



Climate change may reduce litter decomposition while enhancing the contribution of photodegradation in dry perennial Mediterranean grasslands



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ABSTRACT

Understanding how the interactions between solar UV radiation and climate will affect leaf litter decomposition is fundamental to predict how soil and ecosystem biogeochemical cycles will respond to ongoing climate change. We carried out a manipulative experiment to investigate how UV radiation and its interaction with increased temperature (3 °C on average) and a ~35% reduction in precipitation affect the decomposition of “standing” and “on the ground” litter of *Stipa tenacissima*, a dominant species in semiarid Mediterranean grasslands. UV radiation was manipulated using specially designed screens that either passed or blocked 90% of the UV radiation. All climate change manipulation treatments decreased litter decomposition compared to the control treatment. In particular, litter decay rates were reduced by a 34%, 43% and 62% in the rainfall reduction (RE), warming (W), and the combination of warming and rainfall reduction (WRE) treatments, respectively, compared to the control treatment. Across climate manipulation treatments, higher decay rates were observed in litter exposed to UV radiation than in litter non-exposed to UV radiation, and in litter placed on the ground than in standing litter. However, significant interactions were found between climate manipulation and UV exposure or position treatments. In the control and RE treatments, litter on the ground decomposed 25% faster than standing litter. In the W and WRE treatments, litter decomposition rates increased by 29% when exposed to UV radiation despite lower overall decay rates were observed in these treatments. Overall, lignin losses were paralleled by increases in soluble cell materials, particularly when litter was exposed to UV radiation. Our results indicate that predicted climate change scenarios will likely reduce leaf litter decomposition rates, while enhancing the relative contribution of photodegradation to overall litter decomposition in dry perennial Mediterranean grasslands.

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1. Introduction

Plant litter decomposition plays an important role in the formation of soil organic matter, the mineralisation of organic

nutrients, and the carbon balance of terrestrial ecosystems (Berg and McClaugherty, 2008). As a result of a growing concern about climate change, and the increasingly recognized importance of the role of soil organic matter as a sink for atmospheric CO₂, much effort is being devoted to improving our understanding of the factors driving litter decomposition dynamics and subsequent soil C storage in terrestrial ecosystems (Zhang et al., 2008; García-Palacios et al., 2013). Extensive research has focused on predicting litter decay rates based on climate, litter quality and soil biotic

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interactions (e.g., Couteaux et al., 1995; Aerts, 1997). However, models based on climatic drivers consistently underestimate decay rates in arid and semiarid ecosystems (Whitford et al., 1981; Parton et al., 2007), suggesting that factors other than temperature and water availability may act as drivers of surface litter decomposition in these water-limited ecosystems (Throop and Archer, 2009; King et al., 2012; Barnes et al., 2015). A growing body of literature is showing that solar ultraviolet (UV; 280–400 nm) and high-energy visible radiation (400–550 nm) can be important drivers of leaf litter decomposition in arid and semiarid ecosystems (Austin and Vivanco, 2006; Brandt et al., 2007, 2009; Day et al., 2007; Gallo et al., 2009; Austin and Ballaré, 2010; Rutledge et al., 2010). Photodegradation is a process by which solar radiation breaks down directly organic matter components, releasing CO₂ and thus promoting a direct loss of carbon from ecosystems to the atmosphere without being incorporated into the soil organic matter pool (Austin and Vivanco, 2006). Although results differ among litter types, site-specific characteristics and experimental conditions, a recent meta-analysis has shown that litter exposed to solar radiation speeds up decomposition by 32% (King et al., 2012). However, the magnitude and proposed mechanisms for this mass loss remain unclear (Song et al., 2013; Wang et al., 2015). Besides facilitating microbial decomposition through breakdown of large organic compounds into more easily degradable ones (Foereid et al., 2010), photodegradation enhances the solubility of litter leading to increased leaching losses of dissolved organic carbon (Gallo et al., 2006), while promoting direct photochemical mineralisation of litter releasing CO₂ (Brandt et al., 2009; Lee et al., 2012). On the other hand, exposure to solar radiation may directly affect microbial populations by inhibiting microbial activity slowing down litter decomposition rates (Verhoef et al., 2000; Johnson, 2003; Pancotto et al., 2003; Smith et al., 2010) or changing the composition of microbial communities and the chemical characteristics of litter (Anesio et al., 1999; Schade et al., 1999; Smith et al., 2010). Thus, photodegradation is a complex process in which several mechanisms may counterbalance each other so its role on surface litter decomposition remains unclear. Moreover, the interaction between UV radiation and water availability or temperature is not yet fully understood and different responses have been found among studies. Photodegradation generally increases with increasing litter moisture content (Schade et al., 1999; Smith et al., 2010) and air temperature (Lee et al., 2012). However, some studies have observed that UV exposure increases decomposition rates by 25% under dry conditions in high C:N litter, but had no effects under wet conditions (Brandt et al., 2007). Nevertheless, and to the best of our knowledge, the interactive effect of high temperature and decreased water availability on litter decomposition rates by UV radiation has not been evaluated so far.

Alterations in vegetation cover driven by global change drivers, such as land use intensification or climate change, will accelerate degradation of senescent plant material through increased UV radiation exposure, stimulating the CO₂ release and mineralisation of nutrients, and thus limiting soil carbon sequestration and reducing soil fertility in drylands (Sala et al., 2000; Bornman et al., 2014; Williamson et al., 2014). It has been suggested that the Mediterranean region is highly sensitive to global climate change (Sala et al., 2000; Schröter et al., 2005). Recent global and regional models predict a 1.4–5.8 °C warming and 25–30% lower soil water availability over the next three decades in Mediterranean ecosystems as a result of lower rainfall and changes in rain distribution (Giorgi and Lionello, 2008; IPCC, 2013), which may alter litter decomposition dynamics and pathways, and hence soil C storage. Under this scenario, photodegradation could become increasingly more important in semiarid Mediterranean grasslands with sparse vegetation since more dead plant material might be exposed to

solar radiation. Expected reductions in rainfall will result in reduced soil microbial activity, while potentially increased UV radiation resulting from reduced cloud cover will accelerate photo-oxidation of significant amounts of standing senescent plant material (Pancotto et al., 2003; Austin and Vivanco, 2006; Brandt et al., 2009; Throop and Archer, 2009). Therefore, understanding how climate change will impact litter decomposition is fundamental to accurately forecast the ecological consequences of ongoing global environmental change.

