ECOSYSTEMS

Litter Decomposition Rates of Biocrust-Forming Lichens Are Similar to Those of Vascular Plants and Are Affected by Warming

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ABSTRACT

Despite the high relevance of communities dominated by lichens, mosses and cyanobacteria living on the soil surface (biocrusts) for ecosystem functioning in drylands, no study to date has investigated the decomposition of biocrust-forming lichen litter in situ. Thus, we do not know whether the drivers of its decomposition are similar to those for plant litter (for example, importance of abiotic degradation through UV radiation), the magnitude of lichen decomposition rates and whether they will be affected by ongoing climate change. Here we report the results from a litter decomposition experiment carried out with two biocrust-forming lichens (*Diploschistes diacapsis* and *Cladonia convoluta*) that differ in litter chemical quality (C:N ratio) in central Spain. We evaluated how lichen decomposition was affected by warming, rainfall exclusion and their combination. We also manipulated the incidence of UV radiation using mesh material that blocked 10% or 90% of incoming UV radiation. Our results indicate that lichens decompose as fast as some plants typical of the study area ($k \sim 0.3$ y^{-1}). We observed differences among the species studied in line with what is expected according to their chemical composition. Warming increased decomposition rates of both lichen species by 28% and mediated the effects of photodegradation. Although UV exposure accelerated the decomposition of *D. diacapsis*, it slowed that of *C. convoluta*. Our results indicate that biocrust-forming lichens can decompose in the field at a rate similar to that of vascular plants and that this process will be affected by warming. The findings

presented emphasize the need of considering bio-crusts and the decomposition of their tissues when honing ecosystem models aiming to forecast carbon cycling responses to climate change in drylands.

Key words: Lichen litter decomposition; Dry-lands; Biological soil crust; Climate change experiment; Photodegradation; Global warming.

INTRODUCTION

Arid, semi-arid and dry-subhumid ecosystems (drylands, hereafter) cover over 41% of the terrestrial surface (Cherlet and others 2018) but forecasted increases in aridity may increase their global area by 11–23% by the end of this century (Huang and others 2015). Drylands account for over 32% of the total amount of organic carbon stored in the world's soils (Plaza and others 2018) and are the key to understand the inter-annual variability of the global carbon cycle (Poulter and others 2014). In these areas, the highest soil carbon concentration occurs in the first soil centimetres (Ciais and others 2011; Thomas 2012). Thus, soil carbon dynamics in drylands is largely affected by those organisms and communities inhabiting the soil surface, such as biocrusts (communities constituted by cyanobacteria, algae, fungi, lichens, bryophytes and other microorganisms living in an intimate association with soil particles; Weber and others 2016).

Biocrusts are known to affect multiple processes of the carbon cycle. They fix atmospheric CO_2 and increase the amount of carbon stored in soils (Darrouzet-Nardi and others 2015; Delgado-Baquerizo and others 2015a), modulate carbon losses to the atmosphere via soil respiration (Castillo-Monroy and others 2011; Thomas 2012; Escolar and others 2015) and affect the activity of soil enzymes such as β-glucosidase (Bowker and others 2011; Miralles and others 2013). Despite their global extent ($\sim$ 12% of terrestrial surface, Rodriguez-Caballero and others 2018), their dominance across many dryland regions (Eldridge and Greene 1994; Maestre and others 2011, Weber and others 2016) and their well-studied impacts on the dryland carbon cycle, the role of biocrusts on processes such as litter decomposition in these environments is virtually unknown. This is important, especially in a context of climate change, because multiple experimental studies have shown that increases in temperature and/or alterations in precipitation such as those forecasted by climatic

models reduce the photosynthetic performance, growth and cover of biocrust constituents such as mosses and lichens (Maphangwa and others 2012; Reed and others 2012; Ladrón de Guevara and others 2014; Ferrenberg and others 2015; Maestre and others 2015; García-Palacios and others 2018). Maestre and others (2013) observed that increases in recalcitrant carbon compounds in the soil, which are abundant in the lichen thalli, were positively correlated with biocrust cover losses, which were much higher under warming (see also Ladrón de Guevara and others 2018 for longer-term observations). They suggested that the decomposition of dead lichen thalli could help to explain observed increases in overall soil carbon content under warming. However, no previous study has, to our knowledge, evaluated in the field the decomposition of biocrust-forming lichens in drylands, and thus, the rate at which their tissues decompose is unknown. Moreover, we ignore whether ongoing climate change, which is known to affect C cycling processes such as soil respiration and net C uptake in biocrust-dominated drylands (Ladrón de Guevara and others 2014; Darrouzet-Nardi and others 2015; Guan and others 2019), impacts decomposition rates of major biocrust constituents such as lichens.

Litter decomposition is a key process in the global carbon cycle, as more than 50% of net primary production returns to soils via the decomposition of plant litter in terrestrial ecosystems (Wardle and others 2004). Multiple studies have shown that the decomposition of lichen and moss tissues is a usually overlooked part of nutrient cycle in boreal/sub-boreal ecosystems (Wetmore 1982; Lang and others 2009), which is important as N fixed from atmosphere by lichens may not be incorporated to the soil otherwise (Campbell and others 2010). Also in temperate ecosystems, lichen decomposition is studied as a relevant source of soil nutrients for similar reasons (McCune and Daly 1994; Caldiz and others 2007; Li and others 2014). Indeed, the rates at which bryophytes and lichens decompose in these ecosystems can be as fast as those of some vascular plants (Lang and others 2009). Studies conducted in arctic areas have found important differences in the decomposition rates of several lichen species (Lang and others 2009), which are generally attributed to the thallus nutrient content (faster decomposition for species with high N and low C to N ratio) and growing form (faster decomposition for fruticose than for foliose lichens).

