Drought affects biocrust more than increased rainfall in the Tabernas Desert (SE Spain)

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Abstract:

Composed of poikilohydric organisms, biocrusts have the ability to survive during periods of drought, making them particularly important in arid and semi-arid areas. However, despite recent research into climate change, the limits of this tolerance to desiccation and the effects of increased water availability, are not very well known. Our objectives were to analyze the effect of prolonged droughts on the cover and metabolism of various crust types, as well as the effect of increased precipitation. Five types of crusts representative of hypothetic successional stages were studied (Physical, Incipient, Cyanobacteria, Squamarina, and Lepraria). Two representative areas were selected for each crust type. Nine plots were established in each area, delimited by a 10-cm-diameter ring, and distributed in sets of three plots. In each set, three treatments were applied (control, watering, and rain exclusion), and changes in cover, CO_2 fluxes, and chlorophyll *a* fluorescence were analyzed. Rain exclusion led to cover losses due to respiration, although this effect differed among successional stages. However, increased precipitation did not increase biocrust cover, because both photosynthesis and respiration rates increased. Chlorophyll *a* fluorescence was larger in lichens; under watering, it was not different from the control, but decreased under rain exclusion

Keywords: biocrusts, prolonged drought, climate manipulation, semiarid, biocrust succession.

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Impact statement:

Biocrusts are communities of microorganisms, algae, lichen, and mosses that develop in the top few millimeters of the soil. Their poikilohydric condition allows them to become inactive during dry periods and become active when water becomes available again, which is crucial in drylands, where water is a limiting factor for vegetation growth. Biocrusts are common in drylands around the world and are important because perform multiple ecological functions. This high tolerance to desiccation suggests that biocrusts can survive long periods of drought. However, some observations seem to indicate changes in biocrust cover during drought periods. In the current context of climate change, knowing biocrust's limits is essential for the conservation of these areas. This work provides evidence of the impact of increasing drought duration on these communities, analyzing the effects not only on their cover but also on their metabolism (net photosynthesis and dark respiration). On the other hand, analyzing the effect of an increase in precipitation improves our understanding of the limits of biocrust growth. In addition, analyzing various types of biocrusts allows us to better understand the dynamics of the Tabernas Desert's biocrust communities, and provide information for the succession hypothesis.

Introduction

Biocrusts are communities mainly composed of poikilohydric organisms that are capable of surviving in areas where water is a limiting factor. Because their water content tends to equilibrium with that of the environment, they become inactive during dry periods and reactivate when water is available again (Kappen & Valladares, 2007; Green et al., 2011). This condition makes them particularly important in arid and semi-arid areas, where they protect soil against erosion (Chamizo et al. 2012; Rodriguez-Caballero et al. 2013; Chamizo et al. 2017; Lázaro et al. 2023) and can act as main primary producers (Maestre et al., 2016).

Desiccation tolerance mechanisms in these organisms are essential for their survival in these areas, because they allow them to maintain their structural and metabolic integrity during dry periods. Some reviews have highlighted the following mechanisms (Kranner et al., 2008; Green et al., 2011; Heber and Lüttge, 2011): (a) compatible solutes that protect membranes and proteins by replacing water molecules during desiccation (Farrar 1976; Aubert et al., 2007; Oliver, 2008; Hoekstra et al., 2001); (b) late embryogenesis abundant proteins (LEAs) and heat shock proteins (HSPs) that protect proteins from denaturation during desiccation (Hoekstra et al., 2001); (c) thermal energy dissipation that protects against photooxidative damage, preventing the formation of reactive oxygen species (ROS) (Heber and Lüttge, 2011; Kranner et al., 2008); (d) antioxidants that act as scavengers of ROS during desiccation (Kranner et al., 2002; Kranner et al., 2008); and (e) amphiphilic metabolites that, although they cause disturbances in the membrane, promote the insertion of antioxidants (Hoekstra and Golovina, 2002). These mechanisms seem to give biocrusts a certain advantage in dealing with climate change, and they strengthen the belief that biocrusts can survive long periods of drought.

