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Simulated climate change affects how biocrusts modulate water gains and desiccation dynamics after rainfall events

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Abstract

Soil surface communities dominated by mosses, lichens and cyanobacteria (biocrusts) are common between vegetation patches in drylands worldwide, and are known to affect soil wetting and drying after rainfall events. While ongoing climate change is already warming and changing rainfall patterns of drylands in many regions, little is known on how these changes may affect the hydrological behaviour of biocrust-covered soils. We used eight years of continuous soil moisture and rainfall data from a climate change experiment in central Spain to explore how biocrusts modify soil water gains and losses after rainfall events under simulated changes in temperature (2.5°C warming) and rainfall (33% reduction). Both rainfall amount and biocrust cover increased soil water gains after rainfall events, whereas experimental warming, rainfall intensity and initial soil moisture decreased them. Initial moisture, maximum temperature and biocrust cover, by means of enhancing potential evapotranspiration or by soil darkening, increased the drying rates and enhanced the exponential behaviour of the drying events. Meanwhile, warming reduced their exponential behaviour. The effects of climate change treatments on soil water gains and losses changed through time, with important differences between the first two years of the experiment and five years after its setup. These effects were mainly driven by the important reductions in biocrust cover and diversity observed under warming. Our results highlight the importance of long-term studies to understand soil moisture responses to ongoing climate change in drylands.

Keywords

biological soil crusts; drylands; soil moisture; wetting; drying; rainfall exclusion; warming

Introduction

Arid, semi-arid and dry-subhumid ecosystems (drylands) have rainfall regimes characterized by long periods without rainfall, which also takes place as discrete pulses that largely control the activity of organisms and the rate of ecosystem processes such as nutrient cycling, soil respiration or plant productivity, to name a few (Austin et al., 2004; Huxman et al., 2004; Reynolds et al., 2004). Ongoing climate change is increasing the variability of rainfall in

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many drylands worldwide (D'Odorico & Bhattachan, 2012; Singh & Kumar, 2015), a trend that will likely continue and be enhanced in the future (Easterling, 2000; Hughes & Diaz, 2008; Weltzin et al., 2003). Current forecasts indicate that the rainfall regime of many drylands worldwide will be characterized by a lower number of more concentrated rainfall events (Dore, 2005). Therefore, understanding the factors affecting water gains and losses after rainfall events is crucial not only to understand how dryland ecosystems function, but also how they are responding to ongoing climate change (Collins et al., 2014).

Biocrusts are communities formed by mosses, lichens and microorganisms (cyanobacteria, fungi, other bacteria and archaea) that live on the soil surface in drylands worldwide (Weber et al., 2016). These communities are a prevalent biotic component in these ecosystems, where they control the exchange of elements and energy between the atmosphere and the soil (Pointing & Belnap, 2012). Biocrusts largely affect the hydrological cycle of drylands by controlling soil properties such as soil water retention (Cantón et al., 2004), albedo (Rutherford et al., 2017), surface roughness (Eldridge & Rosentreter, 1999) and temperature (Couradeau et al., 2016), which affect infiltration and runoff generation and evaporation losses (Belnap, 2006; Berdugo et al., 2014; Chamizo et al., 2012). The hydrological impacts of biocrusts are, however, largely dependent on: i) their composition and degree of development (Chamizo et al., 2012, 2013) and ii) the amount, duration and intensity of rainfall events (Berdugo et al., 2014; Chamizo et al., 2016). However, most of our knowledge on the hydrological impacts of biocrusts come from short-term studies (i.e., typical length below two years; Cantón et al., 2004; Chamizo et al., 2016; Zaady et al., 2014; but see Berdugo et al., 2014). Conducting studies over multiple years is of great importance to capture inter-annual rainfall variability, which is typically very high in drylands (D'Odorico & Bhattachan, 2012), and hence to better understand how biocrusts affect soil water gains (i.e difference between the initial and the maximum moisture achieved during the rainfall event) and losses (i.e the slope of the drying curve) after rainfall events of different amount, duration and intensity (Chamizo et al., 2016).