In drylands, the rate at which plant litter is decomposed depends on the interaction between

its chemical composition and multiple biotic and abiotic factors, including soil nutrients, fauna and microorganisms, and climatic conditions like precipitation and UV radiation (Throop and Archer 2009; Brandt and others 2010; King and others 2012; García-Palacios and others 2013; Delgado-Baquerizo and others 2015b; Almagro and others 2017). In particular, a growing number of studies have shown that solar ultraviolet (UV) radiation (280–400 nm) can accelerate leaf litter decomposition in drylands by directly breaking down organic matter components releasing CO_2, a process called photodegradation (Brandt and others 2007; Day and others 2007; Gallo and others 2009; Rutledge and others 2010). Although the results differ among litter types, site characteristics (for example, solar irradiance, temperature and moisture) and experimental conditions (field vs. laboratory) (Austin and Vivanco 2006; Gallo and others 2006; Brandt and others 2010; Almagro and others 2017), a meta-analysis concluded that solar radiation speeds up decomposition by 32% (King and others 2012). Because biocrust-forming lichens mainly occur in areas devoid of perennial vegetation, the incidence of UV photodegradation might be a key driver of their decomposition, as has been demonstrated with the decomposition of vascular plant litter.

We conducted a manipulative field experiment in central Spain to evaluate, for the first time, the decomposition rates of biocrust-forming lichen thalli from two dominant species [*Cladonia convoluta* (Lam.) Anders and *Diploschistes diacapsis* (Ach.) Lumbsch] and how it is affected by simulated climate change (2.5 °C warming and 35% rainfall reduction) and UV radiation. Specifically, we aimed to: (1) quantify the litter decomposition rates of *C. convoluta* and *D. diacapsis*, two species that differ importantly on litter quality, (2) assess the effects of simulated climate change (warming and rainfall reduction) on the decomposition rate and chemistry of lichen litter and (3) investigate whether UV radiation (photodegradation) accelerates its decomposition. We tested the following hypotheses: (1) given the different tissue chemistry of the two species studied, we hypothesize that they will exhibit different decomposition rates (Lang and others 2009), (2) litter lichen decomposition rate will be reduced by warming and reduced precipitation due to lower water availability (Almagro and others 2015), and (3) the relative contribution of photodegradation to the decomposition of lichen litter will increase under simulated climate change, as previously observed with plant litter in our study area (Almagro and others 2017).

MATERIALS AND METHODS

Study Area

The study was carried out in the Aranjuez Experimental Station, located in central Spain (Figure S1) (40°02′ N–3°32′ W; 590 m a.s.l). The climate is Mediterranean semi-arid, with mean annual temperature and rainfall values of 15 °C and 349 mm, respectively. Precipitation events predominantly occur in autumn–winter and spring. The soil is classified as Gypsiric Leptosol (IUSS Working Group WRB 2015). The cover of perennial plants is lower than 40% and is dominated by the perennial herbaceous species *Macrochloa tenacissima* (L.) Kunth. To a lesser extent, there are also isolated individuals of shrubs such as *Helianthemum squamatum, Gypsophila struthium* Loefl. and *Retama sphaerocarpa* (L.) Boiss. Open areas between plants contain a well-developed biocrust community dominated by lichens such as *Diploschistes diacapsis, Squamarina lentigera* (Weber) Poelt., *Fulgensia subbracteata* (Hoffm.) Räsänen and *Buellia zoharyi* Galun. Mosses such as *Pleurochaete squarrosa* (Brid.) Lindb. and *Didymodon acutus* (Brid.) K. Saito. are also present (mostly under the canopy of *Macrochloa*, where *Cladonia convoluta* can also be found) at the study site, as well as cyanobacteria of the genera *Microcoleus, Schizothrix, Tolypothrix, Scytonema* and *Nostoc* (Cano-Díaz and others 2018). See Maestre and others (2013) for a complete species checklist of biocrust-forming mosses and lichens found at our study site.

Lichen Litter Collection

For this study, we selected *Diploschistes diacapsis,* a crustose lichen, and *Cladonia convoluta*, a fruticose lichen (Figure S2). Both species have preference for gypsum soils and are semi-vagrants or vagrants lichens. Whereas *D. diacapsis* has as photobiont algae of genus *Trebouxia sp.*, *C. convoluta* associates with *Asterochloris sp.* These algae species are very similar and can only be differentiated by the morphology of their chloroplasts (Tschermak-Woess 1980; del Campo and others 2010). The lichens selected are common in the study area, and due to their loose attachment to the soil, can be collected without disturbing the soil surface and affecting other biocrust-forming species. Thalli from *D. diacapsis* and *C. convoluta* were collected in June 2013 at the study area and were transported to the laboratory, where they were gently cleaned with a small brush. Once cleaned, we killed living tissues by keeping them frozen at − 80° C for a week; after that, the thalli were submerged in liquid nitrogen for 5 s (see Lang

and others 2009 for a similar approach). After these treatments, the thalli were oven-dried at 70 °C for 24 h. It must be noted that this killing procedure may exert a traumatic effect on the microbiota living on the lichen tissues (that is, apart from killing the lichen we are sterilizing its tissues). Although this may exert an effect in decomposition rates, we followed the methods used in other lichen decomposition studies (see Lang and others 2009) to make our results more comparable with those available in the literature. This, however, should be considered when interpreting our results.

