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Divergent responses of moss- and lichen-dominated biocrusts to warming and increased drought in arid desert regions

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ABSTRACT

Global warming coupled with increased drought is predicted to have a significant negative impact on desert ecosystems. In arid desert regions, a large proportion of the ground surface is covered by specialized organisms such as mosses and lichens that form biocrusts, which play a vital role in ecosystems. However, the long-term effects of warming and drought on these key biotic components of desert ecosystems remain poorly understood. Using a manipulative experiment conducted for 12 years in the Tengger Desert, northwestern China, we evaluated how both mosses and lichens in biocrust communities responded to 0.5°C and 1.5°C increases in temperature coupled with 5% and 8% reductions in total annual precipitation, respectively, using two groups of open-top chambers to approximate climate change conditions that are predicted to occur in this study region. Furthermore, surface soil carbon uptake by the biocrusts was also evaluated. Twelve years of warming coupled with increased drought resulted in a significant decrease in the cover and biomass of mosses but did not change the cover or biomass of lichens. These changes in the mosses were positively correlated with the duration and intensity of the treatments. Warming coupled with reduced precipitation significantly reduced the carbon uptake of the moss-dominated biocrusts by reducing the availability of moisture content. However, lichen carbon uptake was insensitive to the warming and reduced precipitation treatments. The reduction in cover and biomass of moss-dominated biocrusts might be attributed to large amounts of carbon loss, which further alters biocrust multifunctionality in desert ecosystems. In addition, our findings suggest that coupled warming and drought conditions could increase the dominance of lichens in biocrust communities to partly maintain the multifunctionality of biocrusts in this desert ecosystem.

1. Introduction

Climate models predict rapidly increasing temperatures for already hot and soil water-limited arid regions (IPCC, 2013; Jardine et al., 2014). The forecasts of precipitation patterns are less certain, but overall drier conditions with changes in precipitation event size and frequency are likely (Seager et al., 2007). Specifically, some climate models have predicted increases in drought frequency and duration coupled with substantial warming (Belnap and Lange, 2003; Huang et al., 2015) as well as significant alterations in the amount and timing of rainfall (Christensen et al., 2007). Likewise, a model from China predicted that by 2050, a temperature increase of 1.5°C and uncertain rainfall changes will occur in the northwestern deserts of the country (Qing, 2002), where biological soil crusts (biocrusts) are key biotic components (Li et al., 2017).

Biocrusts are important for the cycling of key nutrients, such as carbon and nitrogen, in desert ecosystems (Chamizo et al., 2017; Delgado-Baquerizo et al., 2012; Maestre et al., 2013; Su et al., 2011); additionally, biocrusts stabilize surface soil (Park et al., 2017) and influence soil hydrological cycles (Kidron and Tal, 2012; Kidron, 2015; Prorada et al., 2018), creating microhabitats for both vascular plants (Belnap and Lange, 2003; Song et al., 2017) and invertebrates (Li et al., 2012; Liu et al., 2018). However, biocrusts are also one of the most sensitive components of drylands to climate change (Ferrenberg et al., 2017; Reed, Maestre et al., 2016; Darrouzet-Nardi et al., 2018). In general, global warming coupled with drought is predicted to have a significant negative effect on desert ecosystems by influencing the diversity and productivity of dominant plant species (Bita and Gerats,

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2013) and altering the soil water balance (Chamizo et al., 2016). Thus, changes in biocrust components such as mosses, lichens and cyanobacteria are likely to directly affect multiple functions of desert ecosystems (Bowker et al., 2011; Escolar et al., 2012). Numerous studies have demonstrated that the multifunctionality of biocrusts is mainly characterized by the performance and dominance of keystone species in communities, such as the proportion of moss, lichen and cyanobacteria coverage (Belnap et al., 2018). Because of biocrust community complexity, little is understood about how warming and precipitation changes will affect the diversity, abundance and structure of biocrusts. A few previous studies have determined that increasing temperature and precipitation have substantial effects on nonvascular biocrust components, such as mosses, lichens (Ferrenberg et al., 2015; Escolar et al., 2012; Maestre et., 2015) and microbial communities (Johnson et al., 2012; Sheik et al., 2011; Steven et al., 2015; Dacal et al., 2019). In particular, watering treatments, rather than warming treatments, had a notable negative effect on mosses and lichens, and increasing rainfall rapidly reduced the cover of mosses and lichens, even resulting in the death of the moss *Syntrichia caninervis* (Coe et al., 2012). Almost all of the abovementioned studies were carried out in semiarid ecosystems on the Colorado Plateau, Utah (Darrouzet-Nardi et al., 2018; Reed et al., 2012; Ferrenberg et al., 2015) and in semiarid Spain (Maestre et al., 2013; Maestre et al., 2015; Escolar et al., 2012; Lafuente et al., 2018), as well as in southern Africa (Maphangwa et al., 2012). However, the response of biocrusts to increased drought in the unique dryland ecosystem of the Tengger Desert in Asia has not been previously studied. In addition, the abovementioned studies were carried out using manipulative experiments with short-term observations (<5 years) of the increases in temperatures (>2°C) and watering amounts (>30% of rainfall). Furthermore, little is known regarding the responses of biocrusts to global warming in extremely arid ecosystems. In addition to warming and watering treatments, a few studies have addressed the response of lichen-dominated and moss-dominated biocrusts to warming coupled with a reduction in precipitation during long-term observations in arid temperate deserts (Lafuente et al., 2018). Undoubtedly, long-term studies are crucial to understand the mechanisms of biocrust responses to ongoing climate change.