Although several studies have been conducted on climate change in biocrust communities, studies on the effects of changes in precipitation are scarce. Simulations of climate change in southeast Spain found that an increase in soil temperature of 2–3 ºC led to losses in biocrust cover because of increased respiration; however, no cover losses were observed with a 30% reduction in precipitation (Maestre et al., 2013; Ladrón de Guevara et al., 2014). In contrast, in a similar experiment, 5%–8% losses in moss cover (but not in lichens) were observed because of both increased temperature and reduced precipitation (Li et al., 2021). On the other hand, research on the effect of altered precipitation patterns by increasing the frequency of small precipitations also revealed losses of biocrust cover related to negative carbon balances (Belnap et al., 2004; Reed et al., 2012; Zelikova et al.,2012; Johnson et al., 2012). Water availability was shown to increase crust biomass and even to change the crust type (Kidron et al., 2010). Nevertheless, the effects of prolonged droughts on biocrusts are not very well known; although, droughts drastically affected the crust structure and stability in the Negev (Kidron et al., 2017). Some research has observed that the duration of droughts can hinder the reactivation of the metabolic activity in lichens and mosses (Munzi et al., 2019; Kranner et al., 2003; Harel et al., 2004; Proctor et al., 2007), while field observations seem to reveal a relationship between periods of drought and cover loss (Belnap et al., 2006). On the other hand, the effects of increased rainfall on cover and gas exchange of biocrusts are poorly understood.

The objectives of this work were to analyze the effects of prolonged droughts and increased precipitation on biocrust cover and gas exchange. The state of the photosynthetic systems of the main biocrust components after three years of continuous drought were also recorded. We studied five crust types hypothetically representative of successional stages (according Lazaro et al., 2008, and Rubio and Lázaro, 2023, among others). We hypothesized that (a) episodes of hydration insufficient to produce positive net photosynthesis would lead to a decrease in biocrust biomass due to respiration and biocrust cover would be visibly reduced after a few years of drought; and (b) an increase in precipitation would lead to an increase in net photosynthesis rates promoting the growth of biocrust, which could visibly increase its cover.

Material and Methods

Study area

This study was performed at the El Cautivo field site, in the Tabernas Desert (Almería, Spain). This widely studied area (Alexander et al. 1994; Raggio et al. 2014; Miralles et al. 2020; among others) has a mean annual rainfall of about 230 mm, distributed mainly during autumn and winter, and a mean annual temperature of 18 ºC, which can reach 45 ºC in summer and -5.5 ºC in winter (Lázaro et al. 2001, 2004). The weathering of marine marls from the Upper Miocene has generated a landscape of badlands, heterogeneously colonized by vascular vegetation and biocrusts (Lázaro et al., 2008). The vegetation is patchy, concentrated in certain landforms, and is mainly made up of three biotypes: tussock grasses, dwarf shrubs, and annual herbs. Vegetation covers approximately one third of the territory, while another third features eroded regolith with hardly any vegetation, and the final third is covered with biocrusts, which are also in the plant interspaces.

Experimental design

Five crusts types characteristic of the area were analyzed, which could represent stages of a hypothetical succession (Lázaro et al., 2008; Rubio and Lázaro, 2023); ordered from earliest to latest, they were as follows:

- Physical crust (P): Bare soil with a low amount of microorganisms not visible to the naked eye in the field. Smooth surface and beige, pale grey or whitish color.
- Incipient cyanobacterial biocrust (I): Located in flat and sun-exposed areas undergoing a relatively frequent trampling. It has a slight bacterial colonization. The five main phyla are: Proteobacteria (14.8%), Bacteriodetes (14.6%), Actinobacteria, (14.4%), Cyanobacteria (12.4%) and Chloroflexi (11.3%) (Miralles et al., 2020). Smooth compact surface and pale brown or yellowish color.
- Mature cyanobacterial biocrust (C): A widespread biocrust becoming dominant on sun-exposed areas, with a higher microbial concentration than I (Miralles et al., 2020). The five main phyla are: Cyanobacteria (21.9%), Bacteriodetes (14.3%), Proteobacteria (13.2%), Actinobacteria (9.8%) and Chloroflexi (9.7%) (Miralles et al., 2020). Büdel et al. (2014) found 14 cyanobacterial genera, highlighting Nostoc, Leptolyngbya, Scytonema, and Phormidium. Some filamentous cyanobacteria have been identified to the species level, such as the heterocystous Tolypothrix distorta, and Scytonema hyalinum; and the non-heterocystous Leptolyngbya frigida, Microcoleus steenstrupii, and Trichocoleus desertorum (Roncero-Ramos et al. 2019). Rough surface and brown color. Some small pioneer lichens such as *Fulgensia desertorum* Poelt*, Fulgensia poeltii* Llimona and *Endocarpon pussillum* Hedw are often present.