To study the decomposition of lichen thalli in the field, we used the litterbag method (Lang and others 2009; García-Palacios and others 2013). Samples of lichen litter (~ 1.6 g per litterbag) were weighted and placed in 5×5 cm litterbags with a mesh size of 1 mm^2 (Figure S2 C). We used intact thalli (oriented in their natural position) as lichen litter. Litterbags were placed directly on the soil surface to mimic their natural disposition. We used two types of mesh material to build the litterbags (Light treatment): a UV-block screen material made of fibreglass, which blocked about 90% of incoming UV radiation, and a UV-pass screen material made of high-density polyethylene, which blocked only about 10% of incoming UV radiation (Dirks and others 2010; Almagro and others 2015). UV pass material was equally transmittable across all wavelengths of UV radiation (280–400 nm, see Brandt and others 2007). The different litterbag material did not significantly affect temperature within the litterbags (see Figure S3).

Experimental Design

To evaluate the impacts of climate change on the decomposition rates of lichen litter, and their interactions with photodegradation, a factorial experiment was set up with four climatic treatments: warming (W, a ~ 2.5 °C annual temperature increase), rainfall reduction (RE, a $\sim 35\%$ reduction in annual rainfall), the combination of both warming and rainfall reduction (WRE) and a control (C) treatment with no manipulation. The experimental design consisted of five blocks distributed among the different climate manipulation treatments in a split-plot design (Figure 1). The whole-plot factor was the different climatic manipulations used (C, W, RE and WRE; 20 in total). The subplot factor was a factorial combination of Light treatment (UV-block, UV-pass) and litter species (*D. diacapsis* and *C. convoluta*), which were randomly assigned within the plots (80 in
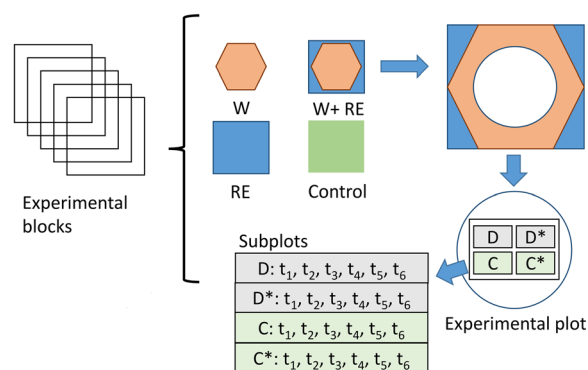
Figure 1. Experimental design used. There were three climate manipulation treatments (W, RE, REW) and control (C) treatments. In each experimental plot ($n = 5$ per treatment), there were four types of subplots, one per combination of litter lichen type (*D. diacapsis*; D, or *C. convoluta*; C), and UV radiation treatment (UV-block, indicated as * or UV-pass, with no indication). Six litterbags were set up at each subplot for collection at different timepoints (t_1–t_6).

total). The experiment was set up in early June 2013.

Climate Manipulation Treatments

To increase temperature in the warming treatment, we used open top chambers (OTCs) with hexagonal design and sloping sides of $65 \times 42 \times 52$ cm. These chambers were built with methacrylate sheets, which ensure high transmittance in the visible spectrum (92%, according to the manufacturer; Decorplax S.L., Humanes, Spain) and a very low emission in the infrared wavelength. Chambers were suspended 3–5 cm over the ground by a metal frame to allow free air circulation at the soil surface level to avoid an excessive heating. With these OTCs we aimed to apply a warming of 2–3 °C, which is in line with several Atmosphere–Ocean General Circulation Models for the second half of this century in Central Spain (Giorgi and Lionello 2008; Stocker and others 2013).

Although precipitation predictions are subject to a higher level of uncertainty in the Mediterranean Basin, projected changes point to an intensification of water scarcity in this region (Giorgi and Lionello 2008; Stocker and others 2013). Thus, passive rainfall shelters based on the design of Yahdjian and Sala (2002) were used to achieve a reduction in rainfall amount of about 30% without changing the frequency of rainfall events. Each RS had an area of 1.68 m^2 (1.4×1.2 m) and a roof composed by six gutters of methacrylate with an inclination of nearly 20° and a mean height of 1 m. The effec-

tiveness of the passive rainfall shelters used has been previously tested (Escolar and others 2012; Maestre and others 2013; Ladrón de Guevara and others 2014).

Our OTCs and RS did not alter substantially the incidence of UV radiation; direct measurements of UV radiation using a UV Meter (UVM, Apogee Instruments Inc, Logan, UT, USA) showed only 9–10% UV reductions when compared to control treatments (Almagro and others 2015).

Environmental Monitoring

Rainfall and solar radiation were monitored by an on-site meteorological station (Onset Corp., Bourne, MA, USA). Air temperature and relative humidity in the different treatments were monitored with automated sensors (HOBO® U23 Pro v2 Temp/RH Onset Corp., Pocasset, MA, USA). Soil surface temperature (first 2 cm) and water content (0–5 cm) were continually monitored with TMC20-HD and EC-5 sensors, respectively (Onset Corp. and Decagon, Inc., Pullman, WA, USA).

Litter Decomposition

Six litterbags per subplot were placed in the field, accounting for a total of 480 litterbags (2 species × 6 timepoints × 2 light treatments × 4 climate treatments × 5 replicates). Five litterbags per combination of treatments and species were randomly removed for dry mass determinations approximately at 3, 5, 7, 11, 15 and 29 months after deployment in the field. Recovered litterbags were put in individual paper bags and were taken to the laboratory, where the lichen litter was carefully cleared of soil, fauna and other lichens species with a soft brush. The litter samples were then dried in an oven at 60 °C for 48 h before weighing.

Mass loss was estimated as the difference of dry mass between the initial and successive litterbag collection dates. The decomposition rate (k) of the litter of each lichen species was determined for climatic and light treatments using the single exponential decay model of (Olson 1963):

$$M_t = M_0 e^{-kt}$$

where M_t and M_0 are the dry mass of the litter at time t and time 0. Thereby, k is the daily litter decay rate, which is commonly used in other experiments of litter decomposition (Lang and others 2009; Campbell and others 2010; King and others 2012; Almagro and others 2017). We used nonlinear estimation of the decomposition rates, as is sug-

gested to be more robust than estimation through logarithmic transformations (Adair and others 2010). The resulting R^2 of these models was high ($R^2 = 0.82 \pm 0.17$).

