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The Contribution of Photodegradation to Litter Decomposition in Semiarid Mediterranean Grasslands Depends on its Interaction with Local Humidity Conditions, Litter Quality and Position

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Abstract

Understanding how UV radiation interacts with prevailing climatic conditions and litter quality to determine leaf litter decomposition is fundamental for understanding soil carbon cycling pathways and ecosystem functioning in drylands. We carried out a field manipulative experiment to investigate how litter quality (labile and nitrogen-rich *Retama sphaerocarpa* vs. recalcitrant and nitrogen-poor *Stipa tenacissima*), position (on the ground vs. standing) and different UV radiation levels (UV pass vs. UV block) affect litter decomposition rates at two semiarid Mediterranean steppes with contrasting climates (continental vs. maritime) in a fully factorial experimental design. As expected, *Retama* litter decomposed faster than that of *Stipa*, and litter placed on the ground decayed faster than standing litter. However, and surprisingly, contrasting effects of UV radiation on litter decomposition were observed between the two sites. At the continental site, UV radiation increased litter decay constants by 21% on average, although the contribution of photodegradation was larger when litter was placed on the ground rather than in standing litter. At the maritime site, decay constants were 15% larger in the absence of UV radiation regardless of litter position. Significant litter type × UV exposure radiation and litter type × position interactions indicate that photodegradation contributes more to

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Author contribution AR and MA designed the experiment; MA and JML conducted field work; MA performed laboratory analyses; FTM contributed microclimate data; MA and JML performed data processing and analysis; MA wrote the paper with inputs from the rest of co-authors.

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litter decomposition under less favorable moisture and substrate availability conditions for microbial decomposers. Our results emphasize the need to consider interactions between moisture availability, litter quality and UV radiation in litter decomposition models to fully understand litter decomposition impacts on soil carbon cycling and storage in drylands under climate change.

Key words: leaf litter decomposition; *Stipa tenacissima*; *Retama sphaerocarpa*; photodegradation; moisture availability; litter chemistry; drylands.

Introduction

Leaf litter decomposition is a key component of global biogeochemical cycles that affects soil carbon and nutrient dynamics in terrestrial ecosystems (Bornman and others 2015). There is a growing recognition of the importance of abiotic (for example, solar UV radiation, temperature, and moisture) and biotic (for example, plant species and decomposer communities) drivers of litter decomposition in drylands (Throop and Archer 2009; King and others 2012; Barnes and others 2015). Recently, extensive research has shown that UV-photodegradation can be an important driver of leaf litter decomposition in these ecosystems, although the magnitude, direction and mechanisms of this process differ among studies (Day and others 2007; Brandt and others 2009; Austin and Ballaré 2010; Pan and others 2015). Photodegradation is a process by which solar radiation breaks down organic matter components directly releasing CO_2, and thus promotes a direct loss of carbon to the atmosphere without being incorporated into the soil organic matter pool (Austin and Vivanco 2006). This process could become increasingly important in drylands, as predicted increased levels of UV radiation will accelerate photo-oxidation of significant amounts of standing senescent plant material while microbial activity will be reduced by forecasted long-term droughts and increases in aridity (Giorgi and Lionello 2008; Zepp and others 2011; IPCC 2013; Williamson and others 2014; Huang and others 2016).

The relative contribution of photodegradation and microbial decomposition to overall litter decomposition in drylands may vary with prevailing environmental conditions (for example, temperature, moisture, UV radiation, and substrate availability), which ultimately influence microbial activity (Throop and Archer 2009; Smith and others 2010; King and others 2012; Barnes and others 2015). Photochemical reactions increase with litter moisture content (Schade and others 1999; Smith and others 2010; Mayer and others 2012) and air temperature (Lee and others 2012). However, photodegradation rates may become more relevant under dry than under wet conditions because microbial activity may be suppressed under less suitable environmental conditions (Brandt and others 2007; Smith and others 2010; Almagro and others 2015). In addition, species with low-quality litter (that is, high C:N and lignin:N ratios) often show greater mass losses as a result of abiotic processes such as photodegradation, leaching and fragmentation by soil abrasion than do species with high-quality litter (Brandt and others 2007; Throop and Archer 2009; Almagro and Martínez-Mena 2012; Lee and others 2012). Besides litter quality, local microbial communities may also influence decomposition responses to UV radiation exposure. Although several studies have reported that photodegradation facilitates microbial litter decomposition through photopriming in drylands (Feng and others 2011; Baker and Allison 2015; Lin and others 2015a; Wang and others 2015), many others have shown either microbial photoinhibition or a decrease in the biodegradability of litter promoted by UV radiation (Moody and others 1999; Duguay and Klironomos 2000; Verhoef and others 2000; Lin and others 2015b). Consequently, photodegradation is a complex process in which several mechanisms may counterbalance each other, and thus its net effect on overall litter decay largely depends on the balance between abiotic (photodegradation) and biotic (microbial) processes (King and others 2012; Barnes and others 2015).

Despite the recent interest in the role of photodegradation as a driver of litter decomposition in drylands, it is largely unknown how photodegradation will be affected by prevailing environmental conditions (that is, temperature, moisture) and litter substrate quality. We conducted a multifactorial 15-month litterbag decomposition experiment in the field at two grassland sites to investigate how local climatic conditions and litter quality influence the magnitude and direction of UV radiation on litter decomposition of the tussock grass *Stipa tenacissima* L. and the N-fixing shrub *Retama sphaerocarpa* (L.) Boiss., two dominant species in semiarid Mediterranean perennial grasslands (Valladares and Pugnaire 1999; Le Houérou 2001). Specifically, we aimed to: (1) investigate the

role of photodegradation in the decomposition dynamics of two contrasting perennial species; and (2) test how this role varies with local climatic conditions (continental vs. maritime climate), litter quality (labile and nitrogen-rich vs. recalcitrant and nitrogen-poor), and litter position (standing litter *vs*. litter on the ground).

We hypothesized that UV radiation plays a significant role in the decomposition of *Retama* and *Stipa* litter via photodegradation, and that its relative importance will be modulated by prevailing climatic conditions, litter chemistry and its position. Given that decreasing moisture availability reduces microbial activity, the effect of UV radiation is expected to be larger under the driest conditions (Brandt and others 2010; Smith and others 2010). Because a low-quality litter (that is, high C:N and lignin:N ratios) may limit microbial degradation, the effect of UV radiation is expected to be larger for litter with high C:N ratios (Gallo and others 2009; Brandt and others 2007). As microbial colonization is enhanced in litter placed on the ground relative to standing litter, a higher contribution of photodegradation to overall decomposition rates is expected in standing litter compared to that resting on the ground (Throop and Archer 2009; Barnes and others 2012).

Material and Methods

Study Sites and Litter Collection

Our study was conducted in two representative semiarid Mediterranean perennial grasslands with contrasting climates located in central (Aranjuez, 40°02′N–3°32′W; ~285 km from the coast and 590 m a.s.l.; hereafter referred as the continental site) and south-eastern (Sorbas, 37°05′N–2°04′W; ~23 km from the coast and 397 m a.s.l.; hereafter referred as the maritime site) Spain (Figure S1). These ecosystems were selected because they had significant standing dead biomass exposed to high levels of solar radiation due to their latitude and elevation, low cloud cover, and sparse vegetation cover (Figure S1). Both sites are characterized by a semiarid Mediterranean climate, with warm dry summers and cold wet winters. According to the aridity index (mean annual precipitation in mm/mean annual potential evapotranspiration in mm; 36-year average, 1960–1996; FAO 1989), the maritime site (0.2–0.5) is more arid than the continental site (0.5–0.75). Annual temperature averages 15 ± 0.1°C (Aranjuez) and 16.5 ± 0.1°C (Sorbas). Annual rainfall averages 362 ± 13 mm (Aranjuez, 1951–2013) and 248 ± 19 mm (Sorbas, 2000–2013), and it is concentrated in the autumn and spring months. Soils at both study sites are derived from gypsum, have pH values *ca*. 7, and are classified as Gypsiric Leptosols (IUSS Working Group WRB 2006). Perennial plant cover is below 40%, and is dominated by *Stipa* and *Retama*.

