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Photodegradation effects are related to precipitation amount, precipitation frequency and litter traits in a desert ecosystem

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ABSTRACT

Photodegradation due to litter exposure to solar UV radiation (UV) is presumed to contribute to the surprisingly fast decomposition in some arid and semi-arid regions; however, precipitation may affect the relative importance of photodegradation versus microbial decomposition in litter decomposition. To assess the dependence of photodegradation effects on precipitation, we subjected litters from three plant life forms (spring annual, summer annual and shrub) to two UV treatments (UV block and sunlight) combining four precipitation treatments (two frequencies plus two amounts) over 2.5 years. UV radiation increased k, and it interacted with litter type, with the strongest stimulating effects on low lignin content litter. Precipitation amount and frequency both affected k, and UV photodegradation was dependent on precipitation, with the strongest photodegradation effects in low frequency and low amount of precipitation. UV radiation decreased microbial PLFAs, and altered microbial community in two litters by depressing fungi development. High precipitation frequency significantly increased microbial PLFAs in *E. oxyrrhynchum* litter. Litter decomposition rate was negatively correlated with initial lignin concentration, and UV photodegradation effects increased with increasing lignin loss, suggesting that the increased decomposition rate under UV radiation may primarily result from photochemical mineralization of lignin, rather than from facilitation of microbial decomposition. Our results demonstrate that UV radiation plays an important role in desert litter decomposition. The dependence of photodegradation on litter type and precipitation underscores the importance of incorporating UV radiation-induced C release into modeling of C cycling in desert ecosystems.

1. Introduction

Litter decomposition is dependent on local climate and litter quality (Moorhead and Reynolds, 1989; Abelho, 2016; Ma et al., 2016). Litter decomposition models are in line with enzymolysis kinetics, showing the dominance of microbial decomposition in litter degradation (Moorhead et al., 1999; Moorhead and Sinsabaugh, 2006). However, in arid regions, litter mass loss declines linearly with time, and cannot be well predicted by exponential decomposition models (Austin and Vivanco, 2006; Parton et al., 2007). Photodegradation is recognized as one of the most important mechanisms for this unexpected rapid litter decomposition in arid regions (Brandt et al., 2007; Day et al., 2007, 2015; Gallo et al., 2009; Austin and Ballare, 2010). UV radiation can break down resistant substrates, and thus facilitate microbial degradation (Brandt et al., 2009; Lee et al., 2012a, b). Laboratory studies have shown increased gas release during litter decomposition under UV radiation (Smith et al., 2010; Lee et al., 2012a), while how litter mass loss and microbial communities respond to UV radiation remain controversial (Duguay and Klironomos, 2000). A model study at the global scale demonstrated limited photodegradation effects because of the low organic matter content in drylands (Foereid et al., 2011). However, this study may have underestimated the significance of the break/shortcut of C cycling resulting from photodegradation in these regions; especially in temperate deserts, where the temporal synchrony of intense solar radiation and high litter production can lead to the feasibility of photodegradation (Austin and Vivanco, 2006).

Photodegradation alone cannot fully explain litter decomposition dynamics, and two reasons are attributable to the controversial photodegradation effects (Brandt et al., 2007; Smith et al., 2010). On the one hand, photodegradation can break down resistant

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substrates and facilitate microbial decomposition; on the other hand, UV radiation can inhibit microbial growth and activities, inhibiting microbial decomposition (Epp et al., 2007; Austin et al., 2009). Besides UV radiation, precipitation is another primary factor microbial communities, and microbial decomposition can be initiated even with low available water in arid areas (Austin et al., 2004). Moreover, because of the sporadic precipitation in arid regions, microbes may experience dormancy or death in dry periods, leading to decreased microbial decomposition (Salamanca et al., 2003); thus, changes in precipitation have significant consequences for microbial decomposition, and it is reasonable to expect that photodegradation would interact with precipitation patterns to affect litter decomposition in arid and semiarid regions.

Plant traits also contribute to the large variation in litter decomposition (Pugnaire and Valladares, 2007). For instance, litter decomposition rates are positively related to plant relative growth rate (Kazakou et al., 2006) and to specific leaf area (Cornelissen and Thompson, 1997). In arid regions, litter lignin and cellulose contents are low, and plant leaves are characterized by special structural traits, including higher water conservation tissues and fewer palisade cells; all these traits can cause plant litter to be more fragile and decomposable (Cepeda and Whitford, 1987; Cornwell et al., 2008; Vanderbilt et al., 2008). Lignin is demonstrated to be the primary contributor to mass loss in photodegradation due to its high UV absorption ratio (Gallo et al., 2009; Austin and Ballare, 2010), therefore, mass loss is dependent on lignin loss (Brandt et al., 2007; Uselman et al., 2011). Litter stoichiometric ratio affects microbial decomposition, which can lead to alterations in decomposition rate and nutrient release during decomposition (Perez-Harguindeguy et al., 2000; Brandt et al., 2007). Despite the profound differences in litter traits, few studies have examined photodegradation effects in association with litter traits in arid and semiarid regions (Throop and Archer, 2009). Further studies examining photodegradation effects on litter decomposition with contrasting litter traits can help to understand the photodegradation role in litter decomposition (Brandt et al., 2007; Austin and Ballare, 2010).

The Gurbantunggut Desert is a temperate desert in northwestern China, where intense litter production is in synchrony with peak solar radiation (Huang et al., 2015a), leading to the feasibility of litter photodegradation. Future climate change scenarios have predicted increasing precipitation with more extreme events in northwestern China (Wang and Zhou, 2005). In this study, a manipulative field experiment was conducted to understand how UV radiation, precipitation frequency and amount, and their interactions would affect litter decomposition of five native plants exhibiting different initial litter qualities. We hypothesized that (1) UV radiation would increase litter decomposition of all species, and the magnitude of UV photodegradation effects would depend on litter quality, with the highest UV photodegradation effects on high quality litter; (2) UV photodegradation effects on litter decomposition would depend on precipitation, specifically, precipitation frequency would exert stronger effects on litter photodegradation than precipitation amount; (3) the positive UV photodegradation effects on litter decomposition would be associated with changed microbial communities, and it would be enhanced under high precipitation frequency.