The duration of our study allows us to compare the decay rates observed with those from previous studies (for example, Lang and others 2009). When comparing with studies of shorter duration we recalculated the decomposition rate to account for the fact that study duration may have a major impact of measured decays. The correlation between the k for the whole experiment and that obtained after 1 year (the duration of many litter decomposition experiments) was high ($r = 0.71$, $P < 0.01$), and thus, we report k vales obtained from the whole experiment.

Determinations of Lichen Mass Chemistry

The contents of organic carbon (OC) and total nitrogen (TN) in the litter were determined at months 0, 11 and 29 after the set-up of the experiment in five replicates per combination of treatments. Organic C was analysed with a colorimetric method after oxidation with a mixture of potassium dichromate and sulphuric acid (Anderson and Ingram 1994). Total N was determined with a Skalar Nutrient Autoanalyzer model SAN ++ (NUTILAB, URJC) after the sample digestion according to the Kjeldahl method, wherein a $Cu + KSO_4$ catalyst is added to the sample and N-organic is oxidized to NH_3–N by a digestion with H_2SO_4 (Radojevic and Bashkin 1999).

Statistical Analyses

Differences in initial chemical composition (OC_0, TN_0 and $C:N_0$) between species were analysed with Student's t-tests. Also, we conducted statistical analyses on the remaining biomass of lichens, on the differences in their chemical composition 11 and 29 months after the beginning of the experiment and on the decomposition rates obtained. We analysed the results at 11 and 29 months from experiment initialization because mechanisms of litter degradation change throughout the decomposition process (García-Palacios and others 2016). We conducted three-way ANOVAs to evaluate the effects of climate manipulations (C, RE, W and REW), light treatment (UV-block and UV-pass) and lichen species (*D. diacapsis* and *C. convoluta*) on remaining litter biomass ($n = 5$), decomposition rates ($n = 5$) and litter chemical composition ($n = 3$). These factors were considered as fixed

factors in these analyses. We added block as a random factor to control for microsite-specific differences among plots. To evaluate differences between levels within each fixed factor, the Fisher's least significant difference (LSD) mean comparison test was applied. Data were tested for ANOVA assumptions before analyses; k (y^{-1}) values were $\log_{10}$-transformed to fulfil ANOVA assumptions. We additionally calculated the power (1-Type II error) of our analyses to test whether sample size was adequate and found that the chosen sample size was not affecting our results (Table S1). All statistical analyses were performed using SPSS 18.0 (SPSS Inc., Chicago, IL, USA). Data are available through figshare (Berdugo and others 2020).

RESULTS

Effect of Climate Manipulation on Environmental Conditions

Accumulated rainfall during the experiment was 690 mm: 249, 386 and 55 mm for the first year, second year and the last five months of the experiment, respectively (Figure S4a). Mean monthly maximum air and soil temperatures (Figure S4b) were reached in July and August of both years (27 °C and 32.5 °C, respectively). On average, warming increased air temperature by 2.5 °C with respect to the control, with maximum effects during the summer (when differences reached up to 3.2 °C). However, in the WRE treatment, the average increase with respect to the control was 1.4 °C (Figure S5). Annual average relative humidity was 62%, with autumn and summer having the highest (80%) and lowest (40%) values, respectively (Figure S5). On average, relative humidity was lower in the W and WRE treatments than in the control treatment by 4% and 3%, respectively. Variations in soil moisture closely followed rainfall events. Mean soil moisture values during the experiment period were: 6.8% for C, 7.7% for RE and 4% for W and WRE treatments.

Treatment Effects on Litter Decomposition Dynamics

After 1 year, the litter mass loss of both *D. diacapsis* and *C. Convoluta* was over 20% (Table S2, Figure 2). No significant effects of the treatments evaluated were observed on litter mass loss at this time ($P > 0.05$; Table S3). Nearly two and a half years after experimental set-up, *D. diacapsis* lost almost 20% more mass than *C. convoluta*. These effects were, however, modulated by the amount of UV
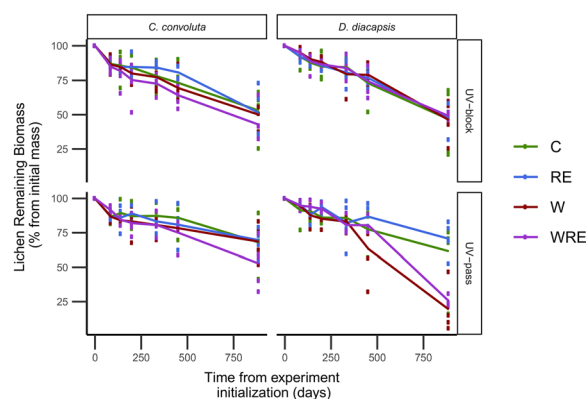
Figure 2. Lichen decomposition dynamics for *Diploschistes diacapsis* and *Cladonia convoluta* (columns) under two UV treatments (rows) and different climatic conditions. Lines are smoothed trends of the data. *RE* rainfall exclusion, *W* warming, *WRE* warming and exclusion combination and *C* control.