Despite the recent interest in the role of photodegradation as a driver of litter decomposition, it is uncertain how the process of photodegradation will be affected by climatic change. We carried out a multi-factorial 15-month field litter decomposition experiment designed to understand the role of UV-photodegradation on litter decomposition and its interaction with climate change and litter position. The main purpose of this study is to investigate how climate change will influence the impact (magnitude and direction) of UV radiation on litter decomposition of *Stipa tenacissima*, a dominant species in semiarid Mediterranean perennial grasslands (Le Houérou, 2001). Specifically, the objectives of this study were to: (i) assess the effect of increased temperature, decreased precipitation, and their interaction, on leaf litter decomposition dynamics of *Stipa*, (ii) quantify the contribution of photodegradation to overall leaf-litter decomposition, and (iii) evaluate how the position of the litter (standing vs. on the ground) affects these rates. We tested the following hypotheses: (i) expected increases in temperature and reductions in rainfall inputs will diminish overall litter decomposition because decomposition processes are highly dependent on soil moisture and dew events in semiarid Mediterranean areas (Dirks et al., 2010), which can be lessened by these climatic changes (Maphangwa et al., 2012; Maestre et al., 2013); (ii) photodegradation is an important mechanism of leaf litter decomposition in semiarid Mediterranean perennial grasslands, and thus, even during the dry season, important leaf litter decomposition will take place; (iii) the contribution of photodegradation will increase with warming and rainfall reduction, as microbial activity will be suppressed under less suitable environmental conditions (Brandt et al., 2010; Smith et al., 2010); and (iv) changes in the initial chemistry of plant material exposed to UV radiation are expected since photodegradation promotes the preferential degradation of lignin with respect to other relatively less recalcitrant carbon fractions (Pancotto et al., 2005; Austin and Ballaré, 2010) and the solubility of litter (Gallo et al., 2006; Foereid et al., 2010).

For the purposes of this study, and following previous research (Brandt et al., 2010; Barnes et al., 2015), we defined the net effect of photodegradation as the balance between positive direct (e.g., photo-lysis, photo-oxidation, fragmentation, thermal degradation, photo-dissolution) and indirect (e.g., changes in litter chemistry that facilitate leaching, fragmentation, or microbial decomposition) effects minus indirect negative (e.g., microbial photo-inhibition) effects. Thus, litter decomposition may be enhanced, lessened or unaffected by UV radiation exposure.

2. Material and methods

2.1. Soil and litter collection

Standing senescent leaf-litter from *Stipa* and soil were collected in a semiarid Mediterranean perennial grassland from Sorbas (Almería, SE Spain) dominated by this species (37° 05' N, 2° 04' W; 397 m a. s. l.). The soil from this site is derived from gypsum, has a pH value ca. 7, and is classified as a Gypsic Leptosols (IUSS Working Group WRB, 2006). Recently senescent leaves of *Stipa* were collected on May 20th 2012, and were 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 in order 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 (and standard deviation) of carbon ($47.3 \pm 0.46\%$), nitrogen ($0.18 \pm 0.01\%$), cell solubles ($17.4 \pm 1.54\%$), cellulose ($49.7 \pm 1.43\%$), hemicellulose ($27.9 \pm 0.75\%$), lignin ($5.00 \pm 0.71\%$), and ash content ($2.09 \pm 0.10\%$). Analytical procedures are explained below. Soil samples were collected to a depth of 5 cm from several randomized sampling points, sieved (2 mm mesh) to remove gypsum fragments and homogenized.

2.2. Experimental design

The litter decomposition experiment was initiated on July 13th 2012 at the Climate Change Outdoor Laboratory (CCOL) of Rey Juan Carlos University located in Móstoles, in the centre of the Iberian Peninsula ($40^{\circ} 20' 37''$ N, $38^{\circ} 52' 00''$ W, 632 m a. s. l., Fig. S1). The climate is semiarid Mediterranean, with mean annual temperature and rainfall of 14.4 °C and 449 mm, respectively. Rainfall follows a bimodal distribution with two rainy seasons (autumn and spring) and a dry period in summer.

To evaluate climate change impacts on litter decomposition rates and the interaction effects with photodegradation, a factorial experiment was set-up at the CCOL with four treatments: warming (W, a 3 °C annual temperature increased), rainfall reduction (RE, an approximately 35% reduction in annual rainfall), the combination of both (WRE) and a control treatment with no manipulation (Fig. S2). The experimental design consisted of eight blocks distributed among different climate manipulation treatments in a split-plot design (32 whole plots and 128 subplots total; Fig. S3). This design was used to increase the level of precision in the UV exposure and litter position factors, as climate change was expected to have the greatest overall effect. The whole-plot factor were the different climatic manipulations used (warming, rainfall reduction, and the combination of both). The subplot factor was a factorial combination of UV radiation (UV block, UV pass) and leaf litter position (on the ground, standing), which were randomly assigned within whole plots. Four litterbags were placed in each subplot, which were removed at different times over 15 months.

To achieve an annual increase in air temperature of 2–4 °C, as it has been predicted by models for Central Spain at the end of twenty-first century (De Castro et al., 2005), we used open top chambers (OTCs) similar to those employed in warming experiments carried out in other dryland areas (Maphangwa et al., 2012; Maestre et al. 2013). Briefly, OTCs were built with six methacrylate plates, using a hexagonal design with sloping sides of 65 cm × 52 cm × 42 cm (Fig. S2). This material was selected because it has very high transmittance of both visible and ultraviolet wavelengths, while very low transmittance of infrared wavelengths. The OTCs were open on top to allow precipitation and air to enter inside, and were suspended 5 cm aboveground to allow air circulation and prevent overwarming. To achieve a ~35% reduction in annual rainfall similar to that forecasted by recent global and regional climatic models (Giorgi and Lionello, 2008), passive rainfall shelters (1.2 m length × 1.2 m width × 1 m height) modified from the design used by Escoler et al. (2012), were set-up (Fig. S2). Each rainfall shelter roof has an inclination of 20° and is composed of six gutters of methacrylate that cover approximately 30% of the surface, and were connected to containers that collected the excluded water. The effects of the OTCs and rainfall shelters on air temperature and relative humidity were monitored using

automated sensors (HOBO Pro v.2 Temp/RH and H8 Data Loggers, Onset corporation, Bourne, MA, USA).