2. Material and methods

2.1. Site description

This study was conducted in the vicinity of the Fukang Station of Desert Ecology, Chinese Academy of Sciences, on the southern edge of the Gurbantunggut Desert (44°17′N, 87°56′E and 475 m a.s.l.). This region has an arid temperate continental climate, with a hot dry summer and cold winter. The annual mean temperature is 6.6 °C, and the annual mean precipitation is 160 mm, of which 70%–80% is distributed in the plant growth season from April to September. The soil is desert solonetz, with aeolian sandy soil at the top (0–100 cm). The soil surface in lowland and the slope of sand dunes is covered with cyanobacterial-lichen crusts (Su et al., 2013), which is very common in desert ecosystems in northern China (Liu et al., 2006; Su et al., 2007; Li, 2012). The shrubs and semi-shrubs are primarily *Haloxylon ammodendron*, *H. persicum*, and *Seriphidium santolinum*, with coverage of ca. 30%. The herbaceous layer is composed of spring annuals and summer annuals, with peak coverage reaching 40%. The dominant herbaceous plants are *Schismus arabicus*, *Erodium oxyrrhynchum*, *Salsola passerine*, *Alyssum linifolium*, *Lactuca undulata*, *Salsola subcrassa*, and *Ceratocarpus arenarius*.

2.2. Experiment design

Three treatments, UV radiation, precipitation amount and precipitation frequency, were used in this study. Two levels of UV treatment were used, UV block from full sunlight and full sunlight. The UV block treatment was manipulated by deploying litters under frames (1.5 m × 2.0 m) with special acrylic sheets (Plexiglass 2458, China), which can resist solar radiation below 380 nm and allow more than 85% transmission of 400–700 nm solar radiation (Fig. S1). The film frames were propped up with steel, fixed by four rebar lengths, and pounded into the soil to a height of 30 cm above the surface. In the sunlight treatment, the same frame without film was fixed in the same way. The frame horizontally covered litter bags. The soil surface temperature was continuously monitored using a thermocouple (Fourtec MicroLab Lite, Israel) near the corner of the frame; the soil temperature under UV block was 0.33 °C higher than that under sunlight (Fig. S2).

Precipitation amount and precipitation frequency were determined based on the nearly 20-year meteorological record; two levels of annual precipitation amount (150 mm and 75 mm) and frequency (an interval of three days and 15 days) were applied from May 10th to October 4th in each year. Precipitation treatment was conducted by evenly spraying distilled water on the surface of litter bags using a sprayer, and this was conducted in late afternoon to prevent excessive evaporation. The combination of precipitation amount and frequency generated four precipitation treatments (Fig. S3): high amount and high frequency (HAHF), 3 mm of distilled water was supplied every three days (Fig. S3a); high amount and low frequency (HALF), 15 mm of distilled water was supplied every 15 days (Fig. S3a); low amount and high frequency (LAHF), 1.5 mm of distilled water was supplied every three days (Fig. S3b); and low amount and low frequency (LALF), 7.5 mm of distilled water was applied every 15 days (Fig. S3b). Natural precipitation was excluded by covering the experimental plots with a piece of plastic film during rainfall throughout the experimental period. The combination of UV and precipitation treatments resulted in eight experimental groups: Sunlight + HAHF, Sunlight + LAHF, Sunlight + HALF, Sunlight + LALF, UV block + HAHF, UV block + LAHF, UV block + HALF, and UV block + LALF.

The deployment of treatments followed a random split-plot design process. Nine blocks were arranged on flat inter-dune ground, and each block was divided into two main plots. UV block and full sunlight transmission treatments were arranged randomly into each main plot in each block. Each main plot was split into four subplots, and the four precipitation treatments were arranged randomly in each subplot. In total, each treatment had nine replicates, totally 72 subplots were arranged, with an area of

1.5 m × 3 m for each subplot. A 2-m buffer zone was established between adjacent subplots. The experiment began in October 2010 and ended in April 2013, lasting 2.5 years.

2.3. *Litter sample deployment, collection and analysis*

Based on plant dominance, lifeform and major litter organs in the native community, five species, *S. arabicus* and *E. oxyrrhynchum* (spring annuals), *S. passerine* (summer annual), *S. santolinum* and *H. ammodendron* (shrubs), were chosen. The whole aboveground section of spring and summer annuals and current year fallen stems (photosynthetic branches) of the two shrubs were collected at leaf falling in 2010.

Collected litters were air-dried to constant weight for 3–5 days and then oven-dried at 65 °C for 48 h until a constant weight was obtained. Both air- and oven-dried litters were weighed to develop a conversion from air-dried mass to dry litter mass. After that, oven-dried litters were mixed uniformly, and ten replicates of each species were randomly selected for initial C, N, P and carbon fraction measurements, and the results showed that initial litter chemistry differed substantially among species (Table 1). Fibreglass mesh bags (10 cm × 25 cm) were used for the litter decomposition experiment. The grid mesh was 1.2 mm on the upper surface and 0.1 mm on the lower surface, which allowed a relatively high exposure area to solar radiation and avoided litter loss from micro-invertebrate activity and pass through the lower surface. The fibreglass mesh blocked approximately 20% of incoming UV irradiation and 13% of incoming visible light. Ten grams of *S. santolinum*, *H. ammodendron* and *S. passerina* litters and 6 g of *S. arabicus* and *E. oxyrrhynchum* of air-dried litter were separately filled in each litterbag. Nine litterbags for each species were randomly laid in each subplot in October 2010, with a distance of 10 cm between adjacent litterbags. The litterbags were fixed at four corners through inserting iron nails into the soil. The litterbags were collected, put into envelopes and transported to the laboratory after 6, 8, 10, 12, 16, 20, 24 and 30 months of decomposition. Sand, litters of other plants and corpses of arthropods were removed from the litter after oven-drying at 45 °C for 48 h, then, the litter was oven-dried again at 65 °C to a constant weight to get mass dry weight. At the last sampling (after 2.5 year), auxiliary litterbags of the spring annual (*E. oxyrrhynchum*) and shrub (*H. ammodendron*) were taken to the laboratory in cooling boxes, and then were hand-sieved and stored at −20 °C for Phospholipid Fatty Acid Analysis (PLFA).

Total carbon was measured using the $K_2Cr_2O_7$ oxidation method (Nelson and Sommers, 1996). Total N was determined by semi-micro-Kjeldahl method with an Alpkem semiautomatic analyser (Kjektec System 1026 distilling unit, Sweden) (Bremner, 1996). Total P was determined by colorimetric analysis (UV−2401PC, Japan) (Kuo, 1996). Ash content was measured using a muffle furnace at 600 °C. Lignin was analysed using the forage fibre technique (Vansoest, 1963). Subsamples (0.5 g) were ground using a Wiley Mill, and then hemicellulose, cellulose and lignin were measured using an ANKOM semiautomatic fibre analyser (ANKOM Technology, Macedon, New York, USA). After obtaining ash content, mass remaining during decomposition was expressed as the ash-free weight, lignin concentration was also expressed as a percentage of the initial lignin content of ash-free weight.