In this study, we conducted an experiment that lasted more than ten years and involved warming coupled with reduced precipitation to evaluate how both lichen-dominated and moss-dominated biocrusts responded to 0.5°C and 1.5°C increases in temperature combined with 5% and 8% reductions in annual precipitation, respectively, using two groups of open-top chambers. These experimental conditions were selected for their consistency with long-term monitoring trends and updated forecasts of temperature in the Tengger Desert (Li et al., 2016). This study aimed to answer the following questions. 1) Which biocrust components, such as lichens or mosses, will be more sensitive to warming and reduced precipitation, which have been predicted by long-term meteorological monitoring in the Tengger Desert, northwestern China (Li et al., 2016)? 2) What mechanisms influence the sensitivity of biocrusts to increased temperature and drought? Related to this question, previous studies have mainly focused on the carbon (C) balance of biocrust mosses, and C loss was associated with a decrease in coverage and an increase in mortality (Reed et al., 2012). Specifically, ongoing warming and frequent watering resulted in higher respiratory loss of C than C uptake by photosynthesis, thus creating a net negative C balance (Maestre et al., 2013; Darrouzet-Nardi et al., 2015). Furthermore, biocrusts cannot persist with a consistently negative C balance (Coe et al., 2012).

2. Materials and Methods

2.1. Site description

The study site is located at the southeastern edge of the Tengger Desert (37°32′–37°26′ N, 105°02′–104°30′ E) in the Shapotou-Hongwei region. The elevation of the site ranges between 1300 and 1350 m above mean sea level (a.m.s.l.). The site has an average annual temperature of 8.6°C and an average annual precipitation of 186 mm, approximately 80% of which falls from May to September. Local climatic measurements are taken at the Shapotou Desert Research and Experiment Station (SDRES) of the Chinese Academy of Sciences, and the records show that the average annual temperature is 0.5°C higher and the average annual precipitation is 4 mm lower in this decade than in the last decade (Li et al., 2016).

The Shapotou-Hongwei region is characterized by orthic sierozem and aeolian sandy soils (Li et al., 2016). Semi-shrubs, shrubs, forbs, and grasses dominate the region's vegetation, including species such as *Artemisia ordosica* Krasch., *Reaumuria soongorica* Maxim, *Salsola passerina* Bunge, *Oxytropis aciphylla* Ledeb., *Caragana korshinskii* Kom., *Ceratoides latens* Reveal et Holmgren, *Stipa breviflora* Griseb., *Carex stenophylloides* Krecz, and *Cleistogenes songorica* Ohwj. However, less than 40% of the land is covered by vegetation. Well-developed biocrusts have colonized open spaces, and these biocrusts are dominated by a patchwork of lichen, moss and cyanobacteria. The cover of biocrusts often exceeds 80%. The lichen species include *Collema coccophorum* Tuck., *Fulgensia desertorum* Poelt, *Squamarina lentigera* Poelt and *Endocarpon pusillum* Hedw (Liu and Wei, 2013), and the moss species *Bryum argenteum* Hedw., *Didymodon constrictus* (Mitt.) Saito., *Syntrichia caninervis* Mitt., and *Tortula bidentata* Bai Xue Liang are dominant in the region (Li et al., 2017).

2.2. Experimental design

The various warming and precipitation treatments of the experiment were based on SDRES observations and recent meteorological research (Li et al., 2016) and implemented open-top chambers (OTCs). OTCs were established to mimic the climatic changes between the past and current decade, specifically, the increase in average temperature and the decrease in average precipitation. The OTC size was adjusted to achieve the desired temperature. To reduce rainfall, the OTC height was increased; a higher OTC receives less rainfall due to the strong wind that frequently accompanies the beginning of a rainfall event (Li et al., 2016). Rainfall shelters were not necessary. This preliminary work was carried out over the course of two years, from 2004–2005. From the 10 existing OTCs, one group of three large OTCs and one group of three small OTCs were selected for the manipulative experiments (Fig. 1). All OTCs were built of glass, and the larger OTCs had sloping sides measuring 100 × 100 × 200 cm and eight aluminium alloy columns. In contrast, the smaller OTCs had sloping sides measuring 100 × 100 × 150 cm and had only four columns. Climatic conditions were characterized by lower rainfall and higher temperature in the small OTCs than in the large OTCs. A control plot was also established and spaced at least 2 m from the OTCs to minimize bias. During the experiment, the conditions in each OTC and the control plot (air temperature, precipitation and soil moisture at 0–5 cm depth) were monitored using an auto-meteorological station (U30 HOBO data logger, Onset Computer Corporation, Bourne, MA, USA). One auto-meteorological station was placed in each of the large OTC, small OTC and control sites. All OTC-induced changes in temperature and rainfall are described in supplemental Table 1. Over the course of the study, the mean annual temperature increased by 0.5°C and 1.5°C and the annual precipitation declined by 5% and 8% in the large and small OTCs, respectively, compared with the conditions of the control treatment.

Based on the surface cover of the dominant biocrust species (>80% of the total biocrust cover), each biocrust sample was classified into one of 2 groups: lichen-dominated or moss-dominated biocrust. In the sites with both lichen-dominated and moss-dominated biocrust samples, the samples were collected using a plexiglass box (length-width-height of 10 × 10 × 5 cm), the bottom of which had 10 equally distributed 0.5 cm-diameter holes, and one side of the box had a 3 cm-diameter hole for inserting a soil moisture probe (S-SMC-M005 of U30 HOBO). All plants