To assess the effect of UV radiation (280–400 nm) on litter decomposition dynamics, 32 paired UV-blocking and UV-passing plastic screens (25 cm length × 29 cm width × 0.3 cm height) were installed within each of the three climate change treatment plots as described above. 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 temperature or photosynthetically active radiation (PAR, 400–700 nm; Brandt et al., 2010). Both plastic screen types were perforated to allow precipitation inputs and to avoid excessive heating while still blocking UV radiation. Moreover, beneath each paired plastic screen a tray filled with soil (21 cm length × 12.5 cm width × 5 cm height) and an upside-down wire cage (21 cm length × 12.5 cm width × 5 cm height) were placed to assess the effect of litter position (with and without contact with soil) (Fig. S2). Between 13th and 14th July 2012, a set of litterbags ($n = 4$) was placed on the above mentioned trays filled with soil simulating leaf litter resting on the ground, and another set ($n = 4$) was suspended 5 cm in the wire cages simulating standing leaf litter (on the ground vs. standing leaf litter), resulting in a total of 512 litterbags (4 climate treatments × 2 UV radiation exposure levels × 2 positions × 4 sampling periods × 8 replicates).

To ensure that our UV treatment was effective, we conducted measurements of UV radiation with a UV Meter (UVM, Apogee Instruments Inc, Logan, Utah, USA) beneath both screen types several times a day once per three or four weeks as an average throughout the duration of the experiment (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.

2.3. Litterbag setup, collection and analyses

Each litterbag (10 cm × 5 cm) contained 2 g of dry litter (recently senescent leaves from *Stipa*). Litterbags were made of high-density polyethylene at the top (transparent screen with mesh size 2.1 × 3.2 mm, 90% UV transmittance; Crystal, Meteor, Petah Tikva, Israel), and window screen at the bottom (1.4 × 1.4 mm). Each litterbag was carried inside an individual envelope to avoid litter losses during transport. Periodic vegetation clipping to prevent shading of litterbags continued until the end of the experiment.

A single litterbag was randomly selected for each treatment and removed for analysis approximately two, six, ten and fifteen months after deployment (i.e., on September 20th 2012, on January 11th 2013, on May 10th 2013, and on October 3rd 2013). Therefore, the first sampling period was representative of the dry season period. 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 was determined by combusting subsamples in a muffle furnace at 550 °C for 5 h. All data were analyzed on an ash-free dry matter basis to exclude any mass gain resulting from mineral soil entering the bags. Litter chemical composition, including 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 et al., 1991). Subsamples were subjected to neutral fibre detergent, acid fibre detergent, and sulphuric acid digestions using an Ankom²⁰⁰⁰ Fiber Analyzer (Ankom Technology Corp., Macedon, NY, USA). After the sulphuric 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 lignocellulose index (LCI) was estimated as the ratio of lignin to lignin plus cellulose, according to Melillo et al. (1989). All these carbon fractions were determined at the beginning and the end of the experiment.

Litter decomposition was estimated as the proportional difference in ash-free dry mass between the initial and successive litterbag collection dates. The decomposition constant k (yr^{-1}) was determined for each climate change treatment by 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.

2.4. Statistical analyses

Changes in litter mass, C content, and N content throughout the study were analyzed using a four-way, split-plot model ANOVA. Warming (W), rainfall reduction (RE), and the combination of warming and rainfall reduction (WRE) treatments, UV radiation exposure, position, and time were considered as main effects. Plot was nested within climate experimental units and was considered as a random factor. Litter decay constants as well as different carbon fractions remaining (% of initial) were analyzed with a three-way, split-plot model ANOVA in which climate change manipulation treatments, UV exposure, and position were considered as main effects. To estimate how climate manipulation, UV radiation exposure and position affected litter carbon fractions throughout the duration of the experiment, carbon fraction remaining (% of initial) was calculated as the ratio between the concentrations of the different carbon fractions (cell solubles, cellulose, hemicellulose, and lignin) at the beginning of the experiment and those found 15 months later. Prior to analysis, data were tested for ANOVA assumptions. All statistical analyses were performed using SPSS 20.0 (Chicago, IL, USA).

3. Results

3.1. Microclimate and UV radiation

The rainfall accumulated during the experiment (from July 13th 2012 to October 3rd 2013) was 459 mm, and occurred mainly during autumn and spring seasons (Fig. 1A). Air temperature reached a maximum in August 2012 (33 °C) coinciding with minimum air relative humidity values in the summer (18%), and then gradually decreased through autumn and winter to reach the lowest value in January 2013 (1 °C), when maximum values of air relative humidity were recorded (96%; Fig. S4). The annual mean air temperature and relative humidity were 18.4 °C and 59.6%, respectively. Mean air temperatures were increased by 3 °C in the warming (W) and the combination of warming and rainfall reduction (WRE) treatments compared to the control treatment (Fig. 1B). On the other hand, mean air relative humidity values were lower in all climate manipulation treatments compared to those observed in the control (Fig. 1C). In particular, the combined effects