2.4. *Phospholipid fatty acid analysis (PLFA)*

The PLFAs were analysed following the protocol described by White et al. (1996) for three replicates in each treatment. Litter was lyophilized for 24 h and then ground into particles <10 μm. PLFAs were extracted from ground litter (250 mg) in dichloromethane-methanol-potassium phosphate buffer (1:2:0.8 v/v/v), vortexed for 30 s, and heated at 37 °C for 0.5 h with vortexing at 10-min intervals. The lipids were separated into neutral lipids, glycolipids and phospholipids in a silicic acid column (Sep-Pak Plus Silica; Waters Corp., Milford, MA) and esterified with HCl methanol (Tokyo Kasei Kogyo Co. Ltd, Tokyo), conversion to fatty acid methyl esters (FAMEs). FAMEs were identified and quantified by running a known standard (Supelco 37-component FAME mix, Sigma-Aldrich Co., St. Louis, MO, USA). The resultant fatty acid methyl esters (FAMEs) were identified using a MIDI peak identification system (Microbial ID. Inc., Newark, DE, USA). Peak areas were converted to nmol lipid g dry litter^{-1} using an internal standard (19:0 non-adecanoic methylester). Though a total of 54 compounds were identified from the extractions, we limited our analyses to the 22 compounds between carbon chain lengths C14 and C19. The total amount of all 22 PLFAs was used to indicate the total microbial biomass.

2.5. *Data analysis*

Decomposition rate (k, year^{-1}) was estimated using the one-component negative exponential decay function of $M_t/M_0 = e^{-kt}$ (Olson, 1963), where M_0 is the initial litter mass, M_t is the remaining litter mass after a given time period t, and t is decomposition time (in years). A four-way split-plot ANOVA with UV treatment as the main-plot fixed factor and precipitation amount and frequency and litter type as the sub-plot fixed factors was used to assess treatment differences in decomposition rate (k), carbon fraction remaining (% of initial) and total PLFAs. We initially included block as a random factor, it was then removed because it was insignificant in all cases. Paired Student's t-test was used to test UV treatment effects on

Table 1
Initial litter chemical traits (mean ± S.E. in parentheses, n = 10) of the five species. *C* carbon, *N* nitrogen, *P* phosphorus, *C:N* the ratio of carbon to nitrogen, *C:P* the ratio of carbon to phosphorus, *DC* dissolved carbon, *H* Hemicellulose, *C* Cellulose, *L* Lignin, *L:N* the ratio of lignin to nitrogen. Percentages were calculated on a percent dry mass (65 °C) basis. Different lower cases show significant difference of the tested parameters among species at $P < 0.05$.

Parameters	Spring annuals		Summer annual	Shrubs	
	S. arabicus	*E. oxyrrhynchum*	*S. passerine*	*S. santolinum*	*H. ammodendron*
C (mg g^{-1})	447.2 (14.2) a	426.8 (8.2) a	345.2 (17.0) b	498.6 (12.5) a	290.7 (18.7) b
N (mg g^{-1})	11.9 (0.4) a	14.0 (0.2) b	11.8 (0.3) a	12.7 (0.8) a	13.6 (0.1) b
P (mg g^{-1})	1.9 (0.06) a	2.1 (0.05) b	1.0 (0.01) c	1.7 (0.01) d	0.8 (0.00) e
C:N	37.7 (2.0) a	30.5 (1.4) a	29.6 (2.0) a	40.4 (2.9) b	21.4 (1.4) a
C:P	235.3 (13.6) a	201.7 (9.4) a	338.1 (20.4) b	290.5 (9.2) b	378.5 (24.4) b
DC	55.0 (0.6) a	64.2 (0.6) a	60.3 (0.8) a	53.8 (0.8) a	80.0 (0.5) b
H (%)	21.8 (0.6) a	9.9 (0.6) b	16.8 (0.9) c	12.7 (0.9) d	10.0 (0.1) b
C (%)	21.1 (0.8) a	22.2 (0.3) a	19.6 (0.5) a	22.7 (1.0) a	7.6 (0.2) b
L (%)	2.1 (0.3) a	3.7 (0.2) b	3.3 (0.2) b	10.8 (0.3) c	2.4 (0.1) a
L:N	1.7 (0.4) a	2.8 (0.2) a	3.0 (0.2) b	8.2 (0.3) c	1.8 (0.1) a

those parameters across the entire dataset. Tukey's multiple comparison tests following ANOVA were used to check the differences among precipitation treatments. The UV photodegradation effect (UVE) was calculated as the ratio of ((sunlight - UV block)/sunlight) decomposition rate (k), with data based on subplot. To assess the effects of precipitation and litter type on UVE, UVE was subjected to a three-way split-plot ANOVA, with precipitation amount, precipitation frequency and litter type as the main factors. To examine the influence of initial lignin content on k and the contribution of lignin loss to mass loss in decomposition, linear regression was used to explore the relationships between initial lignin content and k under two UV treatments, and the relative lignin loss and UVE for precipitation amount and frequency. Standardized major axis (SMA) regression analyses were performed to test the differences between slopes of the linear regressions (SMATR Version 2.0). The relative lignin loss was calculated as the ratio of ((sunlight − UV block)/sunlight) lignin loss. Relative lignin loss and UVE in regression were averaged from nine data points for each treatment. We used all 22 compounds in PCA community analyses. The mole percent of the individual PLFAs was subjected to principal component analysis (PCA) to elucidate major variation patterns. The scores of the first two components from the PCA were then used to compare differences between treatments in the PLFA patterns. All statistical analyses were run using the R software (R Development Core Team). Significance was determined at $P = 0.05$.

3. Results

3.1. UV, precipitation and litter quality effects on litter decomposition rate

UV radiation resulted in significantly faster decomposition rates (k-value) and mass loss than UV block (Fig. 1, Fig. S4, Table S1 and 2). The mean k across precipitation treatments was 0.85, 0.76, 0.49, 0.65 and 0.94 year^{-1} under sunlight, and 0.52, 0.35, 0.37, 0.51 and 0.48 year^{-1} under UV block for *S. arabicus*, *E. oxyrrhynchum*, *S. passerine*, *S. santolinum*, and *H. ammodendron*, respectively (Fig. 1, Table 2). Spring annuals and *H. ammodendron* (shrub) decomposed faster than the summer annual and *S. santolinum* (Tables 1 and 2). The mean k across litter types decreased following the rank of HAHF, LAHF, HALF and LALF (Table 2). Precipitation frequency significantly affected k, and litters decomposed faster under high frequency than low frequency precipitation (Table 2). Precipitation frequency significantly interacted with UV to affect k (Table S1). UV radiation had no significant impact on k under high precipitation frequency, while significantly increasing k under low precipitation frequency (Fig. 1, Table S1). k was higher under high than low precipitation, with higher k on litters containing high initial N and