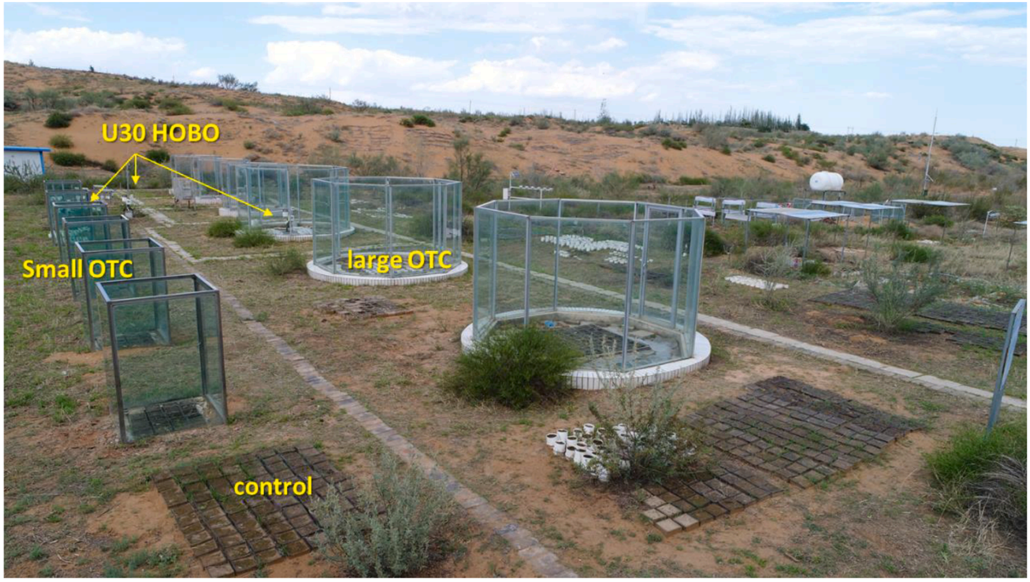

Fig. 1. Open-Top Chambers (OTCs) of different size were employed to simulate warming (photo in 2007). Large OTCs increase temperature by 0.5°C and reduce annual precipitaion by 5%, small OTCs increase temperature by 1.5% and reduce annual precipitation by 8% in comparison with control.

were excluded from the biological soil crust (BSC) samples. For each biocrust type, 90 random replications (boxes) were collected. In spring 2006, ten samples of lichen-dominated and moss-dominated biocrusts were placed into each OTC, and 30 samples of each biocrust type were placed in the control plot to conduct the experiments. Before the experiment, it was expected that there would be nonsignificant differences in each biocrust type between the control and treatment samples (i.e., those placed into OTCs). Soil moisture probes (U30 HOBO auto-meteorological station) were installed in three sample boxes of each biocrust type in one large OTC, one small OTC and the control plot. All sample boxes were inserted into soil and kept at the level of the soil surface.

Instead of determining the independent effects of increasing temperature or decreasing rain, the design of this experiment using OTCs objectively reflects the response of lichen-dominated and moss-dominated biocrusts to the superimposed effects of these climatic factors. In addition, we considered that changes in the biocrust components under these treatments would be a slow and indistinct process in short-term observations. The following traits were measured in the biocrust samples during the experiment: changes in species richness (number of species per sample), cover and biomass before the experiment began and after 6, 10 and 12 years of the experiment and carbon fixation after 1, 6, and 12 years of the experiment. Furthermore, the wet daytime duration for biocrusts after each rainfall event was calculated as the duration of the daytime period when the moisture content of the biocrust soil surface exceeded 1% of the volumetric water content (Belnap et al., 2005; Li et al., 2012). After a rainfall event, the soil moisture in the sample boxes was monitored with a U30 HOBO until the moisture was reduced to 1%. For one-off rainfall, the total diurnal wet time of biocrusts was estimated by determining the duration of the supersaturated time during night when photosynthesis was inhibited (Li et al., 2012). We measured the wet daytime duration for the biocrust samples after each rainfall event in 2007, 2012 and 2018. The temperatures of the biocrust surfaces in the large and small OTCs and in the control plot were measured daily using a manually operated portable infrared temperature sensor (IRT, Minolta/Land Cyclops Compac 3, Land, England).

Species richness was estimated as the number of lichens and mosses present in each sample. The cover was estimated as the proportion of sampling points in a 1 × 1 cm grid (81 points per 8 × 8 cm quadrat) on which mosses and lichens grew (Magurran, 1988). Chlorophyll content was measured as a proxy for biocrust biomass (Li et al., 2012) or potential photosynthetic capacity. Liquid nitrogen was used to pulverize the biocrust samples (0.5 g fresh weight), and then the pigments were extracted with 80% acetone until the samples were completely bleached. Total chlorophyll content was measured according to the method previously described by Lichtenthaler and Wellburn (1983). To identify lichens and mosses easily, the above measurements were conducted in August, which is the moistest month in the study site, of 2012, 2016 and 2018 (Li et al., 2016).

For the field measurements of biocrust photosynthesis, two 10-cm diameter soil collars were inserted into the soil to a depth of 2 cm in the aforementioned sample boxes of each OTC, and three collars were inserted for each biocrust in the control location. Gas exchange measurements were taken on the first clear day after a night-time rainfall event. When a rainfall event occurred during the day, the measurement was taken the following morning at sunrise because photosynthesis is virtually inhibited at the supersaturated water content of crustal thalli (Lange, 2001). For the convenience of simultaneous measurements, all soil collars were marked and collected in places that were adjacent to the control and were returned in situ after a diurnal measurement was taken.

Net photosynthesis (P_n) in the biocrust samples was measured every 2 h from sunrise to sunset. The gas exchange measurements were simultaneously conducted using three Licor 6400 portable photosynthesis systems (LI-COR Inc., Lincoln, NE, USA) with custom chambers that fit over the soil sample collars. We measured P_n after each rainfall event that was > 3 mm in 2007 (after 1 year), 2012 (after 6 years) and 2018 (after 12 years of the experiment) in the OTCs and the control plot. First, we measured gross photosynthesis in the light (P_g), and then an opaque foil cover was placed over the box to determine respiration (R_e). P_n was calculated by the formula $P_n = P_g - R_e$. The measurements for P_g and R_e were recorded until the values became sequentially stable (Brostoff et al., 2002). The photosynthetic rates were then calculated on a surface area basis as μmol CO_2 m^{-2} s^{-1}. Based on these data, we calculated the daily P_n by integrating the area under the diurnal curves (Housman et al., 2006). The daily P_n was transformed to a unit for net carbon fixation of biocrusts (A, g C m^{-2}), where $A = P_n \times 12$ (g•mol^{-1}) $\times 10^{-6} \times 3600$ (s) (Li et al., 2012). Finally, the average daily carbon fixation in each year was combined with the data describing the total wet daytime duration of each biocrust type (biocrusts that were available for carbon fixation) during the different treatments. We then estimated the annual amount of carbon fixation of the two biocrusts under the different warming treatments coupled with reduced rainfall in 2007, 2012 and 2018.