- Lichen biocrust dominated by *Squamarina lentigera* Poelt and/or *Diploschistes diacapsis* Lumbsch (S): It is the most widespread biocrust type at the field site, occupying mainly north and east-oriented hillslopes. Rough surface and whitish color. It includes a diversity of lichens, such as *Buellia zohary* Galun, *Diploschistes ocellatus* Llimona, and *Psora decipiens* Hoff.
- Lichen biocrust characterized by *Lepraria isidiata* Llimona&Crespo (L). It develops on the shadiest north-facing hillslopes, often in spaces among plants (which show 20-40% cover). Others lichens such as *Squamarina cartilagínea* P. James, *Xanthoparmelia pokornyi* Blanco, Crespo, Elix, Hawksw. & Lumbsch, and *Teloschistes lacunosus* Savicz, as well as mosses such as *Grimmia pulvinata* Sm, are also characteristic. Rough surface and a mosaic of whitish (often dominant), green and dark colors.

We selected two representative areas per crust type, and nine representative plots were established in each area, delimited by 10-cm-diameter transparent methacrylate rings, distributed in three sets of three samples. We used six replicates per treatment and crust type; every set of plots including the three following treatments:

- Control (C): samples exposed to the natural rainfall regime.
- Watering (W): samples subjected to irrigation, doubling the natural rainfall. To do so, we measured precipitation and, the day or days following each precipitation event, the samples were carefully watered with an amount of demineralized water equal to that received by precipitation. Watering turned out to be a slow process and, lasting several days in large events and when gas exchange measurements were imminent (see below), in which case the order of the irrigations was used to order the measurements so that they were done under similar moisture conditions.
- Rain exclusion (RE): samples permanently covered with a square, 20-cm-side, transparent methacrylate roof at a height of approximately 20 cm from the ground, preventing the entry of rainwater but allowing light to enter. Although these rainout shelters often condense water,, they probably barely decrease the high relative humidity associated with rain, so they do not exactly replicate the conditions of natural drought.

CO_2 fluxes measurement

The net photosynthesis and dark respiration were measured periodically using an open-circuit infrared gas analyzer LI-6400 (Lincoln, USA) connected to a transparent chamber of 668 cm^3 designed and calibrated by Ladrón de Guevara et al. (2015). To measure respiration, the chamber was covered with an opaque cloth, taking a new record immediately after each light measurement. For photosynthesis and respiration, and for each plot, in each campaign, one record consisted of the average of five consecutive measurements. Ten campaigns were carried out over three years of experimentation: two annual (winter and summer) and some additional ones after heavy rainfall events. Because biocrusts activity peaks during the first light hours of the morning (Raggio et al., 2014; Ladrón de Guevara et al., 2014), only one crust type could be measured per day, so every campaign required five consecutive sunny days. We staggered the irrigations so that each day we measured the crust type watered the day before. We considered positive values to be CO_2 consumption by the biocrust and negative values to be CO_2 loss by the biocrust.

Cover estimation

Each plot was photographed twice per year (winter and summer) to obtain the cover of the main components of the biocrust (bare soil, cyanobacteria, lichens, and mosses). Covers were approximated from the frequencies, using the program GIMP 2.10.34 (GIMP Development Team, 2023) to draw a regular 196-cell grid and to overlap it over each plot photograph. Because 59 grid cells fell outside the plot ring, the frequencies were counted on 137 cells. Frequency counts have been used as a cover subrogate (Maestre et al,, 2013) because it is an objective and repeatable method. This method tends to overestimate the cover of the small-thalli species, however, distinguishing few cover categories, the error can be assumed. We could not monitor the chlorophyll to avoid disturbing the small plots by extracting successive samples, but the small plot size and the grid allowed us to visually check the quality of the cover estimation.