Climate change is impacting the biota of terrestrial ecosystems in multiple ways (Peñuelas et al., 2013), and biocrust constituents are not an exception. Increases in temperature and changes in rainfall regimes such as those forecasted for the second half of this century have been found to negatively affect the performance and cover of lichen- and moss-dominated biocrusts in South Africa (Maphangwa et al., 2012), Spain (Escolar et al., 2012; Maestre et al., 2013, 2015) and the USA (Ferrenberg et al., 2015; Johnson et al., 2012; Zelikova et al., 2012). These changes are leading to shifts in the composition of biocrust communities, with reported increases in cyanobacteria at the expense of mosses and lichens (Ferrenberg et al., 2015), which underlie the dramatic changes in nitrogen (Delgado-Baquerizo et al., 2014; Reed et al., 2012) and carbon (Escolar et al., 2015; Grote et al., 2010; Ladrón de Guevara et al., 2014; Maestre et al., 2013) cycling observed under simulated climate change in biocrust-dominated ecosystems. Despite the growing interest and literature on the impacts of climate change on both biocrusts and the ecosystem processes associated to them (Reed et al., 2016), no study so far has evaluated how climate change-induced changes in biocrust communities, affect their role as modulators of water gains and losses after rainfall events. Given the important roles played by biocrusts as determinants of rainfall infiltration (Berdugo et al.,

2014; Chamizo et al., 2016), such studies are critical to better understand the hydrological impacts of ongoing climate change on dryland ecosystems worldwide.

Here we evaluate how biocrusts modulate the effect of simulated climate change on soil water gains and losses after rainfall events in a semiarid ecosystem from central Spain. For doing so we use eight years of data from an ongoing manipulative experiment where soil moisture is being continuously measured in areas with different biocrust cover and under warming and rainfall exclusion treatments (Maestre et al., 2013). This unique dataset allowed us to explore how: i) forecasted changes in rainfall and temperature may affect water gains and losses after rainfall events across multiple years with contrasting climatic conditions, and ii) simulated climate change alter the role of biocrusts as modulators of these hydrological features. We hypothesize that climate change-induced effects on biocrust communities, being the most noticeable the reduction in the cover and photosynthetic activity of dominant lichen species -already observed during the first years of the experiment (Escobar et al., 2012; Maestre et al., 2013, Ladrón de Guevara et al., 2014), will influence their capacity to affect water gains and losses after rainfall events (Berdugo et al., 2014).

Material and Methods

Site description

This study was conducted in the Aranjuez Experimental Station, located in central Spain (40°01'55.7"N-3°32'48.3"W; 590 m.a.s.l). Its climate is Mediterranean semi-arid, with average annual rainfall and temperature of 358 mm and 15 °C, respectively (data available since 1977 from Aranjuez Meteorological Station, 40°04'N-3°32'W; 540 m.a.s.l, and from an *in situ* meteorological station). The area typically registers a marked dry period from June to September with very few rains of little intensity (June, July, August and September average 19, 9, 9 and 22 mm of precipitation respectively from 1981-2010; see also Figures 1 and S1 and Table 1 for a more detailed description of the climatic conditions throughout the study period). Soils are classified as Gypsic Leptosols (IUSS Working Group WRB 2006), with pH, organic carbon and total nitrogen content values ranging between 7.2-7.7, 9-32 mg/g soil and 0.8-4 mg/g soil, respectively, depending on the microsite (open areas, vegetation and biocrust) considered (see Castillo-Monroy et al., 2010 for more details). The vegetation is dominated by *Macrochloa tenacissima* (L.) Kunth (18% of total cover), *Retama sphaerocarpa* (L.) Boiss and *Helianthemum squamatum* Pers. (6% of total cover for both shrubs). The open areas between vascular plant patches are covered with a well-developed biocrust community that covers ~34% of the soil surface and is dominated by lichens such as *Diploschistes diacapsis* (Ach.) Lumbsch, *Squamarina lentigera* (Weber) Poelt, *Fulgensia subbracteata* (Nyl.) Poelt, *Toninia sedifolia* (Scop.) Timdal, and *Psora decipiens* (Hedw.) Hoffm. (see Maestre et al. 2013 for a full species checklist).