2.3. Statistical analysis

Analysis of variance (ANOVA) followed by Tukey's post hoc tests was employed to compare the measured parameters (P_n values, wet daytime duration, species richness, cover, biomass, and carbon fixation) between the two biocrust types and between the two types of treatments and the control for the years when the measurements were performed. Data were checked for normality and homogeneity of variance before the analysis. Natural changes in the traits of biocrust types and their P_n values during the 12-year experiment were tested by comparing the results with three measured control samples in 2007, 2012 and 2018. The data analyses were conducted using SPSS software version 10 (SPSS, Chicago, IL, USA).

3. Results

3.1. Changes in the species richness, cover and biomass of the biocrusts

There were no changes in the species richness of either lichens or mosses in response to relatively weak warming (0.5°C) coupled with a small reduction in precipitation during the 12-year period. However, we found that after the 12-year treatments with relatively strong warming (1.5°C) coupled with reduced precipitation, the number of moss species notably decreased($p<0.05$), while the number of lichen species was unaltered ($p>0.05$). The two lichen species *Collema coccophorum* and *Endocarpon pusillum* were found in all measured samples during the 12-year period, and *Fulgensia desertorum* and *Squanarina lentigera* occurred in most of the warmed plots and in the control plot. The two moss species *Bryum argenteum* and *Didymodon constrictus* were found in all samples, and *Syntrichia caninervis* and *Tortula bidentata* occurred only in some of the 0.5°C-warmed plots and were absent in the 1.5°C warmed plots and in the control.

Warming and reduced precipitation decreased moss cover, with a marked decrease from 88.5% (control) to 80.0% after 6 years and further decreases to 72.1% after 10 years and 71.6% after 12 years under the 0.5°C warming treatment. The moss cover decreased from 88.5% to 73.5% after 6 years, 53.9% after 10 years and 52.6% after 12 years under the 1.5°C warming treatment. However, under each of the two warming treatments, there was no difference between the moss cover after 10 years and that after 12 years ($p>0.05$). During the 12-year observation period, significant differences were found in the moss cover between the control plot and the 0.5°C-warmed plots and between the control plot and the 1.5°C-warmed plots ($p<0.05$). In contrast, there were no differences in the lichen cover between the control plot and the 0.5°C-warmed plots or between the control plot and the 1.5°C-warmed plots ($p>0.05$), although the lichen cover decreased under both warming treatments (Table 1). In addition, a gradual increase in cover was observed in the control samples of both biocrust types during the experiment.

Warming coupled with reduced precipitation triggered a decrease in moss biomass, and there were significant differences between before the treatments and after 6 years of warming treatments and between 6 and 10 years of warming treatments in the experiments ($p<0.05$); a difference between the last two measurement years (2016 and 2018) was not found. Moss biomass has different responses to different warming intensities, with the moss biomass decreasing more in the 1.5°C-warmed plots than in the 0.5°C-warmed plots after 10 years. At the same time, warming did not alter the lichen biomass.

3.2. Changes in carbon fixation

Based on 15, 10 and 16 measurements in 2007, 2012 and 2018, respectively, the daily mean P_n values in lichen-dominated and moss-dominated biocrusts under the different treatments (control, 0.5°C and 1.5°C warming coupled with reduced rainfall) were determined for the three years with measurements (Fig. 2). After one or 6 years of warming, there was no difference in P_n between the control plot and the 0.5°C-warmed plots or between the control plot and the 1.5°C-warmed plots for either the lichen-dominated or moss-dominated biocrusts ($p>0.05$). Neither the 0.5°C- nor 1.5°C-warmed plots coupled with reduced rainfall had a significant effect on the lichen-dominated biocrusts, even after 12 years, compared with the ambient conditions (control). However, the P_n of the moss-dominated biocrusts notably decreased under the treatment with a 1.5°C increase in temperature ($p<0.05$), while the P_n value in the 0.5°C-warmed plot did not change ($p>0.05$) after the 12-year warming experiment. In general, the P_n values of the moss-dominated biocrusts were higher than those of the lichen-dominated biocrusts in both wet years (2007, 2018) and a drought year (2012), except for in the 1.5°C-warmed plots after twelve years.

The same trends were seen in the daily amount of carbon fixation (A, g C m^{-2} day^{-1}) for both biocrust types during the observation period (Fig. 3). For the moss crusts, 1.5°C warming significantly decreased the daily carbon fixation after 12 years ($p<0.05$), while there was no difference in carbon fixation in 2007 or 2012 ($p>0.05$), even with differences in precipitation. Similarly, there was no change in the daily carbon fixation of lichen crusts in 2007 or 2012 ($p>0.05$), but there was a large increase in carbon fixation after 12 years ($p<0.05$). With the exception of the 1.5°C-warmed plots after 12 years, the moss-dominated biocrusts had a higher daily carbon fixation than the lichen crusts during the observation period. In general, higher warming (1.5°C) has a marked influence on both the daily carbon fixation and annual carbon fixation of moss-dominated biocrusts, which will likely be found after long-term observation (exceeding 10 years).

Table 1
Changes in species richness, cover, and biomass of biocrusts (mean ± s.e., n=30) during warming and rainfall reduction treatments