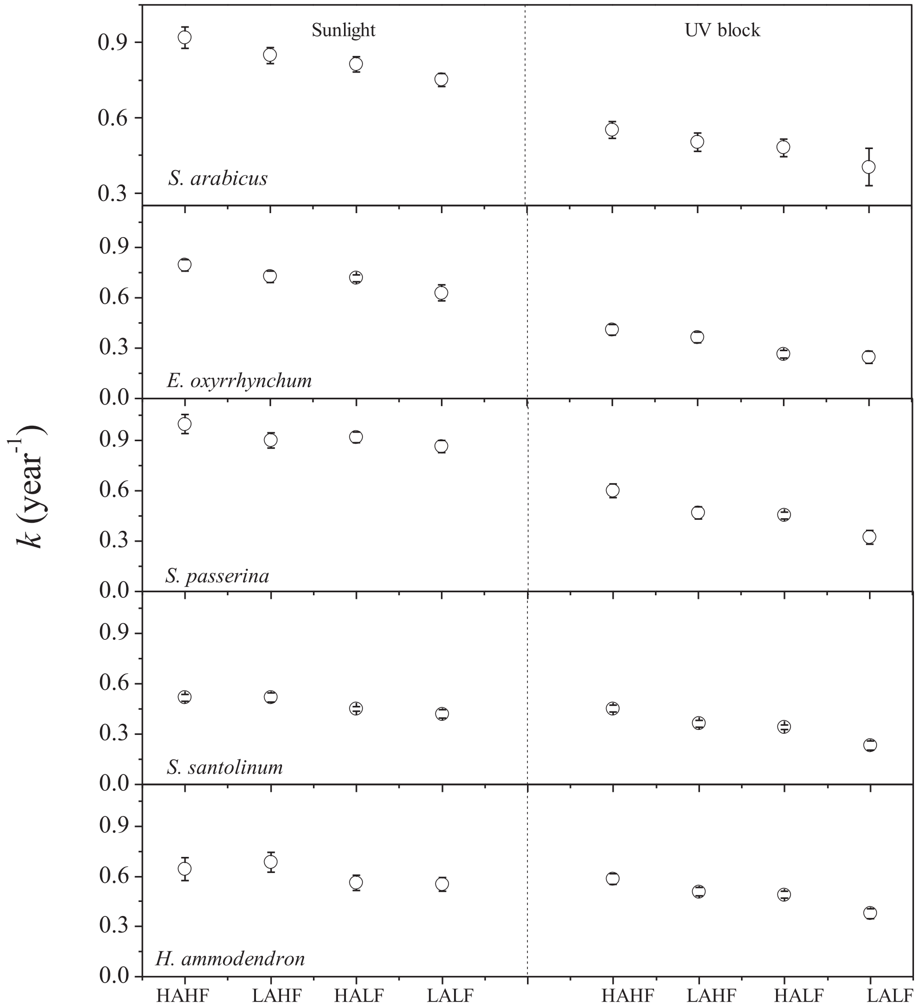

Fig. 1. Litter decomposition rates (k year^{-1}) under different precipitation treatments. The label represents UV treatment-Precipitation treatment. HAHF: high precipitation amount (150 mm) falls in high-frequency; LAHF: low precipitation amount (75 mm) falls in high-frequency; HALF: high precipitation amount (150 mm) falls in low-frequency; LALF: low precipitation amount (75 mm) falls in low-frequency.

Table 2
Litter decomposition constant of mass loss (k, yr^{-1}, mean ± S.E.) under full spectrum sunlight and UV filtering treatments, and the UV radiation effects (UVE) on k for litters of five species (data were averaged across precipitation treatments, n = 36) and four precipitation patterns (data were averaged over litter types, n = 45). HAHF: high precipitation amount (150 mm) falls in high-frequency; LAHF: low precipitation amount (75 mm) falls in high-frequency; HALF: high precipitation amount (150 mm) falls in low-frequency; LALF: low precipitation amount (75 mm) falls in low-frequency. Different capital letters denote a significant difference of k between UV treatments at $P < 0.05$. Different small letters denote a significant difference of k or UV effects between litter types or precipitation patterns at $P < 0.05$. Values for k were determined as the slope of the linear regression of log (mass remaining) against time according to Swift et al. (1979). The UV photodegradation effect (UVE) was calculated as the ratio of ((sunlight - UV block)/sunlight) decomposition rate (k), with data based on subplot. The larger the UVE value, the more decomposition attributable to UV radiation.

Items	k (yr^{-1})		UVE on k
	Sunlight	UV block	
Across precipitation treatments			
S. arabicus	0.85 (0.02) Aa	0.52 (0.02) Ba	0.38 (0.02) a
E. oxyrrhynchum	0.76 (0.02) Ab	0.35 (0.02) Bb	0.53 (0.02) b
S. passerine	0.49 (0.01) Ac	0.37 (0.02) Bb	0.24 (0.03) c
S. santolinum	0.65 (0.03) Ad	0.51 (0.02) Ba	0.17 (0.05) d
H. ammodendron	0.94 (0.02) Ae	0.48 (0.02) Ba	0.48 (0.03) ab
Across litter types			
HAHF	0.78 (0.04) Aa	0.53 (0.02) Ba	0.27 (0.05) a
LAHF	0.75 (0.03) Aa	0.45 (0.02) Bb	0.37 (0.03) ab
HALF	0.72 (0.03) Aa	0.41 (0.02) Bbc	0.39 (0.04) b
LALF	0.69 (0.03) Aa	0.34 (0.02) Bc	0.48 (0.03) b

low lignin concentration (Fig. 1, Tables 1 and 2).

3.2. Precipitation effects on UVE

Precipitation amount, precipitation frequency and litter type all significantly affected UV photodegradation effects (Table S1, $P < 0.001$). Across precipitation treatments, the average UV photodegradation effect was 37% and 53% in *S. arabicus* and *E. oxyrrhynchum* (spring annuals), but only 17% and 24% in the summer annual and shrubs (Table 2). Precipitation amount interacted with litter type to affect UV photodegradation effects (Table S1, $P = 0.01$). UV photodegradation effects were significantly higher under low frequency than under high frequency for *E. oxyrrhynchum* and *H. ammodendron* when high precipitation amount was applied (Fig. 2a), but the reverse was true for *S. santolinum* and *H. ammodendron* when low precipitation amount was applied (Fig. 2b).

3.3. Litter quality effects on UV photodegradation effects

UV radiation significantly decreased the lignin content of all species (Fig. 3a). Precipitation amount and frequency had no impacts on litter lignin content, with an exception of *S. santolinum* under two precipitation frequencies (Fig. 3 b and c). Litter decomposition rates were negatively related to initial lignin concentration, and initial lignin concentration explained 15% and 53% of the variation of decomposition rates under UV block and sunlight, respectively (Fig. 4, $P < 0.05$). UV photodegradation effects were positively related to the relative lignin loss, irrespective of precipitation frequency (Fig. 5a) or amount (Fig. 5b), with a marginally steeper slope under high than low precipitation amount (Fig. 5b, $P = 0.05$).