Experimental design and monitoring

We established a fully factorial experimental design with three factors, each with two levels: biocrust cover (poorly developed biocrust communities with cover <25% vs. well-developed biocrust communities with cover >50%), warming (WA, control vs. ~2.5°C temperature increase), and rainfall exclusion (RE, control vs. ~35% reduction in total annual rainfall).

Ten replicates per combination of treatments were established, resulting in a total of 80 experimental plots. To simulate warming, we used hexagonal open top chambers (OTCs) made of methacrylate and with a size of 40 cm x 50 cm x 32 cm. To intercept rainfall, we built a 1.2 m x 1.2 m x 1 m metallic frame supporting three V-shaped methacrylate gutters that cover ~37% of the surface. The methacrylate gutters had a 20° inclination and on the lower side was a PVC gutter connected by a hose to a tank to collect the excluded rainfall. The WA and RE treatments were setup in July and November 2008, respectively (see Maestre et al. 2013 for additional details on the treatments and on their performance).

Air temperature/humidity, soil moisture, rainfall and biocrust cover have been monitored from 2009 to 2016. Soil moisture (0–5 cm depth) was continuously monitored every 2.5 hours in all treatments using a total of 23 replicated automated sensors, 2–4 replicates per treatment (EC-5 soil moisture sensors, Decagon Devices Inc., Pullman, WA, USA). Relative air humidity, air temperature and rainfall accumulated every 10 min was also monitored using an on-site meteorological station (OnsetCorp 2.8., MA, USA). Within each plot, the total cover of the visible biocrust components (lichens and mosses) were estimated at the beginning of the experiment and once a year hereafter using high resolution photographs, as indicated in Maestre et al. (2013).

Identification and characterization of wetting and drying events

We identified wetting and drying events following the approach of Berdugo et al. (2014). We define a wetting event as any rain registered with the *in-situ* pluviometer. Rainfall events separated by at least 2.5 h without rainfall in between were considered as different wetting events. Drying events are defined as periods of ten consecutive days without any registered rain after a rainfall event. Per these criteria, we described 521 wetting events and 56 drying events from February 2009 to July 2016 (Figure 1).

We used in our analyses different covariates that are important to determine soil water gains and losses after rainfall events in drylands (Berdugo et al., 2014). Four covariates were used when analyzing wetting events: initial soil moisture, rainfall amount, rainfall intensity and the interaction between rainfall amount and intensity. Rainfall intensity was estimated as the maximum rainfall achieved in intervals of 10 minutes. We selected these covariates because they may have opposite effects on soil water gains, i.e. while rainfall amount increases soil water content, a higher intensity of the event may reduce it because it is directly related to runoff (Gardner et al., 1999). Initial soil moisture was estimated as the soil water content before the rainfall event. We used two covariates when analyzing drying events: the maximum temperature reached during the drying event and soil moisture at the beginning of this event, estimated as the water content after the rainfall event.

We characterized water gains as the difference in soil volumetric water content (VWC) between initial moisture preceding a given rainfall event (i.e. minimum moisture) and the maximum moisture achieved during this event. Drying events were characterized by means of the slope and the shape of a drying curve, which describes how soil moisture decreases through time. The drying curves were obtained from the 56 drying events recorded. Each drying curve was fitted to a linear equation

$$bx + c \quad \text{equation 1}$$

to obtain the slope (b) of the drying curve, and to a quadratic equation

$$ax^2 + bx + c \quad \text{equation 2}$$

to obtain the shape (a) of the drying curve. In equation 2, $a = 0$ indicates a linear decay, $a > 0$ an exponential decay and $a < 0$ an inversed exponential decay. To improve the fitting of the drying events, we multiplied a by R^2 , the coefficient of determination from the quadratic regression, to obtain the shape parameter aR^2 (Berdugo et al., 2014). The shape parameter transforms poorly fitted drying curves to an aR^2 value of 0, as these curves are considered artefacts of the statistical method and have no biological meaning.