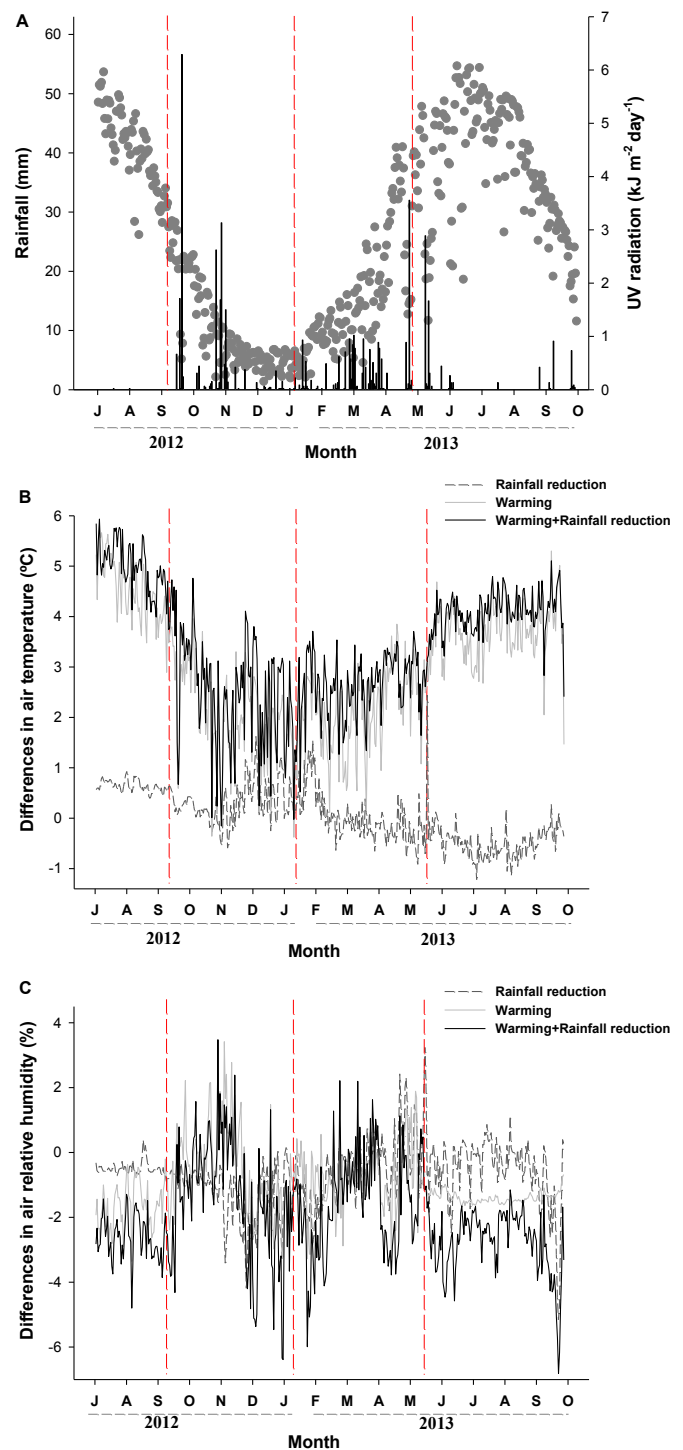


Fig. 1. Environmental variables during the experiment. (A) Rainfall events (mm) and mean daily UV irradiance (kJ m^{-2}). Precipitation data come from the on site meteorological station, and UV irradiance data from the nearest AEMET UV-B monitoring station (Madrid Ciudad Universitaria, $40^{\circ} 27' 10'' \text{ N}$, $3^{\circ} 43' 27'' \text{ W}$, 664 m a. s. l.). Effects of the climate manipulation treatments on air temperature (B) and relative humidity (C) throughout the duration of the experiment (differences with respect to the air temperature and relative humidity registered in the control treatment are shown). Dashed lines indicate different sampling periods throughout the experiment.

of warming and rainfall reduction increased mean air temperature up to 6 °C and decreased mean daily air relative humidity between 2% and 4% during the summer period.

At the beginning of the litter decomposition experiment, UV radiation had already reached its summer peak ($6 \text{ kJ m}^{-2} \text{day}^{-1}$),

although high values of UV radiation were maintained until the middle of August (Fig. 1A). Then UV radiation values started to gradually decrease during the autumn and winter months, when the lowest values ranging from 0.1 to 0.5 $\text{kJ m}^{-2} \text{day}^{-1}$ were observed between November 2012 and February 2013, and increased steadily during spring until it reached a peak in the middle of June 2013 ($6.3 \text{ kJ m}^{-2} \text{day}^{-1}$).

3.2. Mass loss

Stipa litter decomposed slowly and gradually following a single exponential decay model until the last sampling time, when no net mass loss was observed regardless of the treatment considered (Fig. 2). Climate manipulation had significant effects on litter mass loss over the entire duration of the experiment, with a significant interaction between climate and sampling time ($F = 16.225$; $P < 0.001$). At the first sampling period, which corresponded with the first dry season, mass loss rates were 47%, 51% and 115% higher in the RE, W and WRE treatments, respectively, than in the control treatment ($F = 4.01$; $P = 0.008$). However, from the second sampling period onwards, mass loss rates were lower in any of the climate manipulation treatments compared to the control treatment ($F = 5.38, 22.97$ and 28.52 for the second, third and fourth sampling period, respectively; $P < 0.001$ for all sampling periods).

Climate manipulation significantly decreased decay constants (k, yr^{-1}) of *Stipa* litter ($F = 26.067$; $P < 0.001$; Fig. 3). In particular, the WRE treatment caused a reduction of 62% in the litter decay constant compared to that observed in the control treatment, while in the W and RE treatments, litter decay constants were reduced by

ca. 43% and 34%, respectively. Across climate manipulation treatments, significantly higher decay rates were observed in litter exposed to UV radiation ($k = -0.038$) than in litter non-exposed to UV radiation ($k = -0.035$; Table S1). Likewise, significantly higher decay rates were observed in litter placed on the ground ($k = -0.040$) than in standing litter ($k = -0.034$; Table S1). However, significant interactions were found between climate manipulation and UV exposure or position treatments (Table S1). Whereas no differences in decay rates were observed between UV radiation exposure conditions in the control and RE treatments, litter decay rates increased up to 38% and 20% by UV radiation exposure in the W ($F = 5.21$; $P = 0.025$) and WRE ($F = 4.80$; $P = 0.031$) treatments, respectively (Fig. 4A). On the other hand, decay rates of litter placed on the ground were 20% and 30% higher compared to standing litter in the control ($F = 6.83$; $P = 0.011$) and RE ($F = 8.16$; $P = 0.005$) treatments, respectively, but no significant differences in litter decay rates were found between the two positions in the W and the WRE treatments (Fig. 4B).