Measurements of chlorophyll a fluorescence

To analyze the effect of treatments on photosystem II (PSII) efficiency and to determine whether each measured organism was alive, we measured the chlorophyll *a* fluorescence of each sample using a MINI-PAM Photosynthesis Yield Analyzer (Heinz Walz GmbH, Germany). Measurements were performed at night and, 30 min before measuring, the samples were sprayed with demineralized water until saturation was reached in surface horizon (about 4 mm). We distinguished physical crust, incipient and mature cyanobacteria, mosses and the main lichen species. A hard grid of 11 x 12 cm with 99 cells was superimposed on each ring always in the same positions to ensure measurements were taken at the same points or thalli across the dates. A variable number of measurement points were selected to represent each sample, depending on the diversity and abundance of organisms present. We measured on the species and crust types appearing at least in three cells, to obtain three replicates per surface category and sample. Therefore, some plots only had three measurements, for example, those in which there was nothing more than physical crust or incipient cyanobacterial biocrust, whereas other samples were the subjects of many measurements. All measurements obtained in every plot were used in the analyses; for graphical representation we used a single (average) fluorescence value per plot. We carried out three measurement campaigns: March 2020, October 2020, and January 2021.

Climate data

Data on precipitation were obtained from five climate stations installed in one of the two zones for each crust type, measured by Rain-O-Matic-Pro tipping-bucket rain gauges of 0.25-mm resolution (Pronamic, Denmark). The missing data were filled in based on the data of the nearest rain gauge considering the regression between both rainfall data series. For every month, we calculated the amount of precipitation and the number of rainfall events, defined by a minimum inter-event time of six hours.

Data analysis

To test for differences, for each plot, the covers of bare soil, cyanobacteria, lichens and mosses, as well as the net photosynthesis, and dark respiration, were analyzed as dependent variables using generalized mixed models (GLMM), assuming that data follows a gamma log link distribution. Years (in the case of cover) or times of measurement (in the cases of net photosynthesis and dark respiration) were considered within-subject factors and crust type and treatment between-subject factors in the three cases, and their interactions were analyzed.

On the other hand, chlorophyll *a* fluorescence, including all the measurements at the points selected in each sample, was analyzed using generalized models (GLMs), assuming that data follows a gamma log link distribution. Crust type and treatment were considered factors, and their interaction was also analyzed. For all interactions, multiple comparisons were analyzed using the Bonferroni test.

All the analyses were made using SPSS 28.0 (IBM Corporation, USA). Differences were assumed significant at $p < 0.05$.

Results

Precipitation

The averages of total annual precipitation for the years 2018-2021 were 217.80, 212.44, 151.14 and 312.78 mm, respectively

Changes in cover

After the three-years experiment, treatment and crust type, significantly affected the cover of all the components, except for moss, (Table 1). Time itself affected the cover of cyanobacteria, mosses, and (indirectly) the bare soil. However, treatments interacted with time (except in moss cover), and with the type of crust in lichen cover, where the three factors interacted significantly, affecting the bare soil cover.

Bare soil increased significantly under the rain exclusion treatment in all biocrusts (Figure 1), increasing by 23% in Incipient, 52% in Cyanobacteria, 31% in Squamarina and 21% in Lepraria crusts. Nevertheless, watering only significantly affected Cyanobacteria and Squamarina, reducing bare soil cover by 9% and 4%, respectively.

Cyanobacterial cover only changed significantly under the rain exclusion condition, in Physical and Cyanobacteria crusts, where it decreased by 23% and 48%, respectively, (Figure 1). The increase in cyanobacterial cover promoted by watering was not significant. Cyanobacterial cover was not significantly affected by treatments or time in the lichen-dominated crusts (Figure 1).

Lichen cover decreased significantly with rain exclusion in the Incipient and Cyanobacteria crusts (virtually disappearing in both) and in Squamarina crust (where it decreased by 29%; however, its decline in Lepraria crust was not significant (Figure 1). Note that the reduction of lichen cover in control plots of Lepraria was almost 15%. Watering only significantly affected lichen cover in the Incipient crust, where it increased by 5%.