Measured parameters	Biocrusts	Before experiment	6 years of experiment			10 years of experiment			12 years of experiment		
			Control	Increase of 0.5°C	Increase of 1.5°C	Control	Increase of 0.5°C	Increase of 1.5°C	Control	Increase of 0.5°C	Increase of 1.5°C
Sp Richness (number of species presents in samples)	Lichen-biocrust	2.7±0. 7 ^{a}	2.9 ±0.3 ^{a}	2.8±0.4 ^{a}	2.7±0.5 ^{a}	2.8±0.4^{a}	2.9±0.3^{a}	2.9±0.3^{a}	3.1±0.4^{a}	3.0±0.5^{a}	2.8±0.6^{a}
	Moss-biocrust	3.4±0.5 ^{a}	3.30±0.5 ^{a}	3.2±0.6 ^{a}	3.1±0.6 ^{a}	3.4±0.5 ^{a}	3.0±0.6 ^{a}	3.0±0.4 ^{a}	3.3±0.5^{a}	3.0±0.4^{a}	2.5±0.3^{b}
Cover (%)	Lichen-biocrust	86.2±2.3 ^{a}	88.9±1.4 ^{a}	87.9±2.5 ^{a}	88.3±2.3 ^{a}	89.6±1.6 ^{a}	87.1±2.0 ^{a}	88.4±1.7 ^{a}	90.6±1.2^{a}	86.8±1.6^{a}	86.7±2.3^{a}
	Moss-biocrust	88.5±3.4 ^{a}	89.2±1.9 ^{a}	80.0±4.4 ^{b}	73.5±2.8 ^{c}	90.0±1.7 ^{a}	72.1±4.8 ^{c}	53.9±2.3 ^{d}	91.3±1.7^{a}	71.6±2.4^{c}	52.6±2.6^{d}
Biomass (chlorophyll content in mg/cm^2)	Lichen-crust	3.1±0.6 ^{a}	3.19±0.9 ^{a}	3.1±0.4 ^{a}	2.9±1.0 ^{a}	3.4±0.3 ^{a}	3.1±0.4 ^{a}	3.0±0.4 ^{a}	3.6±0.3^{a}	3.2±0.7^{a}	3.3±0.5^{a}
	Moss-crust	4.9±1.5 ^{a}	5.4±0.9 ^{a}	3.6±1.2 ^{b}	3.0±1.1 ^{b}	5.4±1.3 ^{a}	2.8±0.9 ^{c}	1.9±0.9 ^{d}	5.5±0.8^{a}	2.7±0.6^{c}	1.6±0.7^{d}

Note: values of a given measured parameter, different superscripts indicate a significant difference among treatments, different experimental periods at $p<0.05$

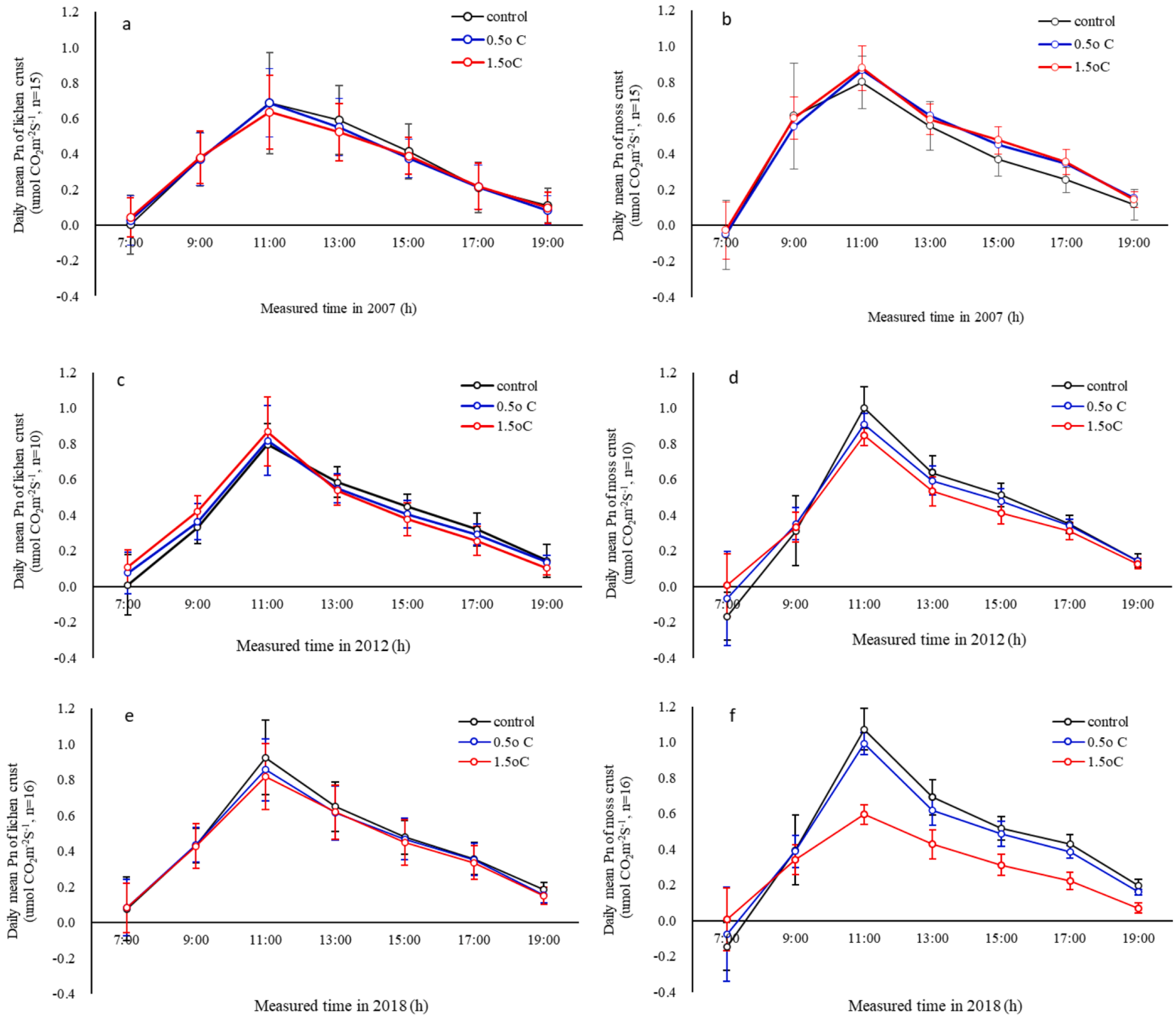

Fig. 2. Daily P_n value (mean±s.e.) in lichen-dominated (a, c, and e) and moss-dominated (b,d, and f) biocrusts under the different treatments and control, one (a and b, n=15), six (c and d, n=10) and twelve (e and f, n=16) years after the experiment was established (measurement was conducted after each rainfall event greater than 3mm)