Statistical analyses

We used generalized linear models to analyze the influence of the experimental treatments on the wetting and drying events. In the case of wetting events, we used the model:

$$WG = Ppt * I10 + H0 + OTC * Cv + RS \quad \text{equation 3}$$

where WG is the maximum water gain at 0–5 cm depth, Ppt is the total amount of rainfall registered during the event, I10 is the rainfall intensity, H0 the soil moisture preceding the rain (hereafter initial soil moisture), OTC is the effect of the open top chambers, Cv is the cover of visible biocrust components (measured from the photograph taken closest to the date of the event) and RS is the effect of rainfall shelters. We introduced the interaction between WA and biocrust cover because we have previously reported negative effects of WA on the cover of biocrusts in our experiment (Escolar et al. 2012, Maestre et al. 2013). In the case of desiccation events, we built two models for the two parameters of the drying curve:

$$\text{Slope} = Tmax + H0 + OTC * Cv + Rs \quad \text{equation 4}$$

$$\text{Shape} = Tmax + H0 + OTC * Cv + Rs \quad \text{equation 5}$$

where Tmax is the maximum temperature achieved during the drying event, H0 is the initial soil moisture of this event, and the other terms are those used in equation 3.

Since biocrusts tend to colonize areas with initial low cover through time (Maestre et al., 2015), and to further investigate whether the effects of the treatments on the wetting and drying events changed through time, we repeated the analyses described above for three periods: 1-2 years, 2-5 years and 5-8 years after the setup of our experiment. We selected these periods because they showed contrasted patterns of biocrust cover under our climate

change treatments (Figure 2). We performed all statistical analyses using the “lm” function of the R 3.3.2 statistical software (R Development Core Team, 2011).

Results

Throughout the study period, mean annual temperature was 15.1 °C, mean annual rainfall was 276.5 mm and rainfall intensity (I10) ranged from 0.02 - 15.2 mm/h (Table 1). Soil moisture content accurately matched rainfall events during this period (Figure 1). Soil water gains under both WA and the combination of WA and RE decreased when the effects of main covariates (i.e., initial soil moisture and biocrust cover) were controlled (Figure 3b). Initial soil moisture of dry soils (i.e., preceding rainfall events) was lower under climate change treatments, especially during the first and last stages of the experiment (Figure 3c). Meanwhile, initial soil moisture after rainfall events showed variations throughout the experiment. In the first stage of the experiment, wetted soils under the WA and WA + RE treatments showed a lower initial moisture (Figure 3d). In the second stage of the experiment, initial soil moisture of wetted soils was lower under the RE and WA treatments, but not under the combination of both (Figure 3d). However, towards the last stage of the experiment, RE, WA and the combination of both had a lower initial soil moisture after rainfall events (Figure 3d).

Climatic covariates (H0, Ppt, I10 and interaction PptxI10 and Tmax) were major drivers of both the maximum water gain during wetting events and the slope and shape of the drying curve (Table 2; Figure 4). During wetting events, rainfall amount increased water gain. However, rainfall intensity decreased soil water gain during these events, even in the case of those with higher rainfall amounts (Table 2, Figure S.2). Initial soil moisture negatively influenced water gains during rainfall events. During the drying events, initial moisture and maximum temperature increased both drying rates and the exponential behavior of the drying curve (Table 2; Figure 4b, c).