Standing senescent leaf litter from *Stipa* and *Retama* was collected from Sorbas on May 20, 2012 and was air-dried in paper bags for seven days until constant mass. Oven-dry mass was determined for ten samples of litter after drying at 55°C for 72 h to establish ''air-dried'' mass to ''oven-dried'' mass relationships for estimating initial dry litter mass. Subsamples were ground in a ball mill and initial determination of litter chemistry was completed using three replicated samples. The litter chemistry characterization included determination of initial concentration of carbon, nitrogen, cell solubles, cellulose, hemicellulose, lignin, and ash content. The water holding capacity (WHC) of each litter type was also determined as an index of its water uptake capacity. Briefly, six subsamples (1 g) for each litter type were submerged in deionised water for 24 h, placed on top of a 5-mm sieve and drained under gravity, weighed, dried for 72 h at 55°C and reweighed. The water holding capacity of each litter type was calculated by subtracting oven-dried mass from wet-drained mass, dividing by oven-dried mass, and multiplying by 100.

Experimental Design

We established a fully factorial experiment with three factors, each with two levels: UV radiation (UV pass vs. UV block), position (on the ground vs. standing biomass), and litter quality (labile and nitrogen-rich *Retama* vs. recalcitrant and nitrogen-poor *Stipa*). The experimental design consisted of six blocks containing a replicate of each treatment combination, resulting in a total of 48 experimental plots at each experimental site (Figure S2). Four litterbags of each species were placed in each plot, which were removed at different times over 15 months.

To assess the effect of UV radiation (280–400 nm) on litter decomposition dynamics, twelve paired UV-blocking and UV-passing plastic screens (75 cm length × 50 cm with × 0.3 cm height) were installed within each of the study sites in a randomized complete block design. UV-transparent acrylic (UV pass, which passes 90% of the solar spectrum, including UV-A and UV-B; PLEXIGLASS 2458, Germany) or polycarbonate (hereafter UV block, which eliminates 90% of UV-A and UV-B, optically equivalent to Lexan XL-1, GE, Pittsfield,

Massachusetts, USA) screens were used. These materials effectively pass or block UV radiation without substantially affecting photosynthetically active radiation (PAR, 400–700 nm; the UV pass and block filters transmit 97 and 92% of PAR, respectively) or temperature (Brandt and others 2010; Lin and King 2014). Both plastic screens were placed 30 cm above the ground in a rectangular-frame design, supported by steel bars to allow adequate ventilation to avoid excessive heating while still manipulating UV radiation. Perforations were made in the filters to allow water infiltration to the litterbags following precipitation events. Screens were oriented southward to achieve the greatest possible UV treatment effect. For half of the paired plastic screens, a set of litterbags ($n = 4$) of each species was placed on the ground simulating leaf litter resting on the ground, and another set ($n = 4$) was suspended 15 cm in a wire screen simulating standing dead leaf litter (on the ground vs. standing leaf litter; Figure S2). A total of 192 litterbags (2 species × 2 UV radiation exposure levels × 2 positions ×4 sampling periods x 6 replicates) were placed at each study site.

To ensure that our UV treatment was effective, we conducted measurements of UV radiation with a UV Meter (UVM, 250–400 nm, Apogee Instruments Inc, Logan, Utah, USA) beneath both screen types several times a day every three or four weeks throughout the study period (July 2012–October 2013). Measurements were compared to readings taken outside of the experimental units. On average, UV was reduced by 90–91% under the UV-block screens, and by 9–10% under the UV-pass screens.

Air temperature and relative humidity, as well as surface soil temperature (0–2 cm depth) and soil moisture (0–5 cm depth), were continuously monitored at both sites using replicated automated sensors located next to the experimental plots (HOBO Pro v.2 Temp/RH and H8 Data Loggers, Onset Corporation, Bourne, Massachusetts, USA).

Litterbag Setup, Collection and Analyses

Each litterbag (10 × 10 cm) contained 2 g of dry litter of *Stipa* or *Retama*. Litterbags were made of high-density polyethylene at the top (transparent screen with mesh size 2.1 × 3.2 mm, 90% UV transmittance and 92.5% of PAR transmittance; Crystal, Meteor, Petah Tikva, Israel), and window screen at the bottom (1.4 × 1.4 mm). Each litterbag was carried to the field inside an individual paper envelope to minimize litter losses during transport. Any remaining material in the paper envelopes after transport was subtracted from the initial litter mass. Prior to the deployment of litterbags, the ground beneath each experimental unit was manually cleared of vegetation by clipping. Litterbags were deployed on 8th and on 21st of July 2012 in Aranjuez and Sorbas, respectively. Litterbags were all placed in the field on the same day within each site, but were delayed by two weeks between sites for logistical reasons. Periodic vegetation clipping to prevent shading of litterbags continued until the end of the experiment.

A single litterbag was randomly selected for each site and treatment and removed for analysis approximately 2, 6, 10, and 15 months after deployment. These dates correspond to the end of the first dry season (September 2012), the middle of the wet season (January 2013), the end of the wet season (May 2013), and the end of the second dry season (October 2013). Retrieved litterbags were placed in sealed plastic bags, weighed immediately after return to the lab, dried for 72 h at 55°C and reweighed. Any material not derived from litter (seedlings, stones, soil fauna or fungi) was removed by hand and litter was carefully brushed to remove mineral soil before weighing. The litter was cut into 2-cm pieces and ground, and subsamples for each litterbag were analyzed for different chemical analyses. Litter C and N content were determined using an elemental analyzer (Flash 1112 EA, Thermo-Finnigan, Bremen, Germany). Ash content from each litterbag was determined by combusting subsamples (0.3 g) in a muffle furnace at 550°C for 5 h. All data were analyzed on an ash-free dry mass basis to exclude any mass gain resulting from mineral soil entering the bags. Nitrogen uptake and release were estimated as the change in N content in the litter for each sampling period relative to initial values on an ash-free dry mass basis. Litter chemical composition, including the cell soluble fraction (that is, soluble carbohydrates, proteins, and lipids; hereafter, cell solubles), hemicellulose, cellulose, and lignin, were analyzed using the sequential extraction technique (Van Soest and others 1991). Subsamples (0.5 g) were subjected to neutral fiber detergent, acid fiber detergent, and sulfuric acid digestions using an Ankom^{2000} Fiber Analyzer (Ankom Technology Corp., Macedon, New York, USA). After the sulfuric acid digestion, samples were combusted in a muffle furnace at 550°C for 5 h to correct for any mineral particles in the lignin fraction. The hemicellulose and cellulose fractions were pooled and considered as holocellulose for statistical analyses given their similar behavior in the decomposition process (Moorhead and Sinsabaugh 2006). The

lignocellulose index (LCI) was estimated as the ratio of lignin to lignin plus cellulose, according to Melillo and others (1989). All these carbon fractions were determined at the beginning and the end of the experiment. Chemical and physical characteristics of the initial litter material of each species are given in Table 1.

Litter decomposition was measured as the proportional difference in ash-free dry mass between the initial and successive litterbag collection dates. The decomposition constant (k, y^{-1}) was determined in each site and by each UV radiation exposure by position combination using a single exponential decay model (Olson 1963):

$$M_t = M_0 e^{-kt} \quad (1)$$

where M_t and M_0 are the ash-free dry mass of the litter at time t and time 0.