3.3. Changes in wet daytime duration and annual biocrust carbon fixation

Biocrusts had a longer wet daytime duration in the wet years (2007 and 2018) than in the relatively dry year (2012), while the 1.5°C-warmed plot after twelve years markedly reduced the wet daytime duration of the moss-dominated biocrusts (Fig. 4). Neither the 0.5°C-warmed plots nor the 1.5°C-warmed plots changed the wet daytime duration of either the lichen-dominated or moss-dominated biocrusts during the six-year observation period in comparison with ambient conditions. In particular, the treatments with lower warming and rainfall reduction weakly affected the wet daytime duration of both biocrust types. In general, the annual mean wet daytime duration of the moss-dominated biocrusts was significantly longer than that of the lichen crusts ($p<0.05$), except for in the 1.5°C-warmed plots after twelve years. The 1.5°C-warmed plots significantly reduced the annual wet daytime duration of the moss-dominated biocrusts after 12 years, even in wet years (annual precipitation of 257 mm), and the annual wet daytime duration of the moss-dominated biocrusts was much less than that of the lichen-dominated biocrusts (Fig. 4).

The annual carbon fixation of the biocrusts is the product of the daily value of carbon fixation (A) and the wet daytime duration. With the exception of the 1.5°C-warmed plots after 12 years, increasing temperature coupled with reduced rainfall slightly decreased the daily mean carbon fixation of both biocrusts after 6 and 12 years of the experiments ($p>0.05$), while a significant reduction in the annual carbon fixation of the moss-dominated biocrusts was found in the 1.5°C-warmed plots after 12 years (Fig. 3). However, the 0.5°C-warmed plots only slightly affected the annual carbon fixation of the two biocrust types.

4. Discussion

The results of our study indicated that the species richness of both lichens and mosses in biocrust communities was insensitive to combined warming and reduced precipitation in the relatively short term (less than 10 years). This result was likely due to the treatments in our study using smaller increases in temperature coupled with smaller reductions in rainfall compared with the treatments in previous studies (Darrouzet-Nardi et al., 2018; Maestre et al., 2015; Reed et al., 2012). However, the species richness of mosses decreased after 12 years of warming, indicating that a small but long-term increase in temperature associated with a small reduction in precipitation affected the species composition of mosses but not lichens. Likewise, the cover and biomass of mosses were sensitive to the treatments, even with a smaller temperature increase (0.5°C) in the short term, while those of lichens had nonsignificant responses to warming coupled with reductions in precipitation (Table 1). These findings suggest that the responses to experimental treatments of moss are divergent in different traits (species richness,

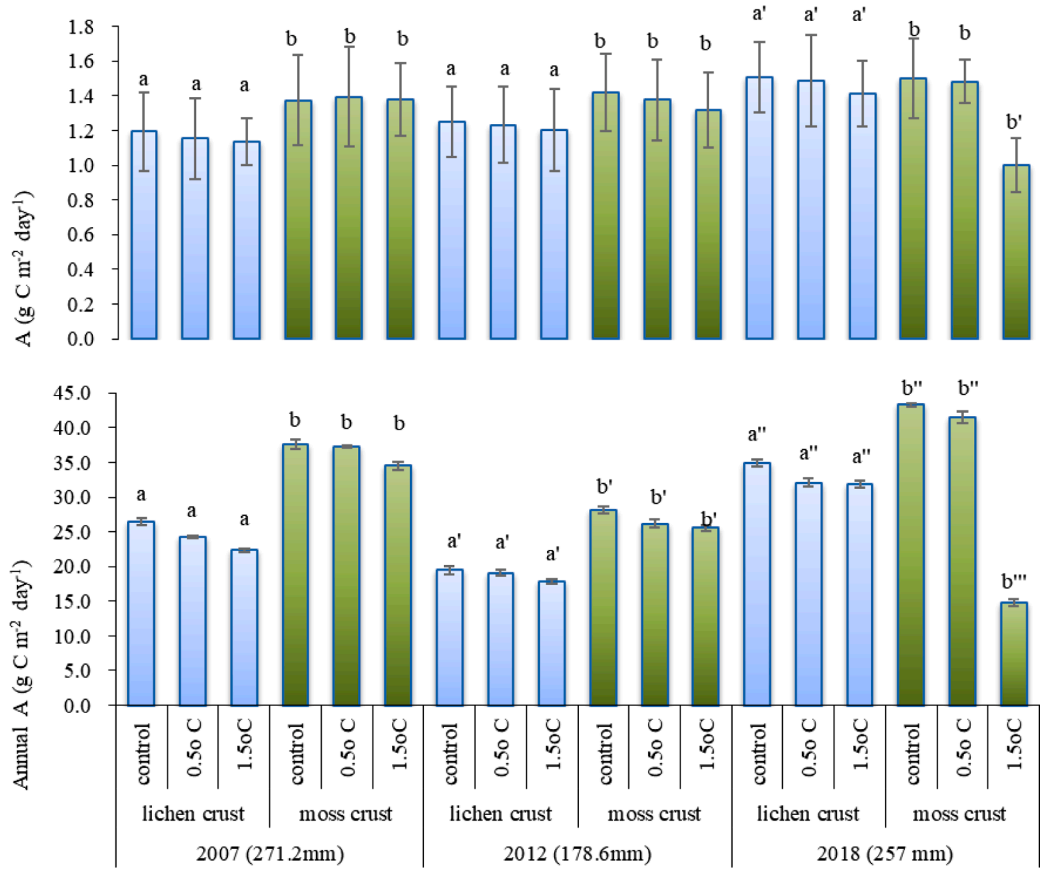

Fig. 3. Daily (A, mean±s.e.) and annual carbon fixation (Annual A, mean±s.e.) of lichen-dominated and moss-dominated biocrusts under the different treatments and control, one, six and twelve years (2007, 2012 and 2018) after the experiment was established. Values with different letters (including a, a' and a'', as well as b, b', b'' and b''') are significantly different, $p<0.05$; Annual precipitation in the years of measurements is shown in brackets.