3.4. UV and precipitation effects on microbial biomass and community composition

Microbial PLFAs differed significantly between *H. ammodendron*

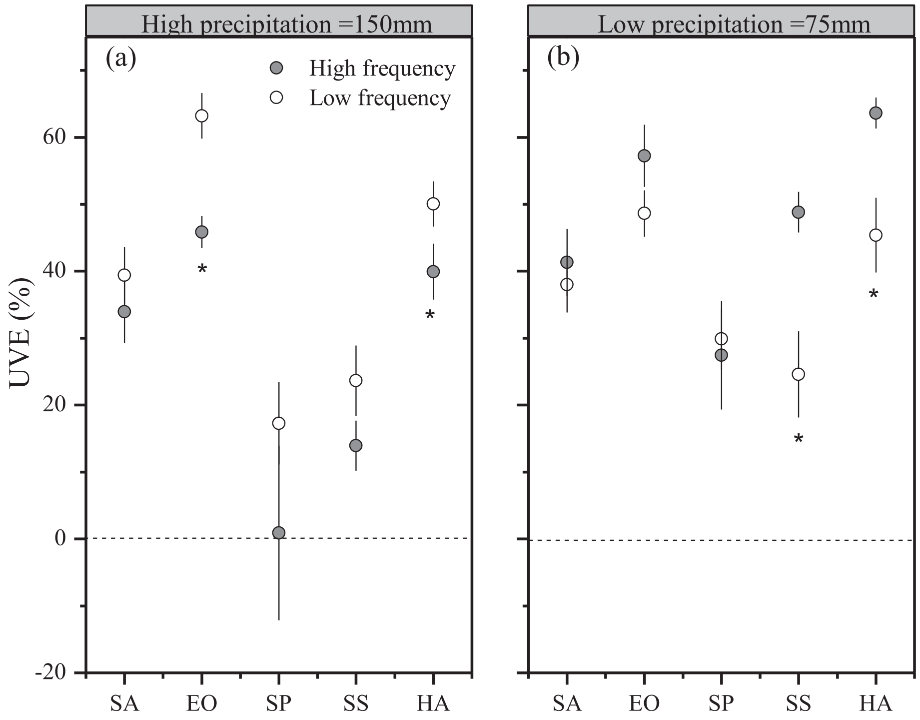

Fig. 2. UV photodegradation effects (UVE was calculated as the ratio of ((sunlight - UV block)/sunlight) decomposition rate (k), with data based on subplot) for each litter type (Mean + S.E.) under 150 mm (a, n = 9) and 75 mm (b, n = 9) of precipitation. Two frequencies of watering every three days (high frequency, grey circles) and every 15 days (low frequency, white circles) were compared in each precipitation amount. Litters are arranged from left to right according to plant lifeform: two spring annuals of *S. arabicus* (SA) and *E. oxyrrhynchum* (EO), one summer annual of *S. passerine* (SP), and two shrubs of *S. santolinum* (SS) and *H. ammodendron* (HA). Asterisks denote significant differences of the UVE between two frequencies of precipitation at $P < 0.05$.

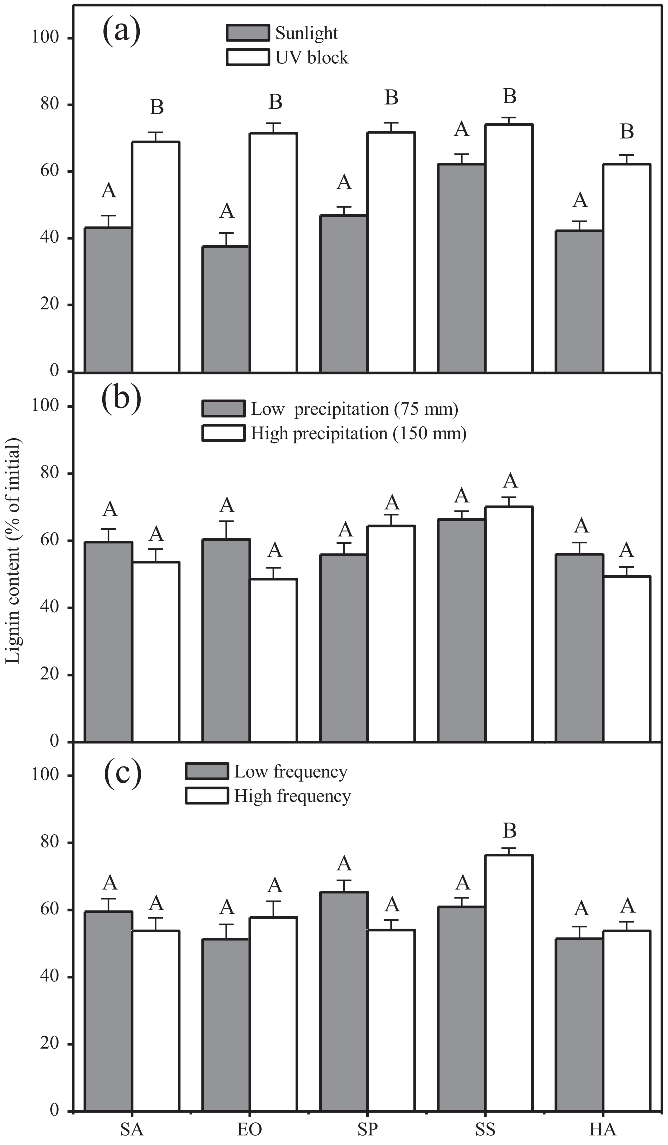

Fig. 3. Litter lignin remaining content (% of initial) under sunlight and UV block (a), two amounts of 150 mm and 75 mm precipitation (b) and two frequencies of watering every three (high frequency) and 15 days (low frequency) (c). All data were over 2.5-year decomposition for five litters (SA, EO, SP, SS and HA, abbreviations refer to Fig. 2). Different capital letters indicate significant pair-wise differences between treatments within a species (Student T test).