3.3. Carbon fraction loss

At the end of the experiment, the fractions of cell solubles, hemicellulose, cellulose and lignin responded differently to climate change manipulation treatments, UV radiation exposure and position (Fig. 5). The remaining cell solubles concentrations were up to 5%, 14% and 16% higher in the RE, W, and WRE treatments, respectively, compared to the amount observed in the control treatment ($F = 4.365$; $P = 0.027$; Fig. 5A). Both, cellulose and hemicellulose contents were not affected by climate manipulation

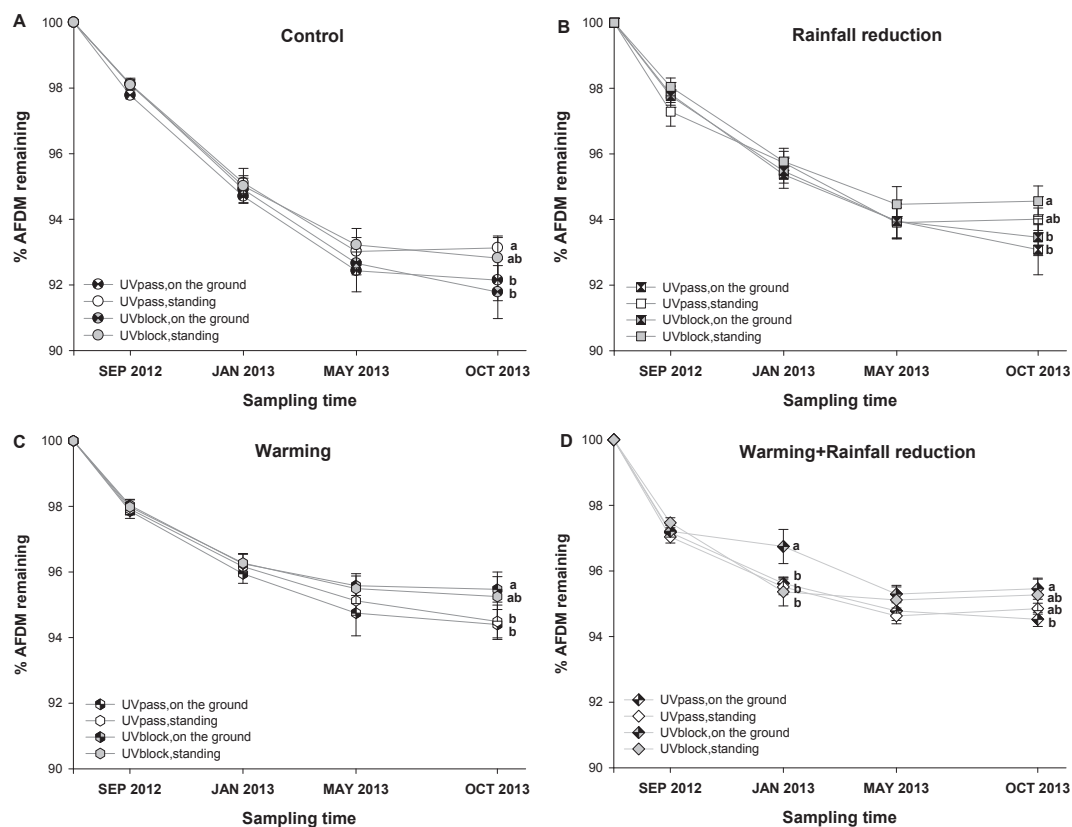


Fig. 2. Mean ash-free dry mass (AFDM, in %) remaining with time for *Stipa tenacissima* leaf litter in different climate change scenarios, UV radiation exposure levels (UV pass and UV block) and positions ("standing" and "on the ground"). Control (A), rainfall reduction (B), warming (C), and combined effect of warming and rainfall reduction (D). Means and standard errors are shown ($n = 8$). Within each climate change scenario and the control, significant differences in mass remaining among combinations of UV radiation and position treatments across sampling periods are denoted by different lowercase letters (a–b) ($P < 0.05$, Tukey's test).

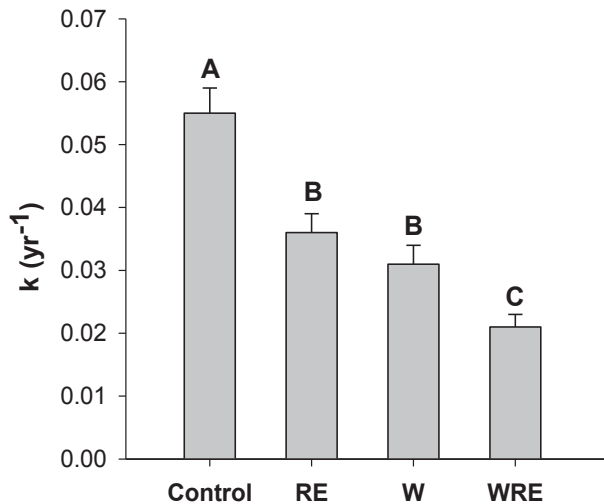


Fig. 3. Average decay constant (k ; yr^{-1}) and standard errors (SE) for *Stipa tenacissima* leaf litter in different climate manipulation treatments (rainfall reduction, RE, warming, W, and the combined effect of warming and rainfall reduction, WRE) and in the control. Among climate treatments, different uppercase letters indicate that means differ significantly between climate treatments ($P < 0.05$), according to Tukey's test.

(Fig. 5C, D), but when both fractions were pooled (holocellulose fraction, according to Moorhead and Sinsabaugh, 2006) marginally significantly greater values were observed in the control and RE treatments than in the W and WRE treatments ($F = 2.84$; $P = 0.083$; Fig. 5E). Lignin concentration decreased in the climate change treatments compared to that observed in the control treatment ($F = 4.01$; $P = 0.034$), being about 14%, 20% and 16% lower in the RE, W, and WRE treatments, respectively (Fig. 5B). At the end of the experiment, the lignocellulose (LCI) index was significantly higher in the control (0.078) compared to the rest of the manipulated climate treatments (0.068 in both RE and WRE, and 0.065 in W treatment; $F = 4.13$; $P = 0.015$). Overall, lignin:N ratios narrowed at the end of the experiment and there were not significant differences among manipulated climate treatments (data not shown).

The fraction of cell solubles remaining was 5% larger in the UV pass treatment than in the UV block treatment ($P = 0.025$), but it was not affected by position (Fig. 5A). A slightly greater loss of lignin was observed in the UV pass treatment than in the UV block treatment ($P = 0.086$), but no differences were observed between litter placed on the ground and standing litter (Fig. 5B). No differences were observed in cellulose or hemicellulose remaining fractions between UV radiation or position treatments.