Statistical Analysis

Changes in litter mass, litter moisture, *C* content, and *N* content throughout the study were analyzed using a five-way ANOVA, in which site, litter type, UV radiation exposure, position, and time were considered as main fixed effects, with repeated measurements of one of the factors (time). Litter decay constants and carbon fractions remaining (% of initial) were analyzed with a four-way ANOVA, in which site, litter type, UV radiation exposure, and position were considered as main effects, and plot was considered as a random factor. Since significant site *x* litter type, site *x* UV exposure, and site *x* position interactions were found on many of these response variables, further analyses were conducted separately for each site and litter type. To estimate how UV radiation exposure and position affected carbon fractions (cell solubles, cellulose, hemicellulose, and lignin) of each litter type throughout the duration of the experiment, carbon fraction remaining (% of initial) were estimated on an ash-free dry mass basis at the end of the experiment. Student's *t* tests were used to compare the initial chemical and physical traits between the litter types. Prior to these analyses, data were tested for ANOVA assumptions, and were log-transformed when necessary. All statistical analyses were performed using SPSS 20.0 software (SPSS Inc., Chicago, Illinois, USA).

Results

Climate Regime and UV Radiation

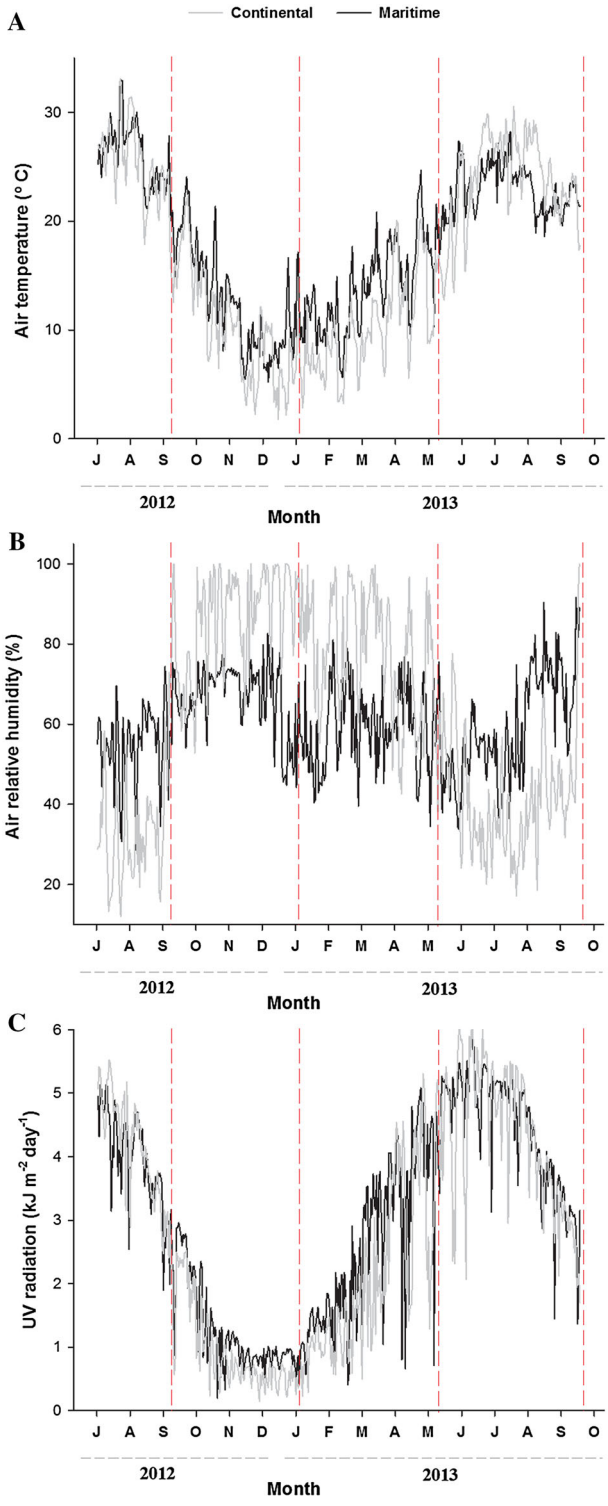
The rainfall accumulated during the experiment (from July 7, 2012 to October 3, 2013) was 398 and 285 mm at the continental (Aranjuez) and maritime (Sorbas) sites, respectively, and occurred mainly during autumn and spring (Figure S3). Accumulated rainfall at the end of the first and second sampling periods was similar at the two sites, but more rainfall was recorded at the continental site compared to the maritime site at the end of the third and last sampling periods.

Mean daily air temperature reached a maximum in August (33°C) at the two study sites coinciding with minimum mean daily air relative humidity values (12 and 28% at the continental and maritime sites, respectively), and then gradually decreased to reach the lowest values in January (~2 and 5°C at the continental and maritime sites, respectively), when maximum values of air relative humidity were recorded (100 and 91% at the continental and maritime sites, respectively; Figure 1A, B). The dynamics of air relative humidity varied among the two study sites during the study

Table 1. Initial Chemical and Physical Characteristics of *S. tenacissima* and *R. sphaerocarpha* Litter

Initial chemistry	*Stipa tenacissima*	*Retama sphaerocarpa*
% Carbon	47.28 ± 0.65a	48.76 ± 0.03a
% Nitrogen	0.18 ± 0.01b	2.88 ± 0.01a
% Cell solubles	17.44 ± 0.50b	49.90 ± 2.12a
% Hemicellulose	27.87 ± 0.41a	12.43 ± 0.98b
% Cellulose	49.68 ± 0.92a	24.35 ± 1.81b
% Lignin	5.00 ± 0.25b	13.31 ± 0.97a
C:N	258.89 ± 14.76a	16.94 ± 0.09b
Lignin:N	27.37 ± 1.56a	4.62 ± 0.32b
Lignin:Lignin + cellulose (LCI)	0.09 ± 0.01b	0.35 ± 0.03a
% Ash	2.1 ± 0.1b	4.57 ± 0.2a
Water holding capacity (%)	55.03 ± 3.99b	131.41 ± 5.78a

Means and standard errors shown (n = 3). Within each row, different letters indicate that means differ significantly between litter types ($P < 0.05$), according to t test



◀**Fig. 1.** Environmental variables throughout the duration of the experiment. Mean daily air temperature **(A)**, relative humidity **(B)** and UV irradiance **(C)** at the continental (Aranjuez) and maritime (Sorbas) site. Air temperature (°C) and relative humidity (%) data come from the on-site meteorological stations, and UV irradiance (kJ m^{-2}) data from the nearest AEMET UV-B monitoring station (Madrid Ciudad Universitaria, 40°27′10″N, 3°43′27″ W, 664 m a. s. l.; and Almería airport, 36°50′47″N, 2°21′25″W, 21 m a. s. l.). *Dashed lines* indicate different sampling periods throughout the experiment. Owing to technical problems, data on air temperature and relative humidity from December 15, 2012 to January 16, 2013, and from July 18 to September 30, 2013, at Sorbas were filled with data from the nearest (~25 km) meteorological station (Tabernas, 37°05′28″N, 2°18′08″W, 435 m a. s. l.).

period (Figure 1B). Mean daily air relative humidity was higher at the continental site (~81%) compared to the maritime site (~63%) during the wet period (from October to May). However, the opposite pattern was observed during the dry period (from June to September), when mean daily air relative humidity values remained at 60% at the maritime site but lowered to 40% at the continental site, with more pronounced differences observed at nights (Figure 2). At this time, and unlike at the continental site, air relative humidity remained steady at 75% at nights at the maritime site. Surface soil moisture (5 cm) closely followed the rainfall events registered at both sites (Figure S3). During the summer dry period, soil moisture remained steady at very low values (below 5%), except after occasional rainfall events, when it increased sharply. During the wet period, soil moisture ranged from 25 to 5% at the maritime site, but it remained steady at 25% at the continental site. Soil surface temperature was substantially warmer in summer and slightly cooler in winter than air temperature at both sites (data not shown), as it is typical in drylands. Overall, and despite its lower aridity index, the continental site had colder winters and drier summers—when UV radiation levels were also high–than the maritime site, leading to less favorable conditions for microbial decomposition.