Finally, moss cover (identified only in Squamarina and Lepraria) decreased significantly over time, irrespective of the treatment and crust types (Table 1, Figure 1).

Changes in CO_2 fluxes

The three factors, treatment, crust type and time, significantly affected net photosynthesis and dark respiration, The interactions of treatments with crust type and time, as well as the triple interaction of the three factors, were significant for both dependent variables (Table 1). Overall, net photosynthesis was mostly negative and was positive only in September 2019, December 2019, and January 2020 under the control and watering treatments (Figure 2).

In the Physical crust, the treatments did not significantly change photosynthesis or respiration after three years. (Figure 2, Figure 3).

In the Incipient crust, net photosynthesis increased significantly under the watering treatment (Figure 2), from -0.19 µmol/m^{2}s in March 2018 to -0.08 µmol/m^{2}s) in January 2021. Punctual increases observed in September 2018 (0.21 µmol/m^{2}s), December 2019 (0.24 µmol/m^{2}s), and January 2020 (0.39 µmol/m^{2}s) coincided with rain events (Figure 2). Dark respiration was significantly higher in the watering treatment (Figure 3).

In the Cyanobacteria crust, net photosynthesis was not significantly different among the treatments (Figure 2), although it increased over the three years by 0.5 µmol/m^{2}s under the watering treatment. As in the case of the Incipient crust, the positive rates of net photosynthesis reached in December 2019, January 2020 and January 2021, coincided with rain events. Dark respiration was significantly higher under the watering treatment and significantly lower under rain exclusion (Figure 3).

In the Squamarina crust, net photosynthesis was significantly higher in watering conditions than in rain exclusion, reaching 0.23 µmol/m^{2}s in January 2021 (Figure 2). Increased photosynthesis was observed in the control and watering samples in January 2020 and January 2021, coinciding with rain events. Dark respiration was significantly higher under the watering treatment, increasing by 0.37 µmol/m^{2}s, and significantly lower under rain exclusion (Figure 3). In September 2020, dark respiration of watering treatment increased to -0.98 µmol/m^{2}s with the first rainfall after summer drought.

In the Lepraria crust, net photosynthesis under watering was not significantly different from that of the control, but did differ from that under rain exclusion (Figure 2). Conversely, dark respiration was significantly higher with watering (thus making it difficult the increase of net photosynthesis) but it was not significantly lower under exclusion, and it peaked at -1.31 µmol/m^{2}s by September 2020 with the first rainfall after summer (Figure 3).

Chlorophyll a fluorescence

Chlorophyll *a* fluorescence was significantly different among crusts and treatments and the effect of the treatments depended on the crust type (Table 1). Fluorescence was significantly lower under rain exclusion than in control or watering treatment in Incipient, Squamarina and Lepraria crusts, while watering did not produce a difference with respect to the control (Figure 4). Fluorescence in lichenic crusts were significantly higher than those of cyanobacterial crusts in both control and watering. Rain exclusion affected fluorescence more in Lepraria than in Squamarina.

Discussion

Our treatments significantly affected the cover and metabolism of biocrusts, and differently according the biocrust types, assumed to be successional stages.

We achieved the maximum possible replication of CO_2 measurements considering that the daily metabolic cycle (Ladrón de Guevara et al, 2014) affects the fluxes if each round of measurements lasts too long, depending on the number of plots. However, the punctual nature of the gas exchange measurements, the seasonality, the erratic nature of rainfall, the inevitable increase in the number of events by watering, and the necessity to water on two or more successive days after the major rains or for the gas exchange campaigns, surely added noise to the data on net photosynthesis and respiration, blurring their relationships with the factors and the cover variations.