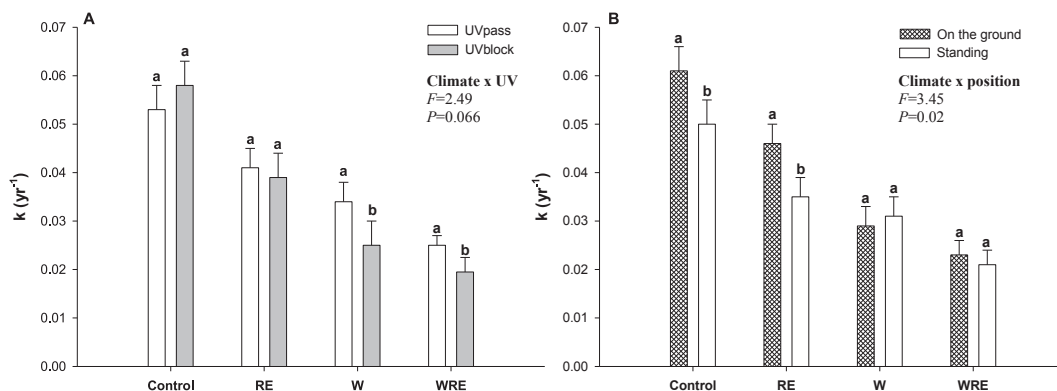


Fig. 4. Effect of UV radiation exposure (A) and position (B) on leaf-litter decay constants (k ; yr^{-1}) of *Stipa tenacissima* in different climate manipulation treatments (rainfall reduction, RE, warming, W, and the combined effect of warming and rainfall reduction, WRE) and in the control. Means and standard errors are shown ($n = 16$). Within climate treatments, means with different lowercase letters differ significantly among UV radiation exposure levels and positions ($P < 0.05$), according to Tukey's test.

Holocellulose remaining was significantly greater in the standing litter than in litter placed on the ground, but it was not affected by UV radiation exposure. No differences were observed in the lignocellulose index or lignin:N ratios between UV radiation or position treatments.

3.4. Nitrogen and moisture dynamics

Significantly higher N uptake and lower N release rates of *Stipa* litter were observed in the control treatment than in the climate manipulation treatments ($F = 13.96$; $P < 0.001$; Fig. 6). During the first sampling period, a N uptake peak was observed in all climate manipulation treatments, being the peak slightly larger in the control and smaller in the WRE treatment. The N uptake peak was followed by a N release period, coinciding with the wet fall period in which the highest mass loss rates occurred during the decomposition experiment. During this period, higher N release rates were observed in all climate manipulation treatments compared to the control treatment despite lower mass loss rates were observed in the formers. After this period, net N uptake occurred during the third and last sampling periods, being significantly larger in the control treatment than in the manipulation climate treatments.

The moisture content of *Stipa* litter was only affected by the climate manipulation treatments (Fig. S5). Significantly higher litter moisture contents were found in the control and the RE treatments than in the warming and the combination of warming and rainfall reduction treatments across collection dates ($F = 3.058$; $P = 0.028$).

4. Discussion

After 15 months, accumulated mass loss ranged from 5 to 8% depending on climate change manipulation, UV radiation exposure and position. These rates are smaller than those reported in other dry Mediterranean species (e.g., Henry et al., 2008; Dirks et al., 2010; Saura-Mas et al., 2012; Lin and King, 2014). In this regard, it is important to note the low quality of *Stipa* leaf litter (i.e., high initial C:N and lignin:N ratios, in combination with a low percentage of labile carbon compounds). However, and despite the small accumulated mass loss observed throughout the decomposition experiment, different effects of climate change manipulation, UV radiation exposure and position treatments were detected.

4.1. Climate change effects on litter decomposition

Results from our experiment show that warming and rainfall reduction reduced leaf litter decomposition rates in dry