The UV ambient radiation varied markedly with season at both sites (Figure 1C). At the beginning of the litter decomposition experiment, UV radiation reached its summer peak (6 kJ m^{-2} day^{-1}), although high values of UV radiation were maintained until the middle of August. UV radiation values gradually decreased during the autumn and winter months, when values ranging from 0.5 to 0.1 kJ m^{-2} day^{-1} were observed. These values increased steadily during spring until the middle of June, when peak values of 6 kJ m^{-2} day^{-1} were observed at both sites. Overall, average daily UV radiation doses were higher at the maritime than at

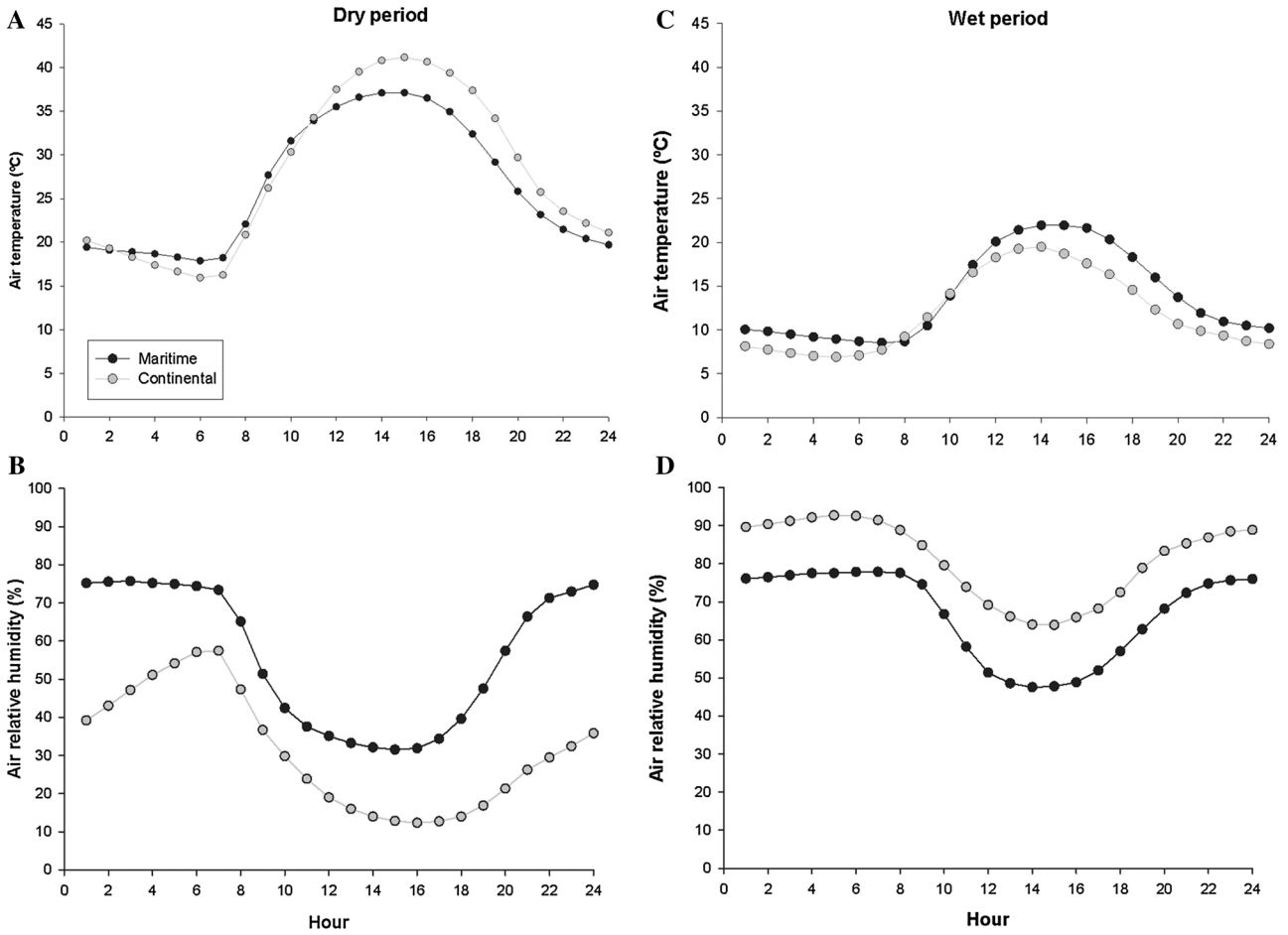


Fig. 2. Mean diel patterns of air temperature (°C) and relative humidity (%) during the dry (**A**, **B)** and wet (**C**, **D)** periods at both study sites. During the study period, mean air temperature and relative humidity were 16.5 and 18°C, and 62 and 60%, at the continental and maritime sites, respectively.

the continental site throughout the study period, mainly during the wet period (Figure 1C).

Litter Mass Loss

Overall, differences in litter mass remaining were observed between the two sites (df = 1; F_{site} = 6.72; P = 0.01) but decay constants were not affected by site (df = 1; F_{site} = 1.00; P = 0.319; Tables S1; S2). Both litter types decomposed following a single exponential decay model until the last sampling period, when very low or even negligible mass loss was observed regardless of the treatment considered (Figure 3). The greatest litter mass loss occurred during the second sampling period, when nearly half of the total rainfall occurred over the experiment at both sites (Figures 3; S3). Overall, litter mass remaining of *Retama* and *Stipa* was affected by position and/or UV radiation exposure treatments from the second sampling period onwards at both sites, with no significant interaction between UV radiation and position treatments at any sampling period (Figure 3; Table 2).

The labile and nitrogen-rich *Retama* litter decomposed about five times faster than the recalcitrant and nitrogen-poor *Stipa* litter at both sites (Figure 4; $P < 0.001$). Decay constants (k, y^{-1}) of *Retama* and *Stipa* litter placed on the ground were 43 and 51% greater compared to those of standing litter at the maritime site. Likewise, at the continental site decay constants of *Retama* litter placed on the ground were 32% higher than those of standing litter, but decay constants of *Stipa* litter showed no difference between the two positions (Figure 4A; Table 2). However, contrasting net effects of UV radiation on decay constants were observed among the two study sites (Figure 4B). As expected, decay constants of *Retama* and *Stipa* litter increased up to 17 and 25%, respectively, by UV radiation exposure at the continental site (Figure 4B; Table 2). On the contrary, at the maritime site UV radiation exposure