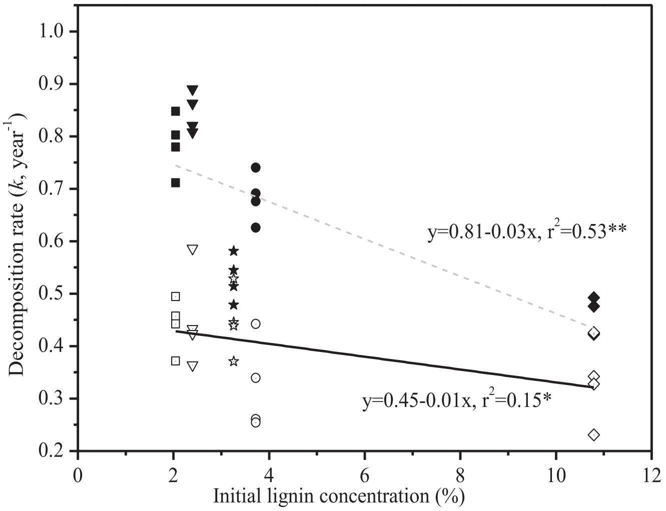

Fig. 4. Linear relationship of decomposition rate (*k*) with initial lignin concentration (%) under sunlight (filled symbols) and UV block (open symbols) for *S. arabicus* (squares), *E. oxyrrhynchum* (cycles), *S. passerine* (triangles), *S. santolinum* (diamonds), and *H. ammodendron* (stars). Each point is the mean of nine replicates. Initial lignin concentration explained 53% of *k* under UV block and 15% under sunlight after 2.5-year decomposition.

and *E. oxyrrhynchum* (Fig. 6, $P < 0.001$), Under sunlight, the average microbial PLFAs across precipitation treatments were nearly two times higher in *E. oxyrrhynchum* than *H. ammodendron* (Fig. 6). UV block increased microbial PLFAs both in *H. ammodendron* and *E. oxyrrhynchum* (Fig. 6). High precipitation frequency significantly increased microbial PLFAs in *E. oxyrrhynchum* (Fig. 6b). Precipitation amount interacted with UV to affect microbial PLFAs under low precipitation (Fig. 6b), microbial PLFAs were higher under UV block than under sunlight, while no difference was observed between UV treatments under high precipitation for *E. oxyrrhynchum* (Fig. 6b).

Principal component analysis (PCA) of the PLFA data from litters of *H. ammodendron* and *E. oxyrrhynchum* showed different patterns (Fig. 7 a1and a2). For *H. ammodendron* litters, microbial PLFA profiles under UV block were compositionally distinct from those under sunlight along PC1 (Fig. 7 a1). It is evident that the fatty acids of 18:2w6,9, 18:1w9 and 16:1w7 were most abundant under UV block (Fig. 7 b1), while litters under sunlight are mainly characterized by the common fatty acids 18:0, the unsaturated fatty acids 18:1w7 and 15:1w6, the cyclopropane fatty acid 17:0cy and the anteiso-branched a16:0 and a17:0 (Fig. 7 b1). The PLFA profiles under UV block + HAHF treatment were separated from others by the high loading value of fatty acid 18:2w6,9, and the PLFA profiles under sunlight + LAHF treatment were separated from others by the high loading values of 16:0 and 18:0 (Fig. 7 b1). Lipid profiles of *E. oxyrrhynchum* also showed a separation between UV block and sunlight along PC2 (Fig. 7 a2). Litters under UV block had high mole percentages of the fatty acids of i14:0 and i15:0, while litters under sunlight are characterized by 18:0 and unsaturated fatty acid 16:1w7 (Fig. 7 b2). Lipid profiles of *E. oxyrrhynchum* under high precipitation frequency were clearly separated from low precipitation frequency by the high loading values of fatty acids of 18:2w6,9, 18:1w9, a15:0 and 16:0 on PC1 (Fig. 7 b2).

4. Discussion

4.1. The role of litter quality on UV photodegradation effect

Consistent with our first hypothesis, litter decomposed faster under sunlight than under UV block. The magnitude of UV photodegradation effects on litter decomposition greatly depended on initial litter quality, with stronger UV photodegradation effects in low lignin content litter (spring annuals) than in high initial lignin content litter. This was supported by the positive correlation between UV photodegradation effects and relative lignin loss, suggesting that lignin loss contributed to litter mass loss in decomposition. Lignin loss of spring annuals might be related to the fast growth rates of these plants (Cornelissen et al., 1999; Kazakou et al., 2006). In our study, spring annuals of *E. oxyrrhynchum* and *S. arabicus* exhibit the high relative growth rates of 0.04 cm cm^{-1} day^{-1} and 0.05 cm cm^{-1} day^{-1}, and seldom develop protective/defensive structures, which make them more sensitive to UV radiation (Cornelissen et al., 1999; Kazakou et al., 2006). Meanwhile, leaf surface area and lignin structure are also critical for UV photodegradation effects (Gallo et al., 2006; Brandt et al., 2009; Day et al., 2015). Higher exposure of leaf surface to sunlight would

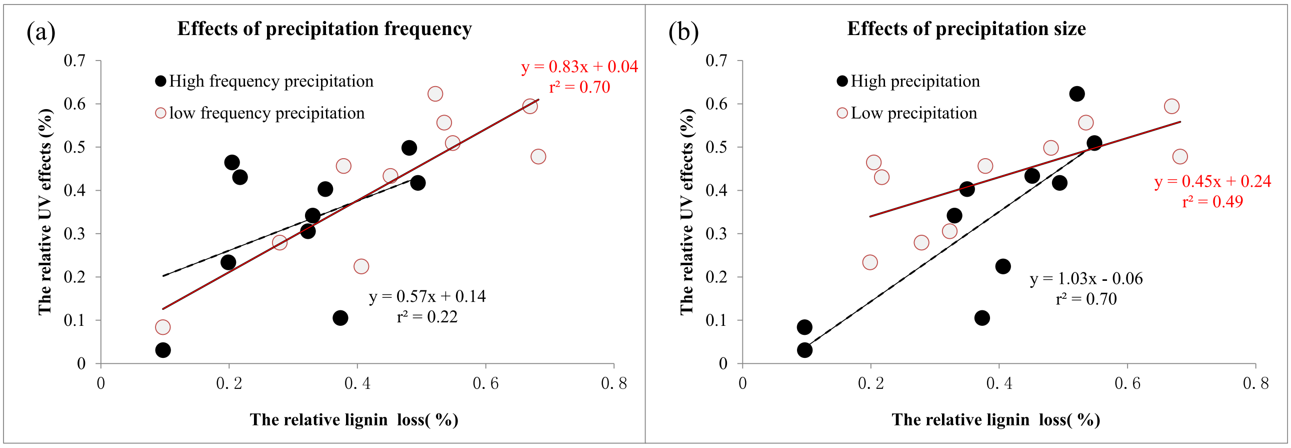

Fig. 5. UV photodegradation effect (UVE) as a function of the relative lignin loss in two precipitation frequencies (a, averaged across precipitation size, n = 18) and two precipitation amounts (b, averaged across precipitation frequencies, n = 18). Standardized major axis regression analyses were performed to test the differences between slopes of the linear regressions.