Effect of prolonged droughts

Rain exclusion negatively and differentially affected both the cover and metabolism of all biocrusts. The Cyanobacteria crust lost more than 40% of its cyanobacterial cover whereas the Incipient lost 20% (Figure 1). Net photosynthesis did not decrease significantly in either (Figure 2); however, dark respiration was significantly lower in the Cyanobacteria crust (Figure 3). Lichen-dominated crusts lost 30% and almost 20% of lichen cover in Squamarina and Lepraria crusts, respectively (Figure 1). However, unlike in the Cyanobacteria crust, they did not lose cyanobacterial cover. This suggests that prolonged droughts (and possibly other disturbances), can reverse the direction of succession. Although lichens displace cyanobacteria under favorable conditions (Lázaro et al., 2008), when lichens recede, cyanobacteria occupy their space. This is the only explanation for the fact that cyanobacterial cover decreased where Cyanobacteria dominate but not where lichens dominate. The space left by the lichen retreat would have particularly suitable conditions for cyanobacteria despite the drought, due to the physical and chemical changes lichens produce in soil. These changes include improvement of soil structure, porosity, stability, water retention and accumulation of fine-grained material (Miralles et al, 2011, Chamizo et al., 2012; 2016); along with increased organic carbon, nitrogen and nutrients: Belnap and Eldridge (2003) showed that Carbon and Nitrogen are fertilizers that increase the amount of chlorophyll a in cyanobacteria. This is consistent with the results of Zelikova et al. (2012), who observed an increase in cyanobacterial cover associated to a decrease in moss cover.

Maestre et al. (2013) found that biocrust cover and metabolism were significantly affected by a 2-3°C temperature increase, but not by a 30% reduction in precipitation although, as Ladron de Guevara et al. (2014) observed, the open-top-chambers used to increase temperature probably caused a decrease in dew, fog, and rain. Non-rainfall water inputs (NRWI) can be relevant for biocrust activity in drylands (del Prado and Sancho, 2007; McHugh et al., 2015). However, to date, there is not enough reliable NRWI data from our study area. Our highest net photosynthesis rates tended to coincide with rainfall periods (Figure 2). Therefore, a 30% reduction in precipitation may not be sufficient to observe short-term decreases in cover. This has not been widely studied in biocrust, but Miranda et al. (2009) found that a 25% reduction in precipitation did not significantly affect plant cover in the short term in the same area; however, a 50% reduction did. Desiccation tolerance is species specific (Green et al., 2011). We have not found data on desiccation tolerance of our main species, but many organisms are able to survive in latent state for drought periods longer than three years (Alpert, 2000). These organisms would not necessarily die or lose cover visibly under our experimental drought.

Effect of increased precipitation

The watering did not significantly increased biocrust cover over the short term (Figure 1). However, it increased net photosynthesis, in all crusts except in Lepraria, (although that increment was not significant in Cyanobacteria). Additionally, watering increased dark respiration in all, but particularly in lichen-dominated crusts (Figures 2 and 3). This is consistently with Lange (1980). The short periods of positive net photosynthesis in Cyanobacteria agree with Büdel et al (2018), who explained that the metabolic active period commences with up to three months of carbon loss, likely due to the reestablishment of the structures of the organisms, prior to about a four-month period of net carbon gain. In the Tabernas Desert, the period of net carbon gain seems to be still shorter than in the Australian Gulf Savannah.

The low increase in cover despite the increase in metabolism could be influenced by the small plot size (Rubio and Lázaro, 2024). However, the control samples did not show significant changes in cover (Figure 1) and it is unlikely that the ring affected only the watering samples. Therefore, we propose two not-exclusive explanations for the low cover increase with watering. (i) The experiment only lasted three years and, although cyanobacteria can grow rapidly, lichens and mosses develop more slowly (Dojani et al., 2011; Rubio and Lázaro, 2023), and their growth rate depends on the species and the environment (Belnap and Eldrige, 2001; Weber et al., 2016). (ii) Since we selected the plots based on their representativeness, they had low bare soil cover. Therefore, an increase in cover of a surface category had to occur mainly at the expense of the cover of another category, and it is unlikely that the competition between lichen and cyanobacteria covers would be resolved in such a short time.