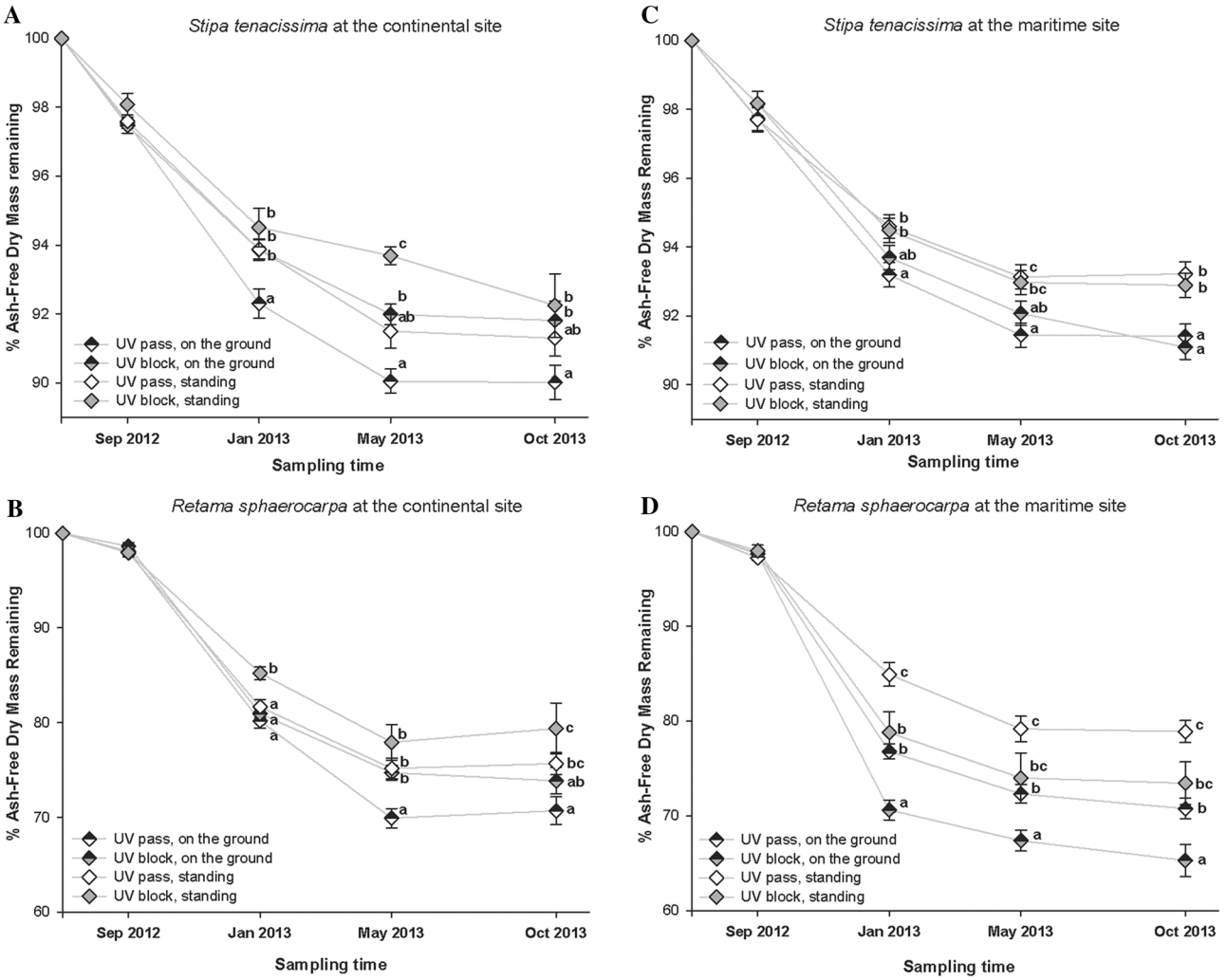


Fig. 3. Mean ash-free dry mass (AFDM, in %) remaining with time for *Stipa tenacissima* (**A**, **B**) and *Retama sphaerocarpa* (**C**, **D**) leaf litter at the continental and maritime sites under different UV radiation exposure levels (UV pass or UV block) and positions (''standing'' or ''on the ground''). After 15 months, accumulated mass loss ranged from 9 to 35% depending on litter type, position, and UV radiation exposure. Means and standard errors are shown ($n = 6$). For each sampling time, significant differences in mass remaining among combinations of UV radiation and position treatments are denoted by different *lowercase letters* (*a–c*) ($P < 0.05$, Tukey's test).

slowed litter decay of *Retama* by 22%, but decay constants of *Stipa* litter showed no difference between the two UV radiation exposure treatments (Table 2).

Carbon Fraction Loss

Lignin remaining (% of initial) was the only carbon fraction affected by the site at the end of the experiment ($df = 1$; $F_{site} = 27.70$; $P < 0.001$; Table S2). Less lignin remaining was observed at the continental than at the maritime site (Figure 5A, B). Contrasting patterns in the carbon fraction remaining were observed among the two litter types (Figure 5; Table S2). *Stipa* litter had less lignin remaining than did *Retama* litter (Figure 5A, B). On the contrary, the amount of holocellulose and labile cell solubles remaining was always higher in *Stipa* than in *Retama* litter (Figure 5C–F).

The carbon fractions of *Stipa* litter were not affected by UV radiation exposure or position at the continental site. However, at the maritime site, *Stipa* litter had less lignin or holocellulose remaining when it was placed on the ground or exposed to UV radiation, respectively (Figure 5B, D; Table S3). Regarding *Retama* litter, holocellulose was the only fraction affected by UV radiation exposure or position at the continental site. At this site, *Retama* litter had less amount of holocellulose

Table 2. ANOVA Results for the Litter Decomposition Experiment

Variable	Effect	*df*	*Stipa tenacissima*				*Retama sphaerocarpa*			
			Continental		Maritime		Continental		Maritime	
			F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
% AFDM remaining	UV	1	**15.36**	**0.001**	0.442	0.514	**13.16**	**0.002**	**17.45**	**<0.001**
	Position	1	**9.27**	**0.006**	**28.71**	**<0.001**	**19.33**	**<0.001**	**41.72**	**<0.001**
	Time	3	**218.22**	**<0.001**	**265.84**	**<0.001**	**411.43**	**<0.001**	**399.6**	**<0.001**
	UV × position	1	0.385	0.542	0.664	0.425	0.031	0.861	0.137	0.715
	UV × time	3	**3.78**	**0.015**	1.033	0.385	**2.28**	**0.088**	**5.84**	**0.001**
	Position × time	3	**2.45**	**0.072**	**7.83**	**<0.001**	**5.24**	**0.003**	**12.6**	**<0.001**
	UV × position × time	3	1.28	0.289	0.417	0.741	0.651	0.585	0.033	0.992
Decay constant (k, yr^{-1})	UV	1	**12.93**	**0.004**	0.132	0.722	**10.71**	**0.007**	**5.70**	**0.030**
	Position	1	0.747	0.404	**7.99**	**0.013**	**29.25**	**<0.001**	**12.36**	**0.003**
	Plot	5	1.01	0.445	1.22	0.346	1.61	0.215	0.857	0.532
	UV × position	1	2.71	0.120	0.248	0.626	0.107	0.748	0.048	0.830

Summary statistics (ANOVA) of treatment effects and their interactions on % ash-free dry mass (AFDM) remaining and decay constant (k, y^{-1}) during the decomposition experiment for each litter type and study site separately
Bold values indicate significant effects ($P < 0.05$)
Changes in % AFDM remaining were analyzed using a three-way (UV, Position, and Time) ANOVA, with repeated measurements of one of the factors (Time). The decay constants (k, y^{-1}) were estimated by fitting a single exponential decay model using litter % ash-free mass remaining (Figure 2). Decay constants were analyzed using a two-way ANOVA, in which UV radiation exposure (UV-pass, UV-block) and position (on the ground, standing litter) were considered as main effects, and plot as a random factor

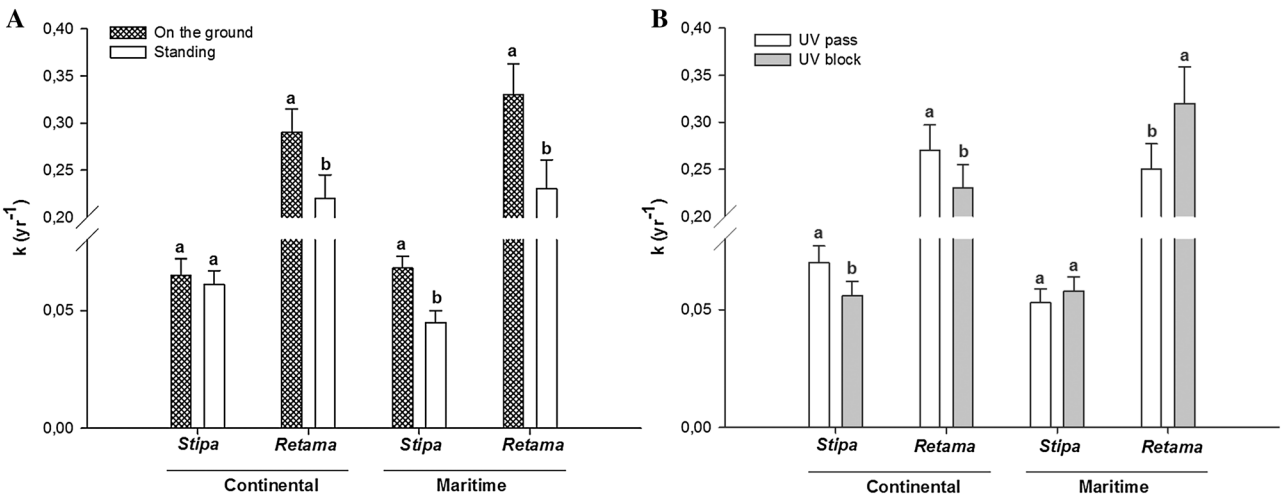


Fig. 4. Effect of position (**A**) and UV radiation exposure (**B**) on average decay constants (k; y^{-1}) of *Stipa tenacissima* and *Retama sphaerocarpa* leaf litter under different UV radiation exposure levels (UV pass or UV block) and positions (''standing'' or ''on the ground'') at the continental and maritime sites. Means and standard errors are shown ($n = 12$). At each site and for each species, means with *different lowercase letters* differ significantly among UV radiation exposure levels and positions ($P < 0.05$), according to Tukey's test.