radiation received, as indicated by a significant species × light interaction ($P = 0.027$; Figure 3). Thus, the differences between species were only detected in the UV-pass treatment ($P = 0.001$; Table S4), and only *C. convoluta* had differences in remaining litter mass ($P = 0.007$) under this UV treatment (Table S4; Figure 2). It must be noted, however, that the species × light × climate and species × climate interactions had P values of 0.082 (Table S3). Indeed, W and WRE resulted in lower mass remaining values than control and RE treat-
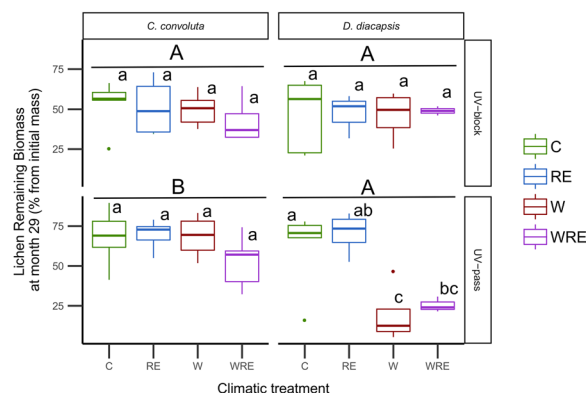
Figure 3. Mass remaining of *Diploschistes diacapsis* and *Cladonia convoluta* litter under different climate change and UV treatments 2.5 years after experimental set-up. Different lowercase letters represent statistically significant differences ($P < 0.05$) when climatic treatments are compared within each panel. Uppercase letters in brackets represent homogeneous groups when comparing the mean of remaining biomass between each of the four panels. *RE* rainfall exclusion, *W* warming, *WRE* warming and exclusion combination and *C* control. Data are median ± SE ($n = 5$).

ments, but this effect was only significant for *D. diacapsis* in the UV-pass treatment ($F = 3.2$, $P = 0.032$, Figure 3).

By the end of the experiment, the decomposition rate of *D. diacapsis* was higher ($k = 0.34$ years^{-1}) than that of *C. convoluta* ($k = 0.22$ years^{-1}). Significant three-way (species × light × climate) and two-way (species × light) interactions were observed when analysing litter decomposition rates (Table S3). Separate ANOVAS conducted for each species revealed that W and WRE accelerated litter decomposition rate in *D. diacapsis* and *C. convoluta*, respectively (Figure 4). Receiving more UV radiation favoured litter decay rate for *D. diacapsis* respect to *C. convoluta* ($F = 12.24$, $P = 0.001$). This effect was more important under warming, where UV exposition increased the decomposition rates in *D. diacapsis* when compared to the UV-block treatment, while showing the opposite effect in *C. convoluta* (Figure 4). Also, *C. convoluta* had in general a higher k (y^{-1}) in the UV-block than in the UV-pass treatment ($F = 7.379$, $P = 0.008$). Contrasting effects were shown between light treatments for *D. diacapsis* depending on the climate treatment (Figure 4), rendering no significant differences overall ($F = 0.719$, $P = 0.400$). There were no differences between species in the absence of UV exposure ($F = 0.004$, $P = 0.947$).
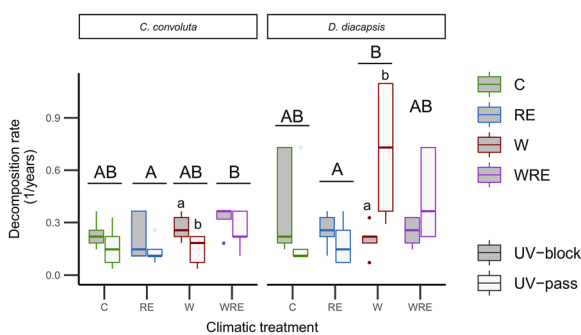
Treatment Effects on Carbon and Nitrogen Dynamics

The litter of *C. convoluta* had a higher concentration of C and N, and a higher C:N ratio than that of *D. diacapsis* at the beginning of the experiment (Table S5). Differences in the C concentration and the C:N ratio between species were maintained throughout the experiment regardless of the treatments, whereas N concentration values re-

mained unaltered for each species throughout the experiment. The light treatment was only significant after 29 months of experiment, promoting increases in the C:N ratio of lichen thalli in the UV-pass treatment (Figure 4). This effect was consistent among species (species × light interactions were not significant). However, depending on the species, different climatic treatments modulated C and N concentrations differently throughout the experiment (Table S6).

Effects of climatic treatments on *D. diacapsis* C and N concentrations were mainly independent from those from light treatments. Some exceptions were the interactions found in the C concentration with the light treatment, which significantly increased this concentration in the RE and W treatments at month 29 and decreased it in the control treatment at month 11. In general, W and WRE treatments decreased the concentration of both C and N with respect to control and RE treatments, respectively (Figure 5). This effect was clearer at month 29 than at month 11, where N concentration in the control treatment was similar to that observed in the warming treatments. Only the RE treatment exhibited lower C:N ratios than the rest of treatments; these were mainly driven by a higher N concentration respect to other treatments, which was also clear at month 11 (Figure 5).

Climate change treatments promoted significant changes in the C and N concentrations of *C. convoluta* at month 29, with significant decreases under RE and W treatments (vs. the control treatment, Figure 5). These differences, however, were modulated by the light treatment. In RE and WRE treatments, UV exposition significantly decreased N concentration while warming (W and WRE treatments) significantly increased C concentration respect to UV-block treatments. Most of these effects cancelled each other when evaluating the C:N ratio. In the WRE and RE treatments, however, UV-pass treatments significantly increased C:N ratios respect to UV-block treatments (Figure 5).