Although we altered the annual timing of rainfall as little as possible by watering after each natural rain event, we could not avoid doubling the number of rainy days in the plots under watering. Regardless of the total amount of precipitation, changes in precipitation pattern can decrease CO_2 fluxes and cover in plants (Knapp et al., 2002) and the increased frequency of small rainfall events significantly decreased biocrust cover (Belnap et al., 2004; Reed et al., 2012); because with increased frequency each precipitation event is less abundant, facilitating water evaporation (Munzi et al., 2019). This can force biocrusts to remain in a desiccated state (William et al., 2014; Kranner et al., 2003; Proctor et al., 2007), and occasionally even to die (Reed et al., 2012). However, in this case an increase in number of raindays does not mean a decrease in rainfall volume per day. Moreover, this negative effect of the increased frequency of small events contrasts with the hypothesis of Lázaro et al. (2001) and Lázaro (2004) from our study area, suggesting that the higher frequency of small rainfall events with regard to the surrounding areas would selectively benefit biocrusts over vascular vegetation, explaining the abundance of biocrusts in this area. Nevertheless, both hypotheses are not mutually exclusive. Belnap et al. (2004) and Reed et al. (2012) investigated in the southwestern USA, where rainfall occurs mainly in summer, when water can evaporate quickly. In the southeast of Spain, rainfall occurs mainly in autumn and winter, when temperatures are lower and the soil remains wet for longer

The succession and the response to changes in precipitation

The successional hypothesis is widely accepted worldwide (Belnap and Eldridge, 2003; Büdel et al., 2009; Zhuang et al., 2009; Drahorad et al., 2013; Geng al., 2024), although not unanimously: Kidron (2019) and Kidron and Xiao (2024) claimed that succession can only be invoked when the successive communities in a recovery space are compared to surrounding ones. The successional hypothesis has been widely assumed in the Tabernas Desert (Lázaro et al., 2008; Chamizo et al., 2015; Miralles et al., 2020; Lopez-Canfin et al., 2022a, 2022b; Rubio and Lázaro, 2023; among others). Our results according to the crust type support this hypothesis; the successional order in the Tabernas Desert would be Physical, Incipient, Cyanobacteria, Squamarina, and Lepraria (Lázaro et al., 2023).

Incipient crust did not show significant cover losses under rain exclusion, maybe because its relatively frequent trampling provides it with greater adaptation to disturbances. Furthermore, Incipient' s net photosynthesis and respiration rates were like those of the Physical crust and lower than those of Cyanobacteria crust. These differences, along with the lower microbial biomass of Incipient (Miralles et al., 2020), its visibility to the naked eye in the field and its persistence over time in trampled places, foster the consideration of Incipient as a successional stage between the Physical and the Cyanobacteria crusts. Rain exclusion caused a decreasing cover loss through the hypothetic succession (50%, 30% and 20% in Cyanobacteria, Squamarina and Lepraria crusts, respectively). The early successional stages might be more sensitive to environmental changes because the later ones involve higher biodiversity and therefore larger functional redundancy, thus achieving greater resilience (Biggs et al., 2020). This growing resistance to cover loss is consistent with the fact that ecosystem services increase accompanying biocrust succession, according various empirical findings, such as decreasing erodibility along succession (Lazaro et al., 2023), increasing water collection and retention (Chamizo et al., 2016) and growing nutrient accumulation (Zhang al., 2022).

Ongoing climate change could reduce biocrust cover; however, this will not necessarily occur because climate change is slower than simulated in experiments and affects several generations of organisms, giving species the opportunity to acclimatize and even adapt (Pintado et al., 2005). The models indicate a progressive concentration and intensification of precipitation, with lengthening droughts (IPCC 2023). However, protecting at least the lichen-dominated biocrusts -the best at resisting droughts and providing ecosystem services- is crucial because, although biocrusts can resist high rainfall intensity (Lazaro et al., 2023), they are at serious risk with the intensification of land uses. Moreover, we have verified here that prolonged droughts indeed increase periods of negative carbon balance. On the other hand, a hypothetic substantial increase in natural precipitation would benefit vascular plants rather than biocrusts (Lazaro, 2004): This area is currently below the forest's lower climatic limit; with double the current rainfall, it would exceed this limit, and the vegetation would barely leave room for biocrusts.

Conclusions

Our results confirm our first initial hypothesis. Although biocrusts can survive long periods of drought, prolonged droughts reduced biocrust biomass by decreasing opportunities to reach the compensation point and accumulate carbon by net photosynthesis, whereas they increased periods of negative carbon balance, potentially causing a significant cover loss. However, this decline in cover will not necessarily occur in the long term because many of these species acclimatize or adapt, as their geographic distributions show. In the experiments, instant artificial climatic changes are often applied to specific individuals, which, in the case of lichens, are sets of symbionts that have organized and developed slowly in equilibrium with the environmental conditions that prevailed until the time of the experiment; so, the results could overestimate the effects of climate change. Moreover, climate change models do not predict years-long droughts in this region.