remaining when exposed to UV radiation, while holocellulose remaining increased when litter was placed on the ground (Figure 5C). At the maritime site, exposure to UV radiation decreased the amount of lignin remaining in *Retama* litter, while it increased that of holocellulose remaining, despite greater litter mass remaining in the UV-pass treatment (Figure 5A, C). On the other hand, the litter placed on the ground had less cell solubles remaining than did standing litter at both sites (Figure 5E, F; Table S3), presumably because of greater microbial consumption.

Nitrogen and Moisture Dynamics

Contrasting patterns in litter N dynamics (uptake vs. release) between the two species were observed throughout the course of the experiment (Fig-

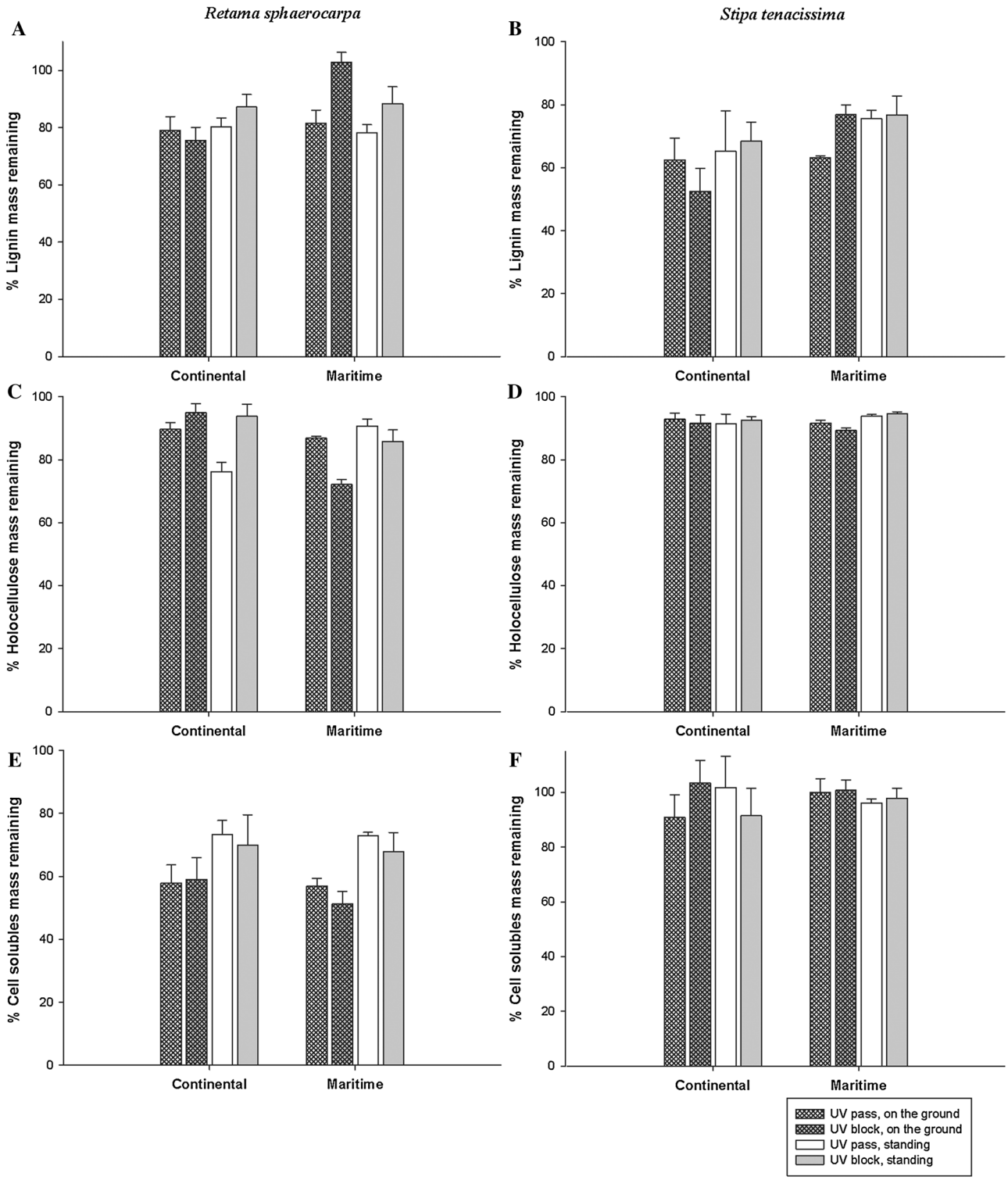


Fig. 5. Fiber fractions remaining (% of initial) of *Stipa tenacissima* and *Retama sphaerocarpa* leaf litter after 15 months under different UV radiation exposure levels (UV pass or UV block) and positions (''standing'' or ''on the ground'') at the continental and maritime sites. Means and standard errors are shown (n = 3).

ure 6). During the first sampling period, a N uptake peak was observed in *Stipa* litter at both sites. This peak was followed by a N release period, coinciding with the wet fall season in which the highest mass loss occurred during the decomposition experiment. After this period, litter N content remained