Biocrust cover increased both water gains after rainfall events and the slope of the drying curve (Table 2). Rainfall exclusion had a positive effect (0.04 as measured with standardized coefficients) only on water gains. Warming decreased (-0.10 as measured with standardized coefficients) water gains, but also substantially reduced the exponential behavior of the drying curve (-0.35, as measured with standardized coefficients). These effects of WA were constant throughout the experiment but their magnitude decreased through time (Table 2; Figure 4). We also found an interaction between WA and biocrust cover when analyzing water gains, as the effect of biocrust cover on this variable was reduced (-0.06 as measured with standardized coefficients) under WA (Table 2).

The effects of the different treatments on water gains and losses varied through time. For instance, the effects of WA on water gains were negative throughout the experiment and particularly important during the first years (Figure 4a). Biocrust cover negatively affected the slope of the drying curves throughout the experiment (Figure 4b, c). In addition, the effects of initial moisture and maximum temperature varied throughout the experiment (Figure 4b,c). The effects of both initial moisture and maximum temperature on the slope of the drying events shifted to negative after the first two years of the experiment. The effect of

these covariates on the shape of the drying events was the opposite. The effect of warming on the response variables evaluated was similar throughout the experiment.

Discussion

Our analyses of an eight-year dataset showed variable effects of simulated climate change on soil water gains and losses after rainfall events in a biocrust-dominated semiarid ecosystem. A 2.5°C warming reduced water gains after rainfall events, and affected the way the soil dried up after them by reducing both the slope and exponential behavior of the drying curve. An important result of our study is that the effects of treatments on soil water gains and losses changed through time, with important differences between the first two years of the experiment and after five years since its setup. These effects were mainly driven by the important reductions in biocrust cover and diversity observed under warming (Escolar et al., 2012), which were similar to those reported in other climate change experiments conducted with biocrusts (Ferrenberg et al., 2015). Our findings thus emphasize the importance of conducting long-term experiments to accurately characterize potential responses to climate change in hydrological variables such as water gains and losses after rainfall events.

Drivers of soil water gains and losses after rainfall events

Soil water gains were dependent on both the amount and intensity of rainfall events. However, there was an interaction between both precipitation attributes. The greater the rainfall event, the larger the soil water gains. Nevertheless, this effect was modulated by rainfall intensity; despite its magnitude, if the intensity of a rainfall event was high, soil water gains turned to be lower than expected. Many studies have evaluated the effects of the amount and intensity of rainfall on infiltration and runoff (e.g., Cantón et al., 2004; Chamizo et al., 2012; Faist et al., 2017; Kidron & Yair, 1997). Our results are similar to those of Chamizo et al., (2012) and Kidron & Yair (1997), who observed that biocrust-dominated soils had the ability to reduce runoff when compared to bare ground soils under low intensity rainfall events. However, when the intensity of the rainfall event was high, biocrusts lost their capacity to reduce runoff. Faist et al., (2017), observed that under high intensity rainfalls the capacity to reduced runoff was dependent on the successional stage of the biocrusts, late successional biocrusts had the capacity to reduce runoff, whereas early successional biocrust lost this capacity. Moreover, the higher the initial soil moisture, the lower the water gains after rainfall events. Fine textured soils show numerous cracks when are dry, which can considerably increase water infiltration. However, these cracks seal when they are wetted, and consequently runoff is favored under these conditions (Chamizo et al., (2012). In addition, wetted soils present a higher total pore volume filled with water, which reduces the capacity of the soil to further gain water (Gardner et al., 1999). As found by Berdugo et al. (2014), soil moisture after rainfall events, combined with the maximal temperature registered during the drying event, affected soil water losses through desiccation.