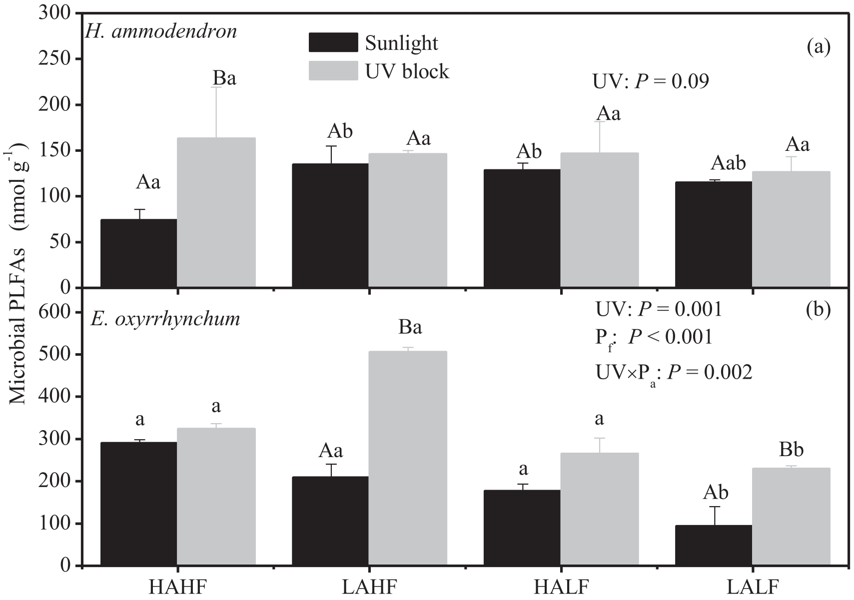

Fig. 6. Microbial extractable phospholipid fatty acids (PLFAs) in *H. ammodendron* (a) and *E. oxyrrhynchum* (b) litters under two UV treatments (sunlight and UV block) and four precipitation patterns (HAHF, LAHF, HALF, and LALF, abbreviations refer to Fig. 1) after 2.5-year decomposition. Different uppercase letters show significant differences between UV treatments within the same precipitation treatment at $P < 0.05$, and different lowercase letters show significant differences among precipitation patterns within the same UV treatment at $P < 0.05$. UV, Pf and Pa indicate UV treatment, precipitation frequency and precipitation amount, respectively.

facilitate photodegradation by increasing photochemical release, and the physical toughness of lignin tissue in shrub stems is stronger than in herbs, leading to a stronger UV photodegradation effect on herb litters (Gallo et al., 2006; Brandt et al., 2009; Austin et al., 2016).

Given that litters with low lignin content contribute significantly to litter composition in this desert ecosystem (Huang et al., 2015a), the increased decomposition rates of desert herbs and photosynthetic branches of *H. ammodendron* by photodegradation in our study suggests a short C retention time. The most important ecological consequence of photodegradation is the direct C release from litter to the atmosphere, leading to a shortcut of C cycling in the atmosphere-plant-soil system by discarding biological degradation (Austin and Vivanco, 2006; Austin et al., 2016). Thus, despite the considerably high vegetation cover and biomass, soil organic matter is still low in this desert (Li et al., 2010). In addition, the temporal synchrony of litter production with high solar radiation increases the possibility of photodegradation in this system. The mean litter production of spring annuals is 83.6 g m^{-2}, representing 75% of the litter production of annuals in this desert (Huang et al., 2015a). UV radiation caused 6% higher litter mass loss via gas release in a lab experiment (Brandt et al., 2009); approximately 5 g litter m^{-2} directly released into the atmosphere through photodegradation, which is comparable to litter production of summer annuals in dry years in this desert (Huang et al., 2015a).

4.2. The role of precipitation in photodegradation

Consistently with many studies across geographic gradients, precipitation significantly enhanced litter decomposition in our study, demonstrating faster litter decomposition rates in wet than in dry areas (Salamanca et al., 2003; Arriaga and Maya, 2007). It is

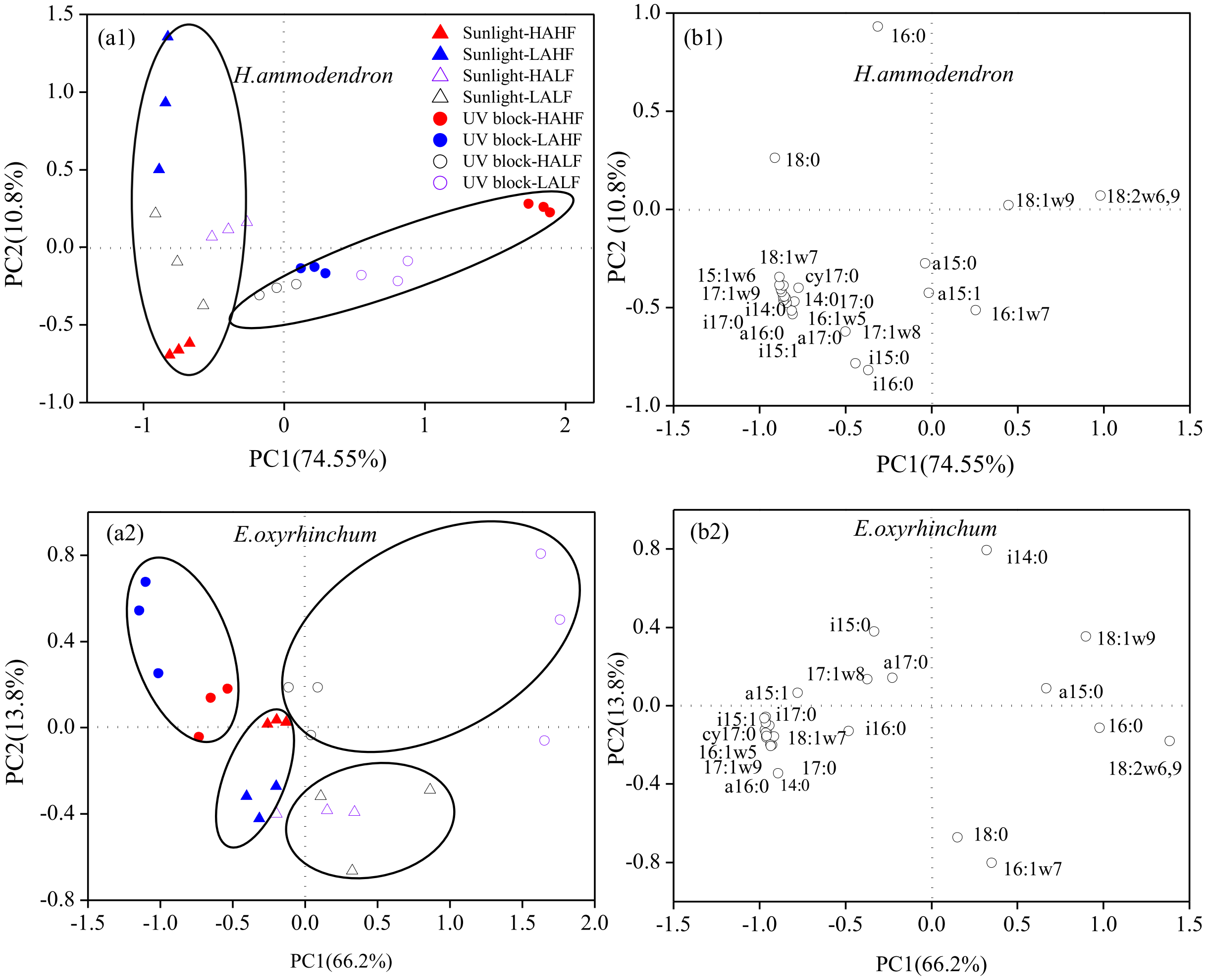

Fig. 7. Ordination of phospholipid fatty acids (PLFAs) extracted per gram litter after 2.5-year decomposition of a shrub (*H. ammodendron*) and spring annual (*E. oxyrrhynchum*) litter experiencing two UV treatments and four precipitation patterns. Labels are presented as "UV treatment – Precipitation treatment" (HAHF, LAHF, HALF, and LALF, abbreviations refer to Fig. 1).