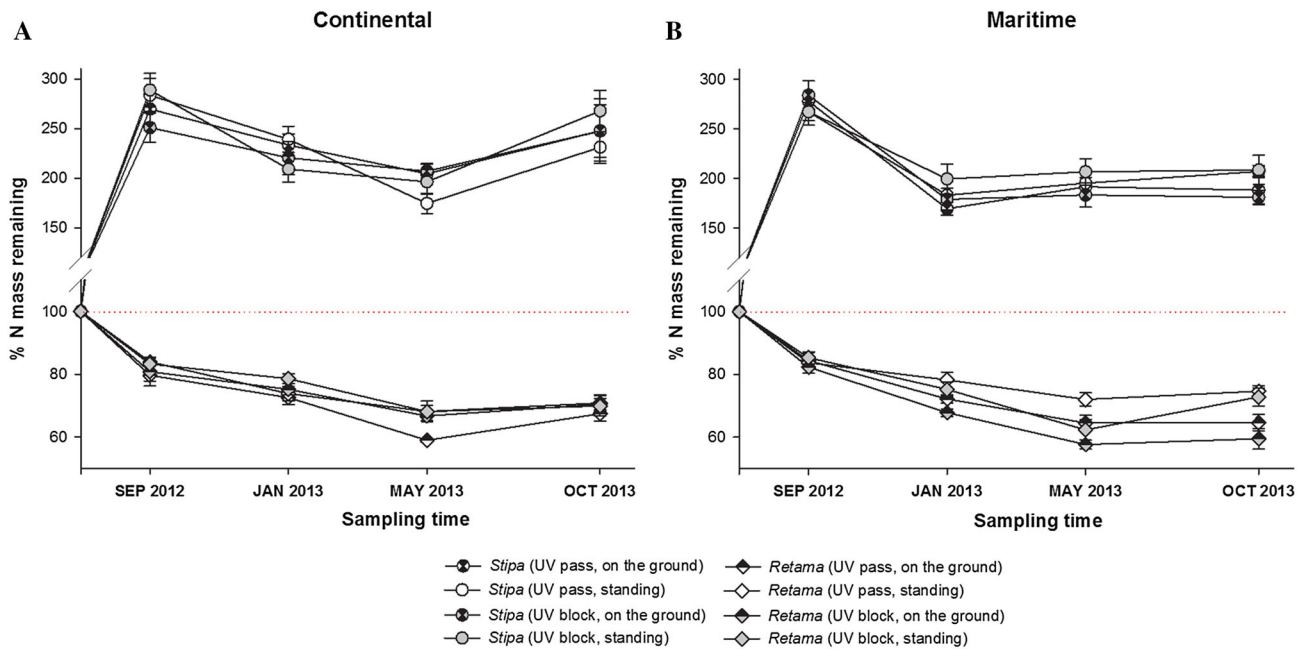


Fig. 6. Changes in N concentration with time for *Stipa tenacissima* and *Retama sphaerocarpa* leaf litter in different UV radiation levels (UV pass or UV block) and positions (''standing'' or ''on the ground'') at the continental and maritime sites. Means and standard errors are shown ($n = 6$). No differences in N uptake (*values above 1*) or release (*values below 1*) rates between UV radiation levels or positions were found over the course of the experiment.

steady until the end of the experiment at the maritime site, while net N uptake occurred during the last sampling period at the continental site. On the contrary, *Retama* litter lost N during the first sampling period and remained steady over the entire decomposition experiment at both sites. Litter N dynamics were affected by the site only in the case of *Stipa* litter (site *x* litter type interaction: $F = 26.27$; $P < 0.001$; Table S1). At the continental site, there was no significant effect of UV radiation or position treatment on N dynamics for any litter type. At the maritime site, larger N losses were observed for both species when litter was placed on the ground (Figure 6).

Retama litter showed higher moisture content than *Stipa* litter throughout the experiment at both study sites (Table S1). For both species and sites, higher litter moisture contents were found in the litter placed on the ground than in the standing litter at the second and third sampling periods (Figure 7).

Discussion

Results from this study show that litter decomposition in dry Mediterranean perennial grasslands can be enhanced, lessened or unaffected by UV radiation depending on local climatic conditions and litter quality. The observed decay constants are lower than (*Stipa*) or in the range of (*Retama*) those reported in other dry Mediterranean species (for example, Henry and others 2008; Dirks and others 2010; Almagro and Martínez-Mena 2012; Saura-Mas and others 2012; Baker and Allison 2015).

Contribution of UV Radiation to Litter Decomposition and its Dependence on Climate

The positive effect of UV radiation on the litter decomposition of both species observed at the continental site (Aranjuez) is in agreement with previous studies reporting enhanced decomposition rates by UV radiation exposure in other arid and semiarid ecosystems (Rozema and others 1997; Austin and Vivanco 2006; Brandt and others 2007; Baker and Allison 2015). On the other hand, the fact that litter decomposition decreased with UV exposure at the maritime site (Sorbas) is consistent with previous findings (Newsham and others 1997; Anesio and others 1999; Pancotto and others 2003; Lin and others 2015b). Such discrepancies may be the result of the different prevailing climatic conditions, litter characteristics, and decomposer communities between studies (Brandt and others

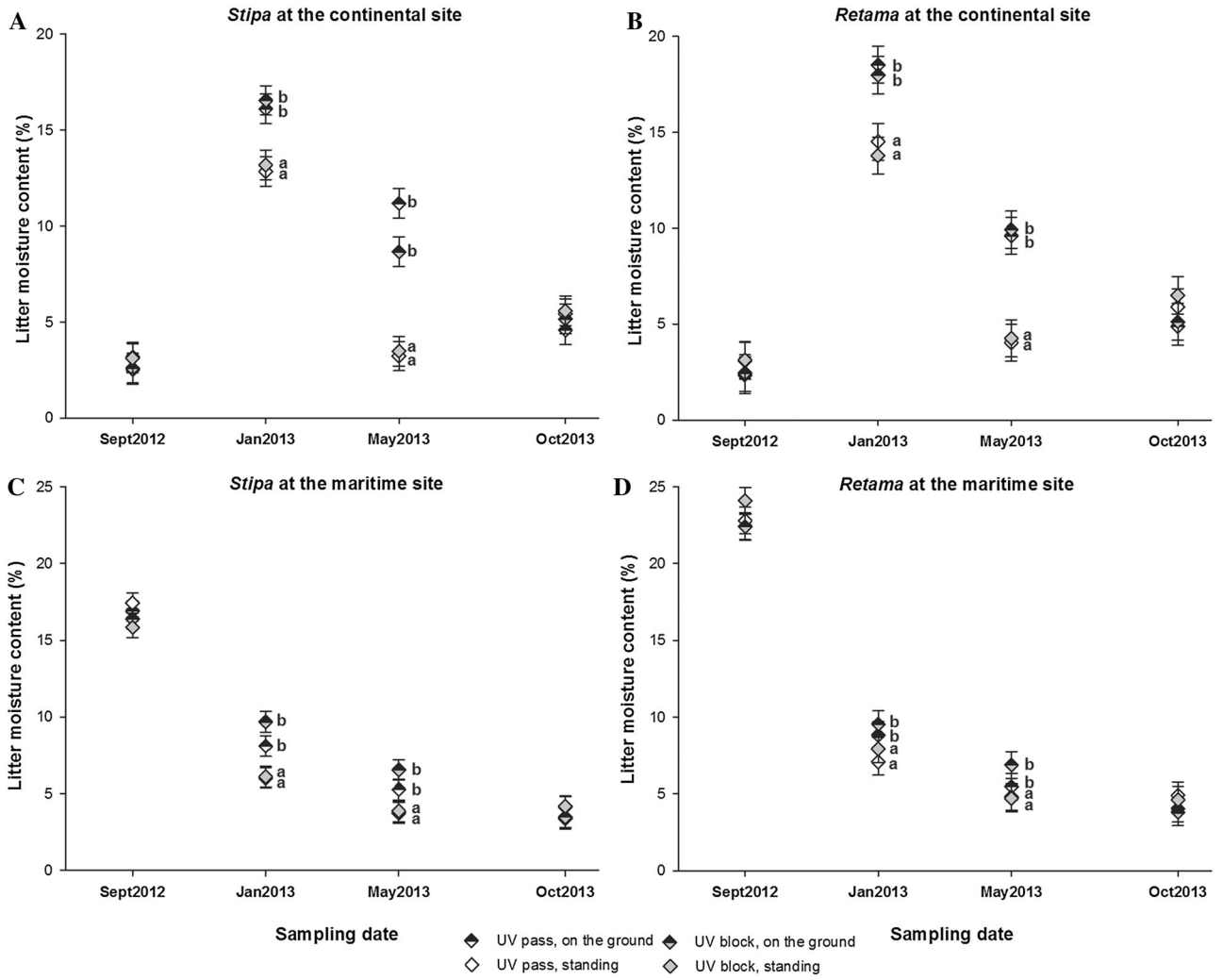


Fig. 7. Moisture content of *Stipa tenacissima* and *Retama sphaerocarpa* leaf litter at different sampling times throughout the litter decomposition experiment. Means and standard errors are shown ($n = 24$). For each species and site, means with *different lowercase letters* differ significantly among combinations of UV radiation exposure levels and positions ($P < 0.05$), according to Tukey's test.

2007; Gallo and others 2009; Smith and others 2010; Day and others 2015).