The effect of biocrusts on water gains and losses after rainfall events is complex but of paramount important since they cover large areas of the soil surface in drylands worldwide. A large body of literature has discussed how biocrusts enhance or decrease infiltration and

runoff (see Chamizo et al., 2016 for a recent review). Reductions in infiltration by biocrusts have been described when these organisms smooth the soil surface (Belnap et al., 2003; Eldridge et al., 2000) and under intense rainfalls due to the production of exopolysaccharides by biocrust-forming cyanobacteria (Warren, 2003). On the other hand, biocrusts increase soil stability (Eldridge & Leys, 2003), porosity (Felde et al., 2014) and surface roughness (Belnap, 2006). Other studies have highlighted how biocrust-dominated soils increase water gains and reduce runoff after rainfall events, maintaining higher moisture conditions in the soil surface (Cantón et al., 2004; Chamizo et al., 2012, 2013, 2016, 2016). Our results agree with these studies, as we found a significant positive effect of well-developed biocrusts on soil water gains after rainfall events (Table 2). This effect is likely to be driven by the increase in soil surface roughness by dominant lichens, which reduces runoff and increases infiltration, and by the positive effects of these organisms on soil pore formation, which positively affect infiltration (Bowker et al., 2013; Chamizo et al., 2012).

We found that well-developed biocrusts increased both the slope and exponential behavior of the drying events (Table 2). Soils with a well-developed biocrust community gained more water after rainfall events, but also had higher drying rates. These results mimic those from Berdugo et al. (2014), who used another mid-term dataset (six years) from the same study area. Our results suggest that evaporation is higher in biocrust-dominated than in bare ground soils. We speculate that this could be consequence of the soil surface darkening by cyanobacteria (Rutherford et al., 2017), which are abundant in our study area (Cano-Díaz et al., 2017), and by some lichen species (e.g. *Toninia sedifolia*), which would thus increase surface heating and enhance evaporation. The increase in soil surface roughness by biocrusts, which also increases the amount of soil surface that can be heated (Kidron & Tal, 2012), can also contribute to explain the results observed.

Soil water gains and losses under simulated climate change

The dynamics of soil wetting and drying after rainfall events was impacted by our climate change treatments, and by warming in particular. The increase in the mean annual temperature imposed by this treatment ($\sim 2.5^{\circ}\text{C}$ on average throughout the experiment) led to drier soils (average reduction in soil moisture $\sim 1\%$ throughout the experiment; Figure 3c and d). Similar responses have also been observed in experimental studies conducted in grasslands (Liancourt et al., 2012) and shrublands (León-Sánchez et al., 2016) from dryland areas. Our warming treatment decreased the observed water gains and reduced the exponential behavior of the desiccation curve, meaning that warmed plots gained less water and desiccated more gradually compared to other treatments (Figure 3b). These findings mimic those of Liancourt et al. (2012), who found that OTCs like those employed in our study significantly reduced soil moisture and decreased soil drying rates in a Mongolian grassland. These authors found that this reduction in the desiccation rate was a consequence of a reduction in wind speed due to the warming structures. However, we believe that the reduction in the desiccation rate observed in our case was due to a reduced water gain that led to a lower initial soil moisture (our OTCs were elevated 5 cm from the soil, hence allowed ventilation), and thus to a more progressive drying (reduction of the exponential behavior), instead of the abrupt drying observed in a more exponential curve.

Our rainfall exclusion treatment increased soil water gains after rainfall events. This result was unexpected because our shelters effectively excluded ~33% of incoming rainfall (Maestre et al. 2013). However, it can be partially explained by the fact that the initial soil moisture of these soils was lower under this treatment (Figure 3). Indeed, the water gains observed under this treatment did not differ from those found in the control plots when least squared means were controlled by the soil moisture at the beginning of each rainfall event (Figure 3b). We believe that the amount of rainfall may be playing a role on this effect of rainfall exclusion because soils are driven to saturation during the most intense events. Indeed, under rainfall events below 2 mm, water gains under rainfall exclusion tended to be slightly lower than controls, whereas for larger rainfall events the exclusion of rainfall did not reduce soil water gains (Figure S2) due to soil saturation. Another possible explanation for these results is the fact that we only placed one sensor under each rainfall exclusion plot, which occupies an area of 2.64 m². As such, the soil moisture registered could have not provided an accurate measure of the soil surface moisture under this treatment. Therefore, the results of our study regarding the effect of rainfall shelters should be treated with caution and must be confirmed by additional studies.