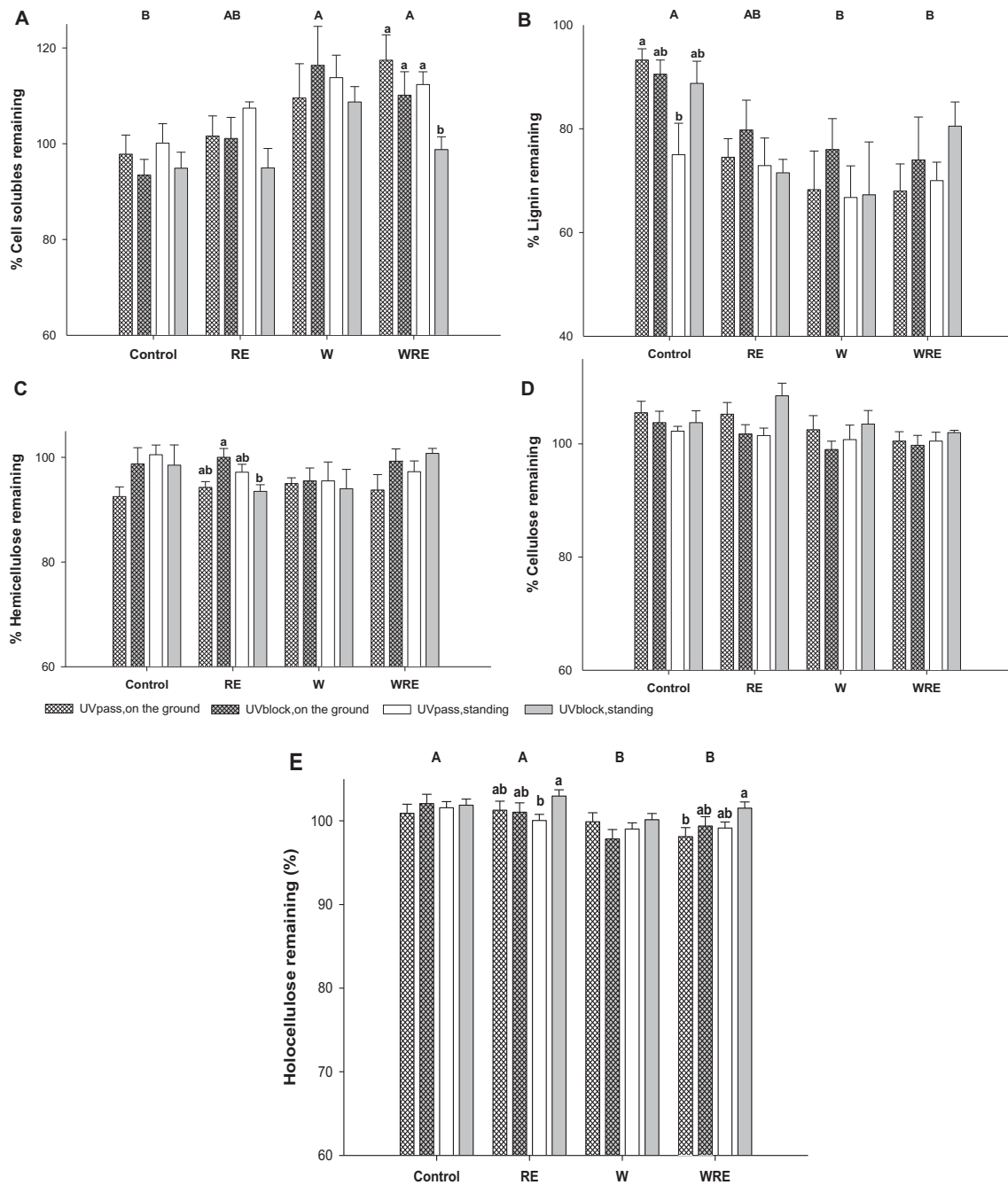


Fig. 5. Fibre fractions remaining (% of initial) of *Stipa tenacissima* leaf-litter after 15 months in different climate manipulation treatments (rainfall reduction, RE, warming, W, and the combined effect of warming and rainfall reduction, WRE) and in the control, as well as different UV radiation exposure levels (UV pass and UV block) and positions (standing and on the ground). Means and standard errors are shown ($n = 4$). Among climate treatments, different uppercase letters indicate that means differ significantly between climate treatments ($P < 0.05$), according to Tukey's test. Within climate treatments, means with different lowercase letters differ significantly among combinations of UV radiation exposure levels and positions ($P < 0.05$), according to Tukey's test.

Mediterranean perennial grasslands, potentially affecting soil organic carbon and nutrient cycling and their subsequent incorporation into soils. Our results are in line with those reported by Saura-Mas et al. (2012) for a Mediterranean ecosystem in North East Spain, in which experimental warming and drought treatments reduced litter decay rates compared to the control treatment after two years. However, we found smaller litter decomposition rates in the W than in the RE treatment, while the opposite pattern was observed by Saura-Mas et al. (2012). These contrasting results could be explained by the differences in the experimental conditions: the increase in temperature (0.6–0.7 °C) induced by their

experiment was much smaller than that induced in our experiment (3 °C), while the decrease in precipitation (~48% reduction) was larger than in our experiment (~35% reduction).

Warming did not speed up litter decomposition in our experiment. This may be explained by the effects of warming on litter moisture. A previous study in a nearby site under similar environmental conditions in which the same climate manipulation methodology was used demonstrated how increasing air temperature largely reduced the duration of suitable conditions for dew formation (*i.e.*, periods in which air relative humidity reaches 100%) and increased soil surface temperature, and therefore

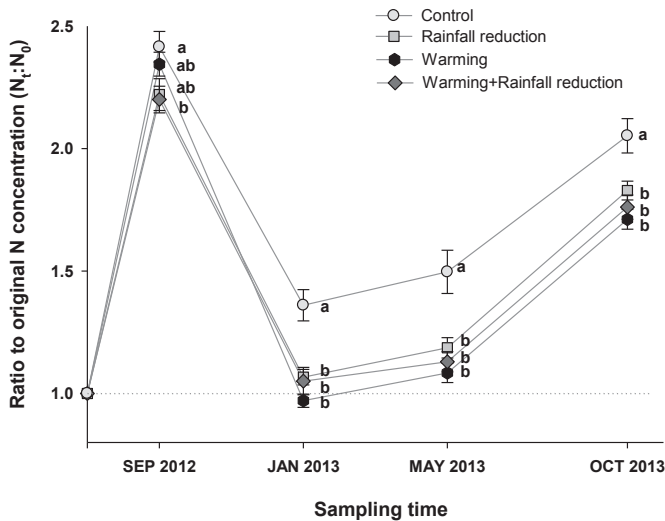


Fig. 6. Changes in N concentration with time for *Stipa tenacissima* leaf-litter in different climate change scenarios (rainfall reduction, RE, warming, W, and the combined effect of warming and rainfall reduction, WRE) and in the control. Means and standard errors are shown ($n = 32$). For each sampling time, different lowercase letters indicate that N uptake or release rates differ significantly between climate treatments ($P < 0.05$), according to Tukey's test.

evapotranspiration, which ultimately caused a reduction in soil moisture (Maestre et al., 2013). This is consistent with the litter moisture patterns (a good indicator of air relative humidity at sampling time; Dirks et al., 2010) observed, as higher litter moisture contents were found in the control and RE treatments than in the W and WRE treatments throughout the experiment (Fig. S5). Given that microbial decomposition enabled by availability of moisture in plant litter has been identified as an important mechanism of litter decomposition in other dry Mediterranean ecosystems (Dirks et al., 2010; Jacobson et al., 2015), microbial activity may have been suppressed in the W and WRE treatments because of the reduction in litter moisture induced by our climate change treatments. This hypothesis is supported by the observed N uptake and release patterns (Fig. 6), as a larger peak of N uptake (considered as an indicator of microbial activity in litter decomposition studies; Hobbie, 2000; Aerts et al., 2006) was observed in the control treatment compared to the climate manipulation treatments.

Changes in litter chemistry provided further evidence that microbial activity slightly enhanced litter decomposition in the control treatment, since larger mass loss rates were paralleled by a slight depletion of the labile cell solubles and lignin fractions (both indicating microbial consumption; Couteaux et al., 1995; Lin and King, 2014). On the contrary, in the W and WRE treatments, a significant depletion of the lignin fraction, and to a lesser extent of the holo-cellulose fraction, were observed and accompanied by an increase in cell solubles (Fig. 5A, B, E). This probably occurred due to thermal degradation-induced changes in litter chemical composition through preferentially degrading the relatively more recalcitrant carbon fractions while increasing its solubility, as observed in other dry ecosystems (Lee et al., 2012).