DISCUSSION

Litter Decomposition Rates of Lichen Species

Overall, the litter decomposition rates of the lichens studied were low (k values between 0.22 and 0.34 y^{-1}). These values are comparable to the litter decomposition rates of some recalcitrant plant species in the Mediterranean (for example, *Retama Sphaerocarpa*, $k = 0.36$ y^{-1}, Almagro and others 2017; *Quercus coccifera*, $k = 0.22$ y^{-1}, Gallardo and

Figure 4. Decomposition rate of *Diploschistes diacapsis* and *Cladonia convoluta* litter under different climate change and UV treatments 2.5 years after experimental set-up. Rest of legend as in Figure 3.
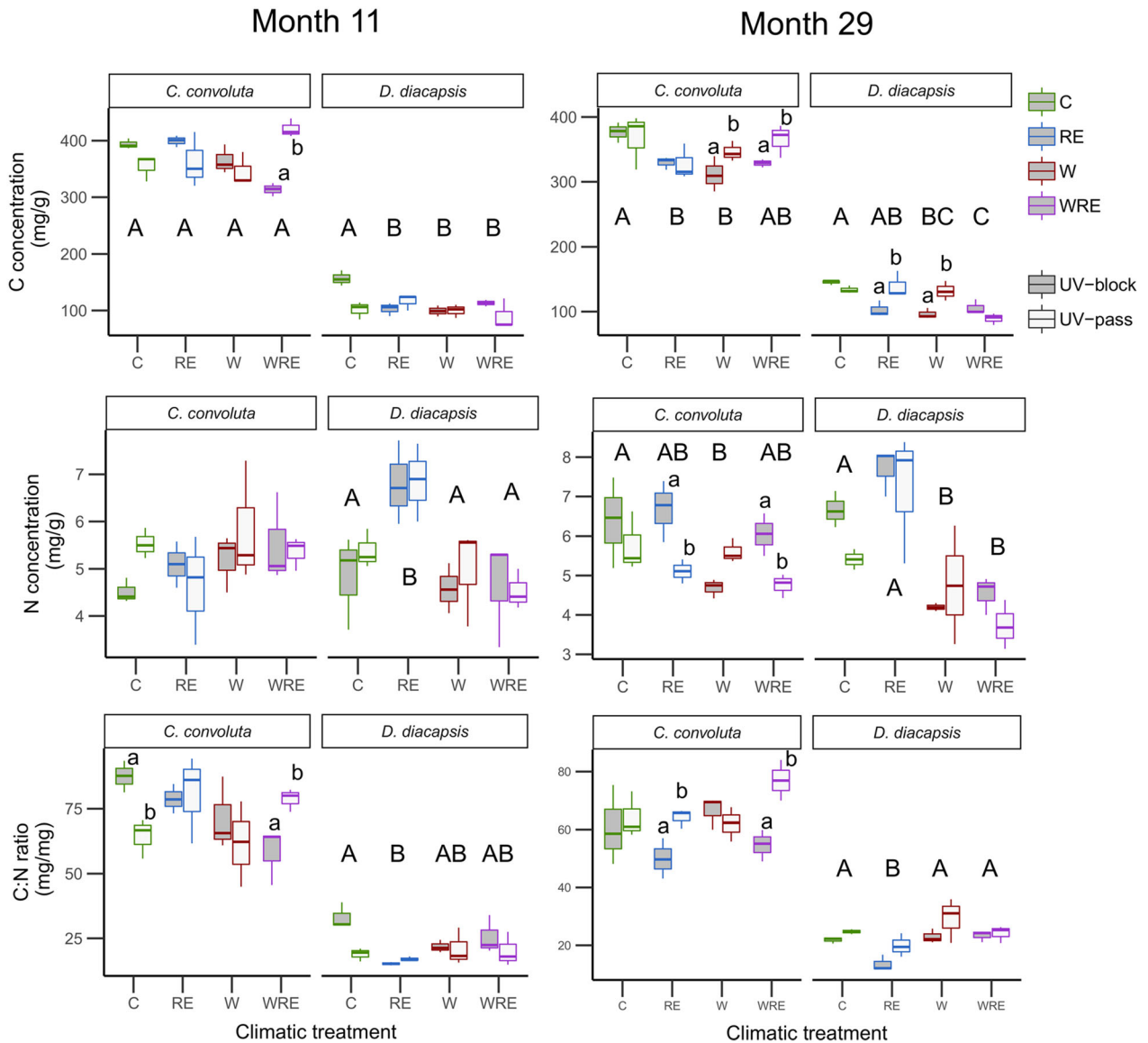
Figure 5. Carbon (top), nitrogen (middle) and C:N ratio (bottom) concentrations at 11 (left) and 29 (right) months after the beginning of the experiment. Data are mean ± SE (*n* = 3). Rest of legend as in Figure 3.

Merino 1993), or other dryland regions (*Bouteloua gracilis*, *k* =0.36 y^{-1}, Brandt and others 2010) but still are faster than the most recalcitrant grass species present in the study area (*Stipa tenacissima*, *k* = 0.06 y^{-1}, Almagro and others 2015) or other species living in the same community (*Helianthenum squamatum*, *k* = 0.15 y^{-1}, Prieto and others 2019). Compared to other lichen species reported mostly in subarctic areas or coniferous forests, the decomposition rates shown here were lower than those of species of the same genus (*C. convoluta* vs. *C. stellaris* *k* = 0.28 y^{-1}, mass remaining ∼ 40%; Lang and others 2009) or morphology (*D. diacapsis* vs. *Umbilicaria hyperborea* *k* = 0.69 y^{-1}, mass

remaining ∼ 20%; Lang and others 2009). This is probably related to site differences in soil and climate, which can limit litter decomposition in plants (Gallardo and Merino 1993). Indeed, although exhibiting lower C:N ratio compared to arctic communities (which indicates higher decomposability, Aber and others 1990), lichens in our experiment still decomposed slower than lichens of arctic communities (Lang and others 2009).