expected that higher water availability can facilitate litter degradation under UV radiation due to the increased labile substrates and microbial decomposition (Throop and Archer, 2009; King et al., 2012; Austin et al., 2016). In our study, both precipitation amount and frequency significantly affected UV photodegradation effects. Increasing precipitation in this desert could reinforce photodegradation directly through increasing litter leaching and indirectly by altering microbial communities (Smith et al., 2010; Lee et al., 2012a). UV radiation decreased microbial PLFAs in *E. oxyrrhynchum* but not in *H. ammodendron* ($P = 0.09$), suggesting that precipitation impacts on UV photodegradation would depend on the direct effects of precipitation on litter quality. The different responses of microbial communities between the two litters to UV block may suggest that microbial colonization differed in the two litters, with the low C:N ratio (21) and lignin:N ratio (1.8) of *H. ammodendron* being more profitable for bacterial colonization.

Precipitation frequency exerted a stronger effect on litter decomposition than precipitation amount, with faster decomposition rates under high precipitation frequency. Frequent precipitation events can alleviate moisture deficit and enhance microbial activity (Austin et al., 2009, 2016; Anaya et al., 2012); moreover, it can also provide abundant labile substrates for microbial decomposers (Salamanca et al., 2003; Lee et al., 2012b). Consistent with our study, Anaya et al. (2012) also found that litter decomposition rate was positively correlated with the frequency of large precipitations (>=10 mm). However, Smith et al. (2010) showed that UV-B radiation of 11.2 kJ m^{-2} day^{-1} decreased decomposition rate under high precipitation frequency but increased under low precipitation frequency. UV radiation can increase labile substrates and litter fragmentation through lignin breakdown in a relatively long wetting-drying cycle, while frequent precipitation can stimulate microbial activity and thus increase litter decomposition (Day et al., 2007; Austin and Ballare, 2010). The opposite effects of high precipitation frequency and UV radiation imply that the direction and magnitude of photodegradation effects can shift with changing precipitation patterns. Therefore, future precipitation patterns would affect litter decomposition by altering the vulnerability of litter C and nutrient pools to extreme events.

4.3. *Effects of UV on microbial biomass and community composition*

Microbial PLFAs is a good index of microbial biomass measured by chloroform fumigation-extraction method (Bailey et al., 2002). In contrast to our third hypothesis, UV radiation decreased microbial PLFAs in both annual and shrub litters. This result falls in line with some previous studies, showing the direct detrimental effects of UV radiation on microbes due to microbial DNA damage (Rohwer and Azam, 2000), growth inhibition (Hughes et al., 2003), and reduced mycelial extension rate and spore germination (Hughes et al., 2003), which can finally alter microbial community composition (Caldwell et al., 2007); The positive effects of UV radiation on litter decomposition are due to UV photolysis of litter, which increases litter solubility and facilitates microbial decomposition (Duguay and Klironomos, 2000).

PLFAs of *H. ammodendron* litter under UV block were set apart from that under sunlight because of the relative higher abundance of two particular PLFAs (fungal PLFA 18:2w6,9 and PLFA 18:1w9 (present in most fungal species)). The higher prevalence of fungal PLFA on *H. ammodendron* under UV block may result from the fact that fungi are more affected by UV radiation than bacteria (Moody et al., 2001). The spore production of litter decomposing fungi is generally inhibited by UV-B (Johnson et al., 2002). Partly, the fungal PLFA 18:2w6,9 on litters under UV block may be related to the persistent wetting of litters after rainfall due to the decreasing evaporation by UV filtering film. In fact, the underlying mechanisms of UV radiation effects on microbial communities are unclear (Paul and Gwynn-Jones, 2003). Some microbial species, such as yeasts and pigmented hyphal fungi, have adapted to extreme environments and are less affected by UV radiation, while others might be damaged by UV radiation (Duguay and Klironomos, 2000).

UV radiation showed strong interactive effects with precipitation on PLFAs in annual litter of *E. oxyrrhynchum*, with stronger UV radiation effect under low than high precipitation, suggesting that high precipitation alleviated the negative UV radiation effects on microbial communities. Microbial PLFA profiles under low precipitation frequency were separated from those under high precipitation frequency by a higher relative abundance of fatty acids 18:2w6,9, 18:1w9, the anteisobranched a15:0 and 16:0. The high fungi prevalence on *E. oxyrrhynchum* under low precipitation frequency may be related to the short litter wetting period and high holocellulose and lignin concentration. Fungi are considered more drought-tolerant than bacteria, so they can survive for a longer dry interval. In particular, fungi have the capacity to decompose substrates with relatively high C:N ratio.

4.4. *Implications for carbon release in the desert ecosystem*

Photodegradation has been proposed to be limited in regions of high solar radiation because of the low vegetation biomass based on a simulative study using averaged solar radiation distribution data at global scale (Foereid et al., 2011); however, using averaged radiation data may underestimate photodegradation. The production of easily decomposable spring-annual litters occurs synchronically with solar radiation peak, leading to a high photodegradation in our study. The critical period of litter decomposition is significant to ecosystem C flux. In our study, precipitation and UV radiation interacted to affect litter decomposition; due to the low precipitation and strong radiation during leaf fall, dissolvable substrates accumulate in litter (Uselman et al., 2011). In early spring, 86% of melted snow (multi-year average: 32 cm in depth) infiltrates into soil (Zhou et al., 2009), initiating microbial activity and litter decomposition (Huang et al., 2015b). Carbon releases from 20th March to 1st April accounted for 27% of the whole year's release in our study (Liu et al., 2013). Moreover, given 20% annual precipitation and 50% litter decomposition occurring in early spring, increasing C storage and improving nutrient utilization from decomposed litter in early spring are important to nutrient retention in this desert ecosystem.

Author contributions statement

GH and YL conceived and designed the experiments. GH performed the experiments, analysed the data and wrote the manuscript.

Data accessibility

All data used in this manuscript are present in the manuscript and its supporting information.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2017.08.034.

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