Temporal trends of the hydrological impacts of climate change treatments

Initial soil moisture after rainfall events was lower under warming throughout the experiment. However, the effect of the combination of warming and rainfall exclusion on this variable differed depending on the period considered. In the first stage of the experiment, the combination of both treatments had no effect on initial soil moisture after rainfall events. After 2-5 years of simulated climate change, the combination of both treatments mitigated the initial soil moisture decrease caused by warming alone. Meanwhile, 5-8 years after the setup of the experiment the combination of warming and rainfall exclusion promoted important reductions in the moisture of wetted soils (Figure 3d). Because the effect of biocrusts cover has been controlled in our analyses, we hypothesize these changes are not directly driven by the loss of lichen cover but indirectly through changes in the soil properties promoted by the loss of lichen cover. These include an increase in hydrophobic compounds originated from the decomposition of lichens, a reduction in the quality of soil organic matter or shifts in the composition of the biocrust community (Asplund & Wardle, 2016; Delgado-Baquerizo et al., 2015).

The effects of initial soil moisture and maximum temperature on the slope and shape of the desiccation curve changed from positive to negative and from negative to positive, respectively, after two years of simulated climate change (Figure 4b,c). In addition, two years after the setup of the experiment, the cover of biocrusts started having a positive effect on water gains, while warming decreased its negative effect on this variable. These results highlighted the existence of feedbacks between soil moisture and biocrust cover, and suggest that the importance of these factors for water gains were altered once biocrusts cover decreased. D'Odorico et al., (2007) also showed a lack of linearity when evaluating the effects of vegetation on soil moisture in the Kalahari. After rainstorms, open areas located between vegetated patches were wetter but also dried faster than plant patches, which is in accordance to what we observed in our experiment.

During our experiment, warming decreased the cover of biocrusts by ~56 % (Figure 2). Just after two years of simulated climate change we already observed a decrease in the water gains under both warming and the combination of warming and rainfall exclusion (Figure 3b). However, the effects of our climate change treatments on initial soil moisture were not evident until five years after the setup of the experiment (Figure 3c, d). These results illustrate the hydrological consequences of reductions in biocrust cover due to simulated climate change. Moreover, some of these consequences took a larger lapse of time to become evident. Our findings further emphasize the importance and value of long-term studies, as some of the observed effects would have gone unnoticed if our study had had a shorter duration.

Concluding remarks

Our results indicate that ongoing climate change, and warming in particular, will affect the hydrological behavior of biocrust-dominated ecosystems both directly, by increasing evaporation, and indirectly, by reducing the cover of lichen-dominated biocrusts and by altering their ability to control water gains and losses after rainfall events. This study emphasizes how after two years of simulated warming, water gains decreased and desiccation occurred more gradually. However, the reduction in water gains consequence of the combined effect of warming and rainfall exclusion was not noticeable until five years of simulated climate change. Most of the hydrological studies focusing on biocrusts have a duration lower than two years (e.g Cantón et al., 2004; Chamizo et al., 2016; Zaady et al., 2014; but see Berdugo et al., 2014). To our knowledge, no previous study focusing on the hydrological impacts of climate change and biocrusts have used a temporal series as large as that employed here. The use of such a dataset provided insights on the hydrological effects of biocrusts under simulated climate change that would not have been evident if our experiment had lasted for a shorter period. These findings point to the importance of conducting mid- and long-term experiments when evaluating the hydrological responses of drylands to climate change, particularly when these are mediated by organisms that are highly sensitive to changes in climatic conditions, such as biocrusts. In addition, and by illustrating how biocrusts modulate the impacts of simulated climate change on soil water gains and losses after rainfall events, our study not only emphasizes the key role of biocrusts on these important hydrological attributes, but also contributes to advance our understanding of climate change impacts on the ecohydrology of drylands.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Figure 1.

Rainfall events registered during the experiment (upper panel, blue bars) and soil moisture (0-5 cm depth) measured by automated sensors in low (L) and high (H) biocrust cover plots (middle and lower panels, respectively). WA = Warming and RE = Rainfall exclusion.