Litter decomposition is tightly linked to litter quality, being faster the lower the C:N ratio of litter (Aber and others 1990). This premise likely explains why *D. diacapsis* (with C:N ratio = 30) decomposed faster than *C. convoluta* (C:N ratio =

56) in our experiment (although this holds true only for certain treatments see Figure 3). However, future studies considering a wider range of species with contrasting C:N ratios are needed to demonstrate that this is the case. (Note that in our study, litter chemistry is nested within the species.) The C:N ratio also controls the mobilization of N into the soil, as N usually is immobilized by microbial decomposers until C:N ratio around 20 (Manzoni and others 2010). Indeed, the C:N ratios of *D. diacapsis* observed at the end of the experiment ($\sim$ 20) suggest that this species reached a stage in which N starts mineralization while *C. convoluta* would still immobilize most of the nitrogen. This can also explain differences in N content of both lichens at the end of the experiment and a faster litter decomposition rate of *D. diacapsis*, especially during the second year of the experiment. However, specific measurements of ammonium and/or nitrate in the soil should be taken to further corroborate this hypothesis.

Decomposition of lichen tissues was accelerated mainly in the second year of our experiment. This response concurs with temporal patterns of decomposition evidenced for other lichen (Hagemann and Moroni 2015) and grass (Wang and others 2017) species in areas with periods of unfavourable conditions such as freezing. However, it contrasts with the rapid mass losses at early stages of decomposition observed in plant litter decomposition experiments in Mediterranean ecosystems (Almagro and others 2015; Prieto and others 2019; Gallardo and Merino 1993). This discrepancy may be partially explained due to the procedure we used to kill the lichens, which involve a necessary sterilization of the tissues prior to the start of the experiment. It is interesting to note that differences between lichen species were only apparent during the second year of the experiment. According to other studies, legacy effects related to litter quality are more apparent on late decomposition stages, when the relative importance of biotic processes linked to microarthropods and nematodes is reduced (García-Palacios and others 2016). Thus, our results also support the hypothesis that differences in litter decomposition rates between species are mainly controlled by litter quality. Other factors, as discussed below, cannot be ruled out as the main cause of these differences.

Apart from the C:N ratio, other chemical components of lichen litter may have a fundamental role on its decomposition (Lang and others 2009). In *D. diacapsis*, almost 40% of the organic carbon present on its thalli is labile (Miralles and others 2013). This carbon can be lost immediately by active microbial synthesis (Chantigny and others 2006) or by microbial respiration of CO_2 via litter decomposition (Delgado-Baquerizo and others 2015b). The two species studied also differ in the content of lichenic substances; *C. convoluta* presents phenolic compounds like fumarprotocetraric acid (aromatic aldehyde), usnic acid, zeorin (Triterpenoides) and psoromic acid (Pino-Bodas and others 2010), while *D. diacapsis* presents diploschistesic, lecanoric and/or sellinic acid (Nash and others 2002). Usnic acid is associated with the protection of lichen thallus against UV radiation, while fumarprotocetraric acid has hydrophobic properties (Barreno and Párez-Ortega 2003). Both compounds have also high antimicrobial activity that inhibit bacteria and fungi. Thus, these lichenic protective substances could affect the decomposition process of their tissues (Kosanić and others 2014). For instance, phenolic compounds have been shown to reduce the positive effects of microarthropods on the decomposition of lichen litter, although these substances reduce rapidly through decomposition after 1 year (Asplund and Wardle 2013).

Effect of Climate Manipulation on Litter Decomposition

According to the previous results in other climate manipulation experiments carried out with plants (Almagro and others 2015, 2017), we expected warming and rainfall exclusion to decrease overall decomposition rates due to lower water availability under these treatments. However, warming increased litter decomposition rates of *D. diacapsis*, a response accompanied by higher N mobilization (as indicated by N concentration rates, Figure 5), and of *C. Convoluta*, albeit in this species this response was only observed when warming was combined with reduced precipitation. Albeit initially unexpected, our results could explain the higher soil respiration rates observed under warming in areas covered by a well-developed biocrust, which co-occurred with large reductions in biocrust cover, during the first years after experimental set-up (Maestre and others 2013). Furthermore, our results indicate that these increases in soil respiration with warming are not only due to a higher lichen mortality, but also to a higher decomposition of their tissues. Interestingly, this positive effect of warming on soil respiration disappears 8–10 years after the set-up of the experiment (Dacal and others 2020), when the mortality of biocrust-forming lichens was mostly halted compared to the initial years of the experiment (Ladrón de Guevara and

others 2018). Using data from these studies and those reported here, we can quantify how the loss of lichen litter may have contributed to carbon cycling under warming. Assuming that 1.6 g of lichen cover 25 cm^2 (based on our experiment observations, thus 640 g/m^2) and that carbon is the major component of lichen thalli, and taking into account the declines in lichen cover reported with warming in previous experiments (up 75% during the first two years, Maestre and others 2013, resulting in a loss of litter of 480 g/m^2) and the decomposition rates we observed (75% of mass lost after two years for *D. diacapsis* under warming), we estimate that decomposition would mobilize around 360 g/m^2 of carbon either to the soil as recalcitrant compounds or as respiration in form of CO_2. These numbers are in the same order of magnitude than what is found in the study by Maestre and others (2013), who roughly found increases of about 100 g C/m^2 of recalcitrant carbon in soils under the warming treatment plus a total respiration of around 227 g C/m^2 in two years (at a rate ~ 0.3 μmol CO_2/m^2/s). Indeed, some authors state that under some stresses the fungal component of the lichen can consume the algal component of the lichen symbiosis and then die because they are not able to thrive without the symbiosis (Ahmadjian and Jacobs 2011). In any case, our results suggest that increased decomposition under warming treatment may be at least partially responsible for enhancing respiration rates observed by Maestre and others (2013).