4.2. Contribution of photodegradation to litter decomposition dynamics

Temporal patterns in mass loss were related to seasonal changes in solar radiation, temperature and precipitation events. However, and contrary to our expectations, a lack of response of litter decomposition rates to UV radiation exposure was observed during the first dry season (Fig. 2). Interestingly, this finding is consistent

with that observed by Baker and Allison (2015) in a Mediterranean ecosystem in which the UV radiation effect on litter decomposition was assessed for the same period than our experiment. This could be explained by the short time elapsed during the first sampling period (i.e., two months), together with the fact that litterbags were deployed in the experimental site few weeks after the peak of UV radiation occurred in mid June. Moreover, since photochemical reactions tend to enhance with increasing moisture content of litter (Schade et al., 1999; Smith et al., 2010; Mayer et al., 2012), photodegradation may have been limited by the low moisture content of *Stipa* litter (~3% on average; Fig. S5) due to the low air relative humidity values and high temperatures observed during this dry period (Fig. S4). Nevertheless, although no significant differences in mass loss rates were observed during the first dry season, partial breakdown and dissolution of litter by solar irradiance and heating probably occurred (Gallo et al., 2006; Foereid et al., 2010; Lee et al., 2012; Mayer et al., 2012). This would make labile substrates more available to decomposers in litter exposed to UV radiation during the following wet period (Henry et al., 2008; Rutledge et al., 2010; Ma et al., 2012), when differences in mass loss rates between UV radiation treatments became apparent. However, it is also important to highlight the negligible contribution of the last sampling period to total mass loss rates, a pattern which was consistent regardless of the treatment considered. No net mass loss or even a slight increase in remaining mass during early, intermediate, and final stages of decomposition experiments has been previously reported in other dry, Mediterranean and mesic ecosystems, and could be related to microbial colonization and growth on the decomposing litter (Quideau et al., 2005; Brandt et al., 2010; Lee et al., 2014; Lin and King, 2014; Baker and Allison, 2015). Nevertheless, we found a trend at the end of the experiment towards increased leaf litter mass loss rates in response to UV radiation exposure in warming treatments, being decay rates 38% and 20% higher in the W and WRE treatments than in the control, respectively (Fig. 4A). This finding supports previous hypotheses stating that, under dry conditions, photodegradation should be easily detectable because microbial activity is suppressed under less suitable environmental conditions (Brandt et al., 2007; Smith et al., 2010). Thus, despite slower decay rates under warming, the contribution of photodegradation became more apparent during the dry period.

As expected, and despite the lower initial lignin concentration of *Stipa* leaf litter (4–5%) compared to other perennial grass species, lignin content decreased up to 7% in the litter exposed to UV radiation compared to that observed in the non-UV radiation treatment at the end of the decomposition experiment. Our results are in line with previous studies showing preferential loss of lignin with respect to other relatively less recalcitrant carbon fractions by photodegradation (Rozema et al., 1997; Day et al., 2007; Henry et al., 2008; Austin and Ballaré, 2010). However, and contrary to other studies (Rozema et al., 1997; Schade et al., 1999; Austin and Ballaré, 2010; Brandt et al., 2010; Lin and King, 2014), we did not observe any significant effect of UV radiation on cellulose or hemicellulose remaining (individually or pooled), and these fractions were much more abundant than lignin or cell soluble fractions in *Stipa* leaf litter. Overall, the larger losses of lignin observed in litter exposed to UV radiation were paralleled by increases in the cell soluble fraction, confirming previous evidence that photodegradation can play a dual role in litter decomposition process, breaking down lignin into more easily degradable fractions while enhancing the solubility of leaf litter (Gallo et al., 2006; Foereid et al., 2010). Simultaneously, the enhancement of cell solubles (the most labile carbon) could favour further microbial decomposition of recalcitrant sources by photo-priming (Barnes et al., 2015). However, the increase of cell solubles or decrease in the lignin

fraction mediated by UV radiation exposure were not affected by position, suggesting that no photo-priming occurred in this experiment, and therefore the photodegradation mechanism was mainly abiotic.

4.3. Interactions between climate, UV radiation, and position on litter decomposition rates

Contrary to our expectations and to previous reports from the literature (Brandt et al., 2010; Smith et al., 2010), the contribution of photodegradation to litter mass loss did not increase under rainfall reduction, but rather increased with warming. In the control and RE treatments, the decay rates of litter placed on the ground increased compared to those of standing litter. On the contrary, in the W and WRE treatments, litter decomposition rates did not differ between positions, but were positively affected by UV radiation (Fig. 4A, B). This finding is consistent with previous studies in other water-limited ecosystems in which abiotic processes such as photodegradation and thermal degradation were identified as important mechanisms of litter decomposition in the absence of microbial activity (Austin and Vivanco, 2006; Smith et al., 2010; Lee et al., 2012). Thus, our results support our hypothesis that warmer and drier conditions will lead to less biologically-driven decomposition while enhancing photodegradation, altering carbon cycling pathways and its incorporation into soils, and thereby impairing ecosystem functioning of dry Mediterranean perennial grasslands.

5. Concluding remarks

Increased temperature and decreased precipitation reduced leaf litter decomposition rates while enhancing the relative contribution of photodegradation to the overall decomposition of *Stipa* litter. We have also demonstrated that the combination of warming and UV radiation exposure favoured changes in the chemical composition of litter enhancing its solubility. Under warmer and drier conditions, lower litter decomposition rates were paralleled by higher losses of holocellulose (more abundant) and lignin (more recalcitrant) fractions, suggesting that climate change could affect litter decomposition pathways promoting preferential degradation of relatively more recalcitrant carbon, which ultimately could affect the long-term stability and storage of soil organic carbon.

The results of this study emphasise the need to incorporate the interaction between warming, moisture availability and UV radiation in litter decomposition models. This is a necessary step towards understanding the relative importance of photodegradation with respect to other environmental controlling factors in litter decomposition dynamics, as well as its implications for soil carbon cycling and storage of dry Mediterranean perennial grasslands, where increases in aridification are expected as a result of climate change.

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Appendix A. Supplementary material

Supplementary data related to this article can be found online at <http://dx.doi.org/10.1016/j.soilbio.2015.08.006>.

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