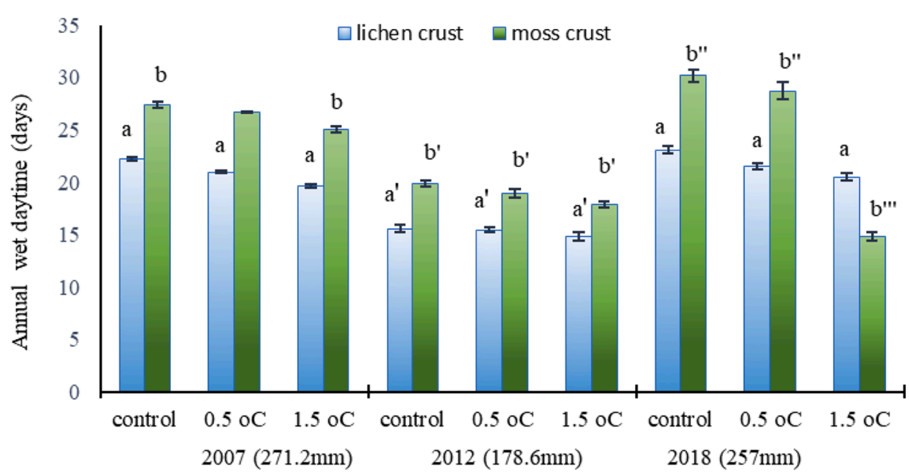

Fig. 4. The annual wet daytime of lichen-dominated and moss-dominated biocrusts under the different treatments and control one, six and twelve years after the experiment was established (mean±s.e., n=3; values with different letters are significantly different, $p<0.05$). Annual precipitation in the years of measurements is shown in brackets.

cover and biomass); therefore, the selection and measurement of multiple traits is important for the objective evaluation of biocrust responses to different treatments.

Compared with mosses, lichens are more likely to be tolerant to changes in temperature and rainfall because they are well adapted to drought and other extreme stresses (Barker et al., 2005; Hui et al., 2014). Lichens have lower moisture requirements for survival (West, 1990). Our previous field observations also indirectly supported this viewpoint, as lichens are frequently distributed in more exposed, drier microhabitats, such as bare areas between shrubby canopies, while mosses are mainly distributed in moister microhabitats under shrubby canopies and on northern exposures in temperate deserts (Li et al., 2017).

In terms of the photosynthetic characteristics and carbon fixation of the two biocrusts, the photosynthetic activities of lichens (Maphangwa et al., 2012; Ladrón de Guevara et al., 2014) and mosses (Grote et al., 2010) are expected to be sensitive to warming in the short term. In addition, the long-term climate change effects on carbon fixation by biocrust photosynthesis differ from those observed in the short term (Darrouzet-Nardi et al., 2018).

The mean carbon fixation per rainfall event differed from the daily P_n for both biocrust types; the moss-dominated biocrusts had higher carbon fixation than the lichen-dominated biocrusts ($p<0.05$, Fig. 3) because the moss-dominated biocrusts are able to maintain a longer wet daytime period after a rainfall event due to thicker topsoil layer coverage and lower evaporation (Kidron and Tal, 2012). The smaller warming treatment had insignificant effects on the mean carbon fixation in both biocrusts. At the same time, moss carbon fixation per rainfall event dramatically decreased with greater warming after 12 years, which might contribute to decreasing P_n and reducing the wet daytime duration per rainfall event. Warming increases the surface temperature of moss-dominated biocrusts more than that of lichen-dominated biocrusts. The 1.5°C warming increased the annual mean temperature on the moss surface more than that on the lichen surface compared with that in the control plot (Fig. 5). Greater warming facilitated moisture loss from a