Although we can only hypothesize the reasons for a higher decomposition under warming treatments, we speculate it could be driven by two alternative hypotheses. First, summer is an unfavourable period for biotic activity in the study area due to the acute water scarcity. In contrast, during winter water is no longer a limiting factor although low temperatures may reduce biotic activity significantly (despite the still warm temperature compared to other areas). Thus, the warming treatment could have accelerated decomposition processes during winter and early spring by creating a warmer microenvironment prone to decomposition when it rains more. Another explanation may be the existence of some kind of antimicrobial effect exerted by lichens (Kosanić and others 2014). The effect of soil humidity on litter decomposition rates is partly mediated by microbial activity, which degrades litter (Manzoni and others 2010; García-Palacios and others 2016). Thus, the antimicrobial compounds present in lichen tissues may have obscured the effect of soil humidity on their degradation by

impeding efficient microbial activity. This is especially relevant for biocrust-forming lichens, which live in tight interaction with soil microorganisms and, unlike plants, developed a series of chemical compounds to compete with them (Kosanic and Ranković 2015).

Effects of UV Radiation on Litter Decomposition

Observed increases in decomposition rates in the warming treatment were partly mediated by the effects of the light treatment. Unlike with previous observations carried out with plant litter (Brandt and others 2010; King and others 2012; Almagro and others 2017; Wang and others 2017), UV exposure only accelerated lichen litter decomposition together with warming in *D. diacapsis*. However, *C. convoluta* litter showed a contrasting behaviour, as decomposition was reduced by warming when exposed to UV. Photodegradation is an increasingly recognized driver of litter decomposition in drylands (Austin and Vivanco 2006; King and others 2012) and may increase degradation by mechanic fragmentation of lichens (Gallo and others 2006; Day and others 2007). On the other hand, increased UV radiation can slow down the decomposition process due to the negative effect on microbial and arthropod life forms (Brandt and others 2007, 2010). Thus, the effect of photodegradation on litter decomposition is the result of a balance between abiotic and biotic processes.

The chemical composition and morphology of the lichen thalli may be an important driver explaining the contrasting decomposition behaviour of the two lichen species studied. For instance, differences in content, number and complexity of carotenoids between some species of *D. diacapsis* and *C. convoluta* have been reported (for example *D. muscorum* and *C. furcaiu*, Czeczuga and others 1995), which is also apparent by their different colour. A higher content of pigments in *C. Convoluta* or other compounds that absorb UV radiation (for example, usnic acid) may decrease the efficiency of direct photodegradation when compared with *D. diacapsis*, which is white and has a lower concentration of usnic acid and different composition of carotenoids than *C. convoluta* (Nash and others 2002). Similarly, *D. diacapsis* is more exposed to radiation due to its plain morphology, whereas *C. convoluta* is a foliose lichen and its higher structural complexity and volume may produce more diffuse impact of radiation in the thallus. These drivers have been previously overlooked in plants, which exhibit less variation in

their morphology and whose composition in UV-absorbing pigments is more homogeneous than in lichens. Future studies need to test these hypotheses by examining the importance of photodegradation in a wider variety of lichens regarding their pigment content. Interestingly, the higher protection of *C. convoluta* (vs. *D. diacapsis*) to UV radiation is counter-intuitive with its living form, as in the study area this lichen lives mainly in more moist/shaded areas whereas *D. diacapsis* develops predominantly in inter-spaces under full sunlight (Castillo-Monroy and others 2011). To better test the hypothesis that pigments influence the relative importance of photodegradation, two populations of the same species with contrasting adaptation to shade/sun conditions (for example, Pintado and others 2005) should be examined.

Apart from the overall decomposition rates, photodegradation was an important driver of the changes in the C and N concentration of lichen litter during our experiment. Our results suggest that these effects are more apparent in *C. convoluta*, the species with the lowest decomposition rates. It is interesting to note that UV exposure effects were more apparent in the climate change treatments. In particular, the lower N concentration rates found in RE and WRE treatments suggest that UV radiation may even mobilize N regardless of the C:N ratio of the thallus, thus increasing abiotic decomposition (Austin and Vivanco 2006). This effect is probably more important in dry lichens, which would explain why this result was significant only in the RE and WRE treatments. An important point is that this N mobilization by UV radiation prevents the C:N ratios to decrease and thus may suppose an impediment to microbes for mobilizing N compounds through the decomposition process. Our results also suggest that the role of photodegradation will be more important with ongoing climate change.

CONCLUDING REMARKS

To the best of our knowledge, this is the first study assessing the decomposition of biocrust-forming lichens under simulated climate change in drylands. Our results showed that these lichens may have similar decomposition rates (or even faster) than plants growing in the same areas and under the same climatic conditions, but slower than lichens from temperate and arctic ecosystems. Altogether, our results show that the degradation of lichen litter is stimulated by UV radiation and warming and that it depends strongly on lichen species. An interesting contribution of our study is

that the effects of climate change on lichen decomposition interact with the abiotic and biotic drivers of this process. Future studies should focus on the biotic drivers of lichen litter decomposition (for example, abundance and identity of lichen decomposers) and the composition of secondary components of lichen tissues (such as antimicrobial peptides and phenolic compounds) to advance our understanding of the decomposition of biocrust-forming lichens in drylands. The production of lichen litter is a relevant component of nutrient cycling not studied here that should be analysed in future studies to achieve a more complete understanding of the overall contribution of lichen litter decomposition to C cycling. The (relatively) high decomposition rates of lichen tissues observed here stress the importance of considering biocrusts and the decomposition of their tissues when modelling carbon cycling responses to climate change in drylands.

DATA AVAILABILITY

Data can be found at: https://figshare.com/s/d5fa 2310717821c6b779. The digital object identifier of these data is: https://doi.org/10.6084/m9.figshare. 11822538.

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