In this study, the contrasting UV radiation effects on litter decay could be explained by the different moisture availability dynamics observed between the two study sites. Overall, relatively drier conditions were expected at the maritime site than at the continental site based on its lower aridity index and accumulated rainfall during the course of the experiment (Figures S1; S3). However, when moisture availability dynamics were explored more deeply, daily mean air relative humidity and soil moisture were substantially higher at the maritime site (60 and 5%, respectively) than at the continental site (40 and 1%, respectively) during the summer dry months, when maximum UV radiation occurred (Figure 1B, C; S3). At this time, and unlike in Aranjuez, air relative humidity remained steady at 75% at night in Sorbas because predominant East winds in summer probably supply moisture directly from the nearby Mediterranean Sea (Figures 2; S1; Uclés and others 2014). Previous studies have highlighted the important role of high air relative humidity during summer nights to enable microbial litter decomposition in Mediterranean and arid ecosystems (Dirks and others 2010; Jacobson and others 2015). We hypothesize that microbial activity may have been stimulated by greater moisture availability at night while inhibited by high UV radiation at day during the summer drought at the maritime site, thus explaining the lower overall decay rates observed when litter was

exposed to UV radiation at this site. On the contrary, the harsher environmental conditions at the continental site (colder winters, drier summers) compared to the maritime site may have slowed down microbial degradation during the winter months while completely suppressing it during the summer drought. This could explain the enhanced contribution of photodegradation to overall litter decomposition observed at the continental site. Our results agree with those from a climate change experiment carried out in central Spain, in which we observed that the relative contribution of UV radiation to overall litter decomposition of *Stipa* increased under drier and warmer conditions (Almagro and others 2015). The fact that litter decomposition of *Stipa* was not affected by UV radiation but by the position at the maritime site is consistent with what observed by Almagro and others (2015) under ambient (control) conditions. However, the opposite pattern observed at the continental site (that is, decay of *Stipa* litter was not affected by position but increased when exposed to UV radiation) is in agreement with what observed by these authors when warming and drought conditions were experimentally induced. Together, our findings indicate that the impact (magnitude and direction) of UV radiation on overall litter decomposition strongly depends on its interaction with moisture availability, particularly during the summer dry months.

Litter quality controls abiotic and biotic drivers of decomposition

The fact that *Retama* litter decomposed about five times faster than *Stipa* litter at both sites was expected based on the differences in initial chemistry and physical quality traits among these species (Table 1). The improved chemical quality of *Retama* litter compared to that of *Stipa* (that is, lower C:N and lignin:N ratios, four times higher labile carbon) in combination with its larger water holding capacity may not only have stimulated microbial degradation, but also extended the environmental conditions suitable for microbial decomposers after rainfall, fog or dew events (Throop and Archer 2009; Barnes and others 2012; Hewins and others 2013; Lee and others 2014). Interestingly, our findings agree with those from a cross-species study in a Mediterranean shrubland (Dirks and others 2010). These authors observed that the lower the litter lignin: N ratio, the higher the capacity for water absorption.

The contrasting patterns in the carbon fractions and N dynamics observed between the two litter types support the idea that different drivers control litter decomposition of both species. Microbial activity may have enhanced overall litter decomposition of *Retama* because its large mass loss was accompanied by a significant depletion of cell soluble materials, whereas the recalcitrant carbon fractions (holocellulose and lignin) were less affected. These results indicate microbial consumption according to microbiologically-driven decomposition models (Coûteaux and others 1995; Adair and others 2008; Moorhead and others 2012; Lin and King 2014). On the contrary, the extremely low litter decomposition of *Stipa* was paralleled by a significant depletion of the relatively more recalcitrant carbon fraction (lignin), whereas the soluble cell materials were unaffected or slightly increased. The low quality of *Stipa* litter may have suppressed microbial degradation, consequently enhancing the relative contribution of abiotic processes such as photodegradation, thermal degradation and photodissolution to the overall litter decay. These processes probably promoted the preferential degradation of lignin with respect to other relatively less recalcitrant carbon fractions and the solubility of litter, as observed in other drylands (Gallo and others 2006; Foereid and others 2010; Lee and others 2012; Mayer and others 2012).

We did not find a clear pattern regarding the lignin fraction response to UV exposure at the continental site. However, at the maritime site, larger losses of the lignin fraction were observed despite lower litter mass loss in the UV-pass treatment. To date, contradictory results have been reported with regard to lignin dynamics during photodegradation. Some studies have observed that UV exposure increased loss of lignin (Henry and others 2008; Song and others 2014), whereas others have found no significant changes in the lignin fraction with UV exposure (Baker and Allison 2015; Brandt and others 2010; Lin and King 2014). Recently, it has been suggested that photodegradation may cause partial degradation of lignin structures without completely breaking down lignin molecules (Lin and others 2015a). This may explain the lack of response of lignin content to UV exposure (Baker and Allison 2015; Brandt and others 2010; Lin and King 2014). Nevertheless, results from a recent meta-analysis (Wang and others 2015) suggest that the combined effect of UV exposure on abiotic (photodegradation) and biotic (microbial) litter decomposition processes contributes to a larger litter mass loss and lignin degradation than abiotic photodegradation alone.

Position effects on litter decomposition and its interaction with UV radiation

Decay constants of litter placed on the ground were larger than those of standing litter, regardless of the site and litter type. Besides much greater microbial colonization and activity in litter resting on the ground compared to standing litter (Barnes and others 2012), the higher litter moisture content observed in the former during the wet season at both sites (Figure 7; Table S1) may have enhanced decomposition by extending the environmental conditions suitable for microbial decomposers after rainfall, dew and fog events (Throop and Archer 2009; Dirks and others 2010; Hewins and others 2013; Lee and others 2014). However, the contribution of photodegradation to overall litter decomposition at the continental site was larger when litter was in contact with the soil rather than in standing litter. This result was contrary to our expectations and to studies reporting photodegradation as an important abiotic mechanism of litter decomposition in the absence of microbial activity (Austin and Vivanco 2006; Smith and others 2010; King and others 2012; Lee and others 2012). Nevertheless, previous research has also reported that photochemical reactions tend to enhance with increasing moisture availability in plant litter (Schade and others 1999; Smith and others 2010; Mayer and others 2012), and that microbial litter decomposition can be enhanced by UV radiation exposure (Baker and Allison 2015; Wang and others 2015). The later mechanism could explain the enhanced photodegradation rates in litter resting on the ground observed at the continental site. Nevertheless, potential synergistic effects or interactions between abiotic and biotic litter decomposition processes remain largely unknown (UNEP 2016).

Concluding remarks

Our results show that litter decomposition in dry perennial Mediterranean grasslands can be enhanced, lessened or unaffected by UV radiation depending on local moisture conditions and litter quality, which ultimately determines the relative balance between abiotic (photodegradation) and biotic (microbial) decomposition drivers. Our findings confirm previous evidence that photodegradation plays a larger role in the decomposition process under less suitable substrate and environmental conditions (for example, *Stipa* litter decaying at the continental site) when microbial degradation is reduced (Gallo and others 2006, 2009; Brandt and others 2007, 2010; Smith and others 2010). On the contrary, when microbial activity is favored by better substrate and moisture availability conditions during the dry summer months (for example, *Retama* litter decaying at the maritime site), litter decomposition decreased with UV exposure presumably as a result of its negative impacts on microbial communities (Moody and others 1999; Verhoef and others 2000; Johnson 2003; Pancotto and others 2003). Unlike for *Retama*, decomposition of *Stipa* litter was not significantly negatively affected by UV exposure at the maritime site. This probably occurred because the low relative contribution of microbial degradation to decomposition of the recalcitrant and nitrogen-poor *Stipa* litter may have been counterbalanced by the positive effects of photochemical degradation, as suggested by the carbon fraction data. Together, our results indicate that the capacity of drylands to storage carbon in plant litter may be substantially hampered in the driest ecosystems dominated by species producing low-quality litter. They also emphasize the need to account for the interaction between moisture availability, litter quality and UV radiation in litter decomposition models to fully understand litter decomposition impacts on soil carbon cycling and sequestration in drylands under climate change.

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