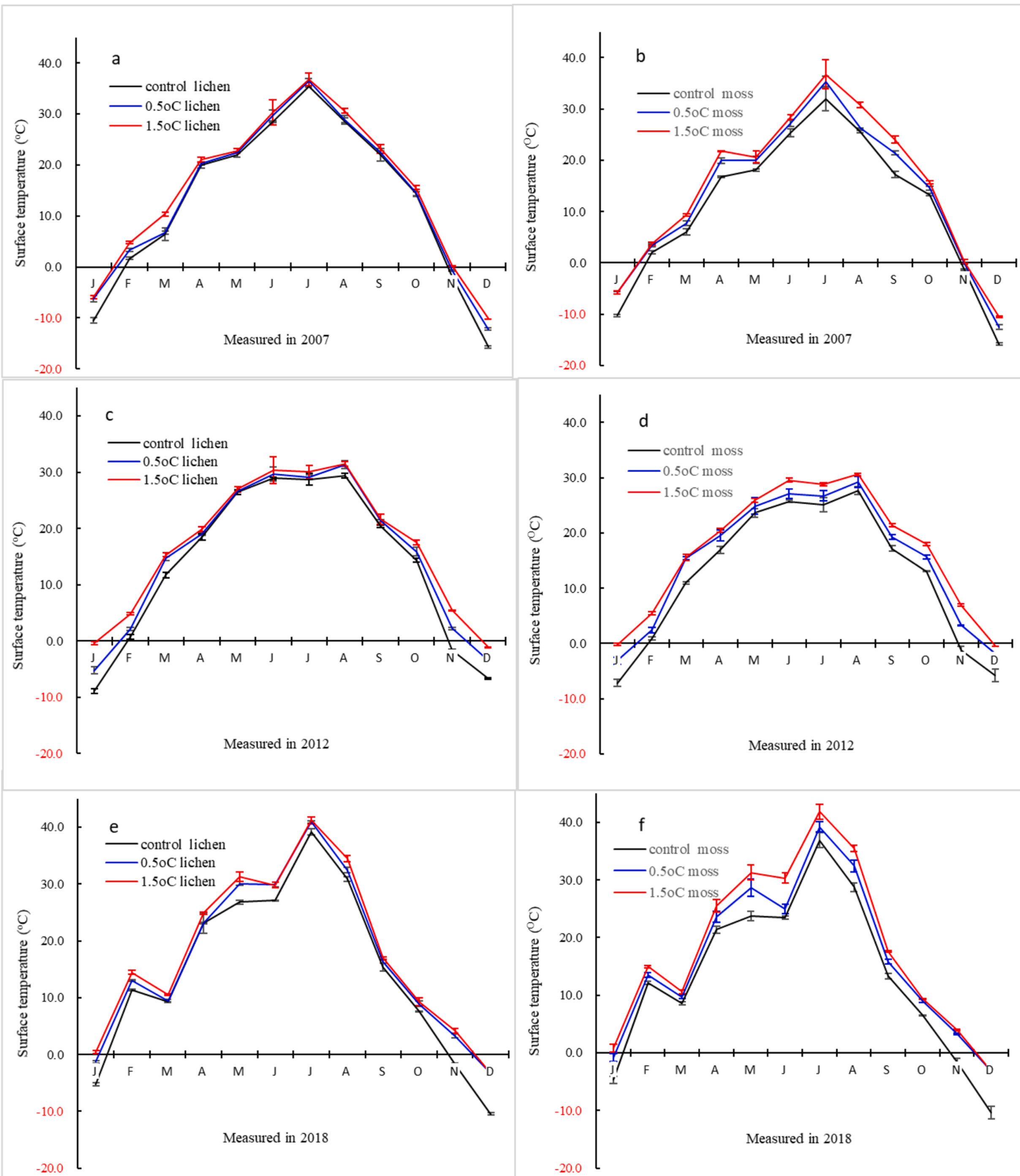

Fig. 5. The effects of warming on the surface temperature of lichen-dominated (a, c, and e) and moss-dominated (b, d, and f) biocrusts (monthly mean±s.e.) on the figure it is indicated 2007, 2012, and 2018 (in lichen-dominated biocrusts, the 0.5°C-warming increased annual mean temperature by 4.9%, 6.2% and 7.9%; the 1.5°C-warming increased annual mean temperature by 8.7%, 10.6% and 10.9% in 2007, 2012 and 2018, respectively; in moss-dominated biocrusts, the 0.5°C-warming increased annual mean temperature by 10%, 9.6% and 10.8%; the 1.5°C-warming increased annual mean temperature by15.3%, 15.8% and 16.1% in 2007, 2012 and 2018, respectively).

biocrust-covered soil surface (Sheik et al., 2011); in this case, the advantages of a greater water-holding capacity and a longer wet daytime duration were likely weaker in the mosses than in the lichens (Li et al., 2010).

Annual carbon fixation of both biocrust types was promoted in wet years, even under smaller warming (2007 and 2018, Fig. 3), because biocrust has a longer wet daytime period for the uptake of available carbon via photosynthesis (Fig. 4), and biocrust photosynthesis is determined by the water content rather than either photosynthetically active radiation or temperature (Li et al., 2012; Tucker et al., 2019). Similarly, the negative effect of the long-term warming of 1.5°C was obvious on the moss-dominated biocrusts and insignificant on the lichen-dominated biocrusts. Based on a 12-year observation period, evidence of reduced photosynthetic capacity of the mosses in response to the coupled 1.5°C warming and reduction in precipitation was found in our study (Fig. 2), while the CO_2 release induced by mosses was unlikely to decrease (Maestre et al. 2013; Guan et al., 2019). This finding supported the explanation that C deficits when the air temperature is high and moisture is limited will likely reduce the productivity and increase the mortality of mosses (Belnap et al., 2008). Compared with the mosses, the lichens seemed to be less sensitive to the notably reduced C budgets under the warming and reduced precipitation treatments. Here, our results contrast with previous results (Ladrón de Guevara et al., 2018).

The contrasting results between our study and previous studies for both biocrust-forming lichens and mosses are likely attributed to differences in the methods, experimental designs, experimental periods, and climatic regimes of the study sites (Lange, 2001; Belnap et al., 2006; Escolar et al., 2012; Reed et al., 2012; Maestre et al., 2013; Ferrenberg et al., 2015; Maestre et al., 2015; Darrouzet-Nardi et al., 2018; Ladrón de Guevara et al., 2018; Lafuente et al., 2018). In particular, previous studies mainly simulated higher warming (2–6°C) coupled with additional rainfall (Maestre et al., 2015; Tucker et al., 2019) or reduced rainfall using a rain shade during short (≤5 years) and medium (≤8 years) periods (Ladrón de Guevara et al., 2014; Ladrón de Guevara et al., 2018; Maestre et al., 2013). However, our study shows how biocrust components are affected by long-term small increases in warming associated with small reductions in rainfall. Nevertheless, the negative effect of warming coupled with reduced precipitation on the biocrust components is indisputable.

In addition, lichens and mosses are dominant components of biocrust communities in the later successional stage in arid and semiarid regions (Belnap and Lange, 2003; Housman et al., 2019). The relatively high species richness, cover and biomass of these biocrusts indicate the health and stability of desert ecosystems (Belnap, 2002; Coe et al., 2012; Delgado-Baquerizo et al., 2013; Chamizo et al., 2017; Li et al., 2017; Lafuente et al., 2018; Liu et al., 2018). The loss of these important species will likely alter the complex structure and multifunctionality of desert ecosystems in arid and semiarid regions (Bowker et al., 2011; Reed et al., 2012; Escolar, Maestre & Rey, 2015; Gross et al., 2017; Rodriguez-Caballero et al., 2018). Therefore, it will be an urgent task for land managers and ecologists to develop reasonable countermeasures for the conservation of desert ecosystems.

5. Conclusions

Long-term warming and reductions in precipitation influenced the moss-dominated biocrust via a decrease in moss cover and biomass, even causing a decrease in moss species richness. This result occurred because the ability of mosses to uptake carbon dramatically decreased due to reductions in their wet daytime period and P_n. At the same time, the lichen-dominated biocrusts did not respond to warming and drought. These differences between mosses and lichens suggest that the responses of the dominant species in desert ecosystems to warming are variable. Reductions in moss cover and biomass in biocrust communities negatively affect the compositions, structures and functions of desert ecosystems, while lichen, as a less vulnerable biocrust component, is likely to sustainably maintain some of the functions of biocrusts in desert ecosystems, such as stabilizing soils, as well as fixing carbon and nitrogen. These findings may help to define appropriate conservation strategies for mitigating the effects of climate change on desert ecosystems.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

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