Figure 2.

Cover of biocrusts in the different treatments throughout the duration of the experiment: 0-2 years (A), 2-5 years (B), and 5-8 years (C). WA = Warming and RE = Rainfall exclusion. Data are means $\pm$ SE (n = 10).

Figure 3.

Least squared means (lsmean) for the slope of the desiccation curve (a), soil water gains (b), initial soil moisture prior to soil wetting (c) and initial soil moisture prior to desiccation (d) throughout the duration of the experiment. WA = Warming and RE = Rainfall exclusion. Data are lsmeans $\pm$ confidence intervals ($n = 21$).

Figure 4.

Standardized effect size of variables involved in predicting water gains (a), and the slope (b) and shape (c) of the desiccation curve after rainfall events throughout the duration of the experiment. Vertical lines represent 95% confidence intervals. Tmax: Maximum temperature during desiccation event; H0: initial soil moisture before the rainfall event; OTC: warming treatment; Cv: cover of biocrust; Ppt: summation of rainfall during the wetting event; I10: rainfall intensity.

Table 1

Description of the climatic conditions registered during the three periods identified in our study (1-2, 2-5 and 5-8 years after the setup of the experiment). Annual Rainfall (mm); Temperature (°C); I10: mean rainfall intensity (mm/h); average and range of water gains (WG), expressed as volumetric water content per day (% VWC), and average and range of water losses, expressed as volumetric water content per day (% VWC).

		Period		
		1-2	2-5	5-8
Mean Annual Rainfall		232.6	288.4	260.6
Mean Temperature		15.8	15.9	14
Mean I10		0.54	0.88	0.58
Maximum WG	Control	1.77 [0 - 9.32]	1.48 [0 - 19.31]	1.24 [0 - 19.55]
	WA	0.70 [0 - 6.55]	1.22 [0 - 26.94]	0.98 [0 - 21.08]
	RE	1.67 [0 - 9.52]	1.66 [0 - 22.61]	1.44 [0 - 21.00]
	WA+RE	0.61 [0 - 4.34]	1.32 [0 - 22.82]	1.03 [0 - 23.11]
Average water loss	Control	-0.51 [-1.19 - 0.18]	-0.53 [-1.66 - 0.77]	-0.41 [-1.45 - 0.58]
	WA	-0.48 [-1.21 - -0.01]	-0.38 [-1.56 - 0.21]	-0.40 [-1.50 - 0.48]
	RE	-0.71 [-1.24 - -0.04]	-0.49 [-1.72 - 0.16]	-0.54 [-1.79 - 0.09]
	WA+RE	-0.58 [-1.07 - -0.26]	-0.56 [-1.76 - 0.02]	-0.41 [-1.45 - 0.37]

Table 2

Estimates of standardized effects of covariates introduced when modelling water gains and losses (slope and shape of the drying curve) after rainfall events. Tmax: Maximum temperature during desiccation event; H0: initial soil moisture before the considered rainfall event; RS: rainfall shelter; OTC: warming treatment; Cv: biocrusts cover; Ppt: summation of rainfall during the wetting event; I10: rainfall intensity (mm/h); F: Fisher statistic; d.f.: degrees of freedom.

Predictor	Water Gain	Slope	Shape
H0	-0.12 ***	-0.51 ***	0.05
Tmax	-	-0.43 ***	0.27 ***
Ppt	0.61 ***	-	-
I10	-0.09 ***	-	-
Ppt × I10	-0.22 ***	-	-
OTC	-0.10 ***	-0.06	-0.35 ***
RS	0.04 *	-0.10	-0.02
Cv	0.08 ***	-0.19 ***	0.07
OTC × Cv	-0.06 ***	0.09	-0.06
Adjusted R ²	0.3945	0.2929	0.1060
F	810.7	55.05	16.47
d.f.	8/9934	6/777	6/777

*** = $p < 0.001$; * = $p < 0.05$