Our results show that increased rainfall would not necessarily imply increased biocrust cover in the long term, because the current biocrust cover is already high; additionally an increase in precipitation would favor the development of vascular vegetation, which ultimately would outcompete biocrusts, as can be observed in the regions surrounding the Tabernas Desert. This strongly suggests that the current precipitation conditions in the Tabernas Desert are close to being optimal for biocrusts to reach their maximum possible extension in the area.

Our results also show that biocrust's response to changes in precipitation depends on the biocrust type. Therefore, the analysis of these various responses is essential to better understand biocrust dynamics and the associated processes, as well as for issues of land management and conservation. Our results support the succession hypothesis. The development of lichens increases community resilience. Changes in biocrust cover as a consequence of rainfall changes appear muffled in the biocrust community hypothetically considered late-successional. Therefore, our results suggest that the dynamic relationships among biocrust types should be considered in future work at other field sites.

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Author Contribution statement

All authors contributed to the conception and design of the study. Roberto Lázaro and Clement López selected the plots and prepared the material, while all authors carried out data collection and analysis. Consuelo Rubio wrote the first draft of the manuscript and Roberto Lázaro and Clement López commented on later versions of the manuscript. All authors read and approved the final manuscript.

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Conflict of Interest statement

Conflicts of Interest: None

Data availability statement

The data that support the findings of this study are available from the corresponding author, R.L., upon reasonable request.

References

Alexander RW, Harvey AM, Calvo-Cases A, James PA, and Cerdá A (1994) Natural Stabilisation Mechanisms on Badland Slopes: Tabernas, Almería, Spain. In Environmental Change in Dylands: Biogeographical and Geomorphological Perspectives (eds. AC. Millington and K. Pye), pp 85-111. United Kingdom: Wiley.

Alpert P (2000) The discovery, scope, and puzzle of desiccation tolerance in plants. Plant Ecol **151,** 5–17

Aubert S, Juge C, Boisson A, Gout E and Bligny R (2007) Metabolic processes sustaining the reviviscence of lichen Xanthoria elegans (Link) in high mountain environments. Planta **226(5)**, 1287-1297.

Belnap J and Eldridge DJ (2003). Disturbance and recovery of biological soil crusts. In: Belnap J and Lange OI (Eds.) Biological Soil Crusts: Structure, Function and Management. Springer Verlag, Ecological Studies, 150, 363 – 383. Berlin – Heidelberg.

Belnap J, Phillips SL and Miller ME (2004) Response of desert biological soil crusts to alterations in precipitation frequency. Oecologia **141(2)**, 306-316.

Belnap J, Phillips SL and Troxler T (2006) Soil lichen and moss cover and species richness can be highly dynamic: The effects of invasion by the annual exotic grass Bromus tectorum, precipitation, and temperature on biological soil crusts in SE Utah. Applied Soil Ecology **32(1)**, 63-76.

Biggs CR, Yeager LA, Bolser DG, Bonsell C, Dichiera AM, Hou Z, Keyser SR, Khursigara AJ, Lu K, Muth AF, Negrete Jr. B, and Erisman BE (2020) Does functional redundancy affect ecological stability and resilience?A review and meta-analysis. Ecosphere **11(7)**:e03184.

Büdel B, Darienko T, Deutschewitz K, Dojani S, Friedl T, Mohr K and Weber B (2009). Southern African biological soil crusts are ubiquitous and highly diverse in drylands, being restricted by rainfall frequency. Microbiology Ecology, **57**, 229–247.

Büdel, B.; Colesie, C.; Green, T.A.; Grube, M.; Suau, R.L.; Loewen-Schneider, K.; Maier, S.; Peer, T.; Pintado, A.; Raggio, J.; et al. Improved appreciation of the functioning and importance of biological soil crusts in Europe: The Soil Crust International Project (SCIN). *Biodivers. Conserv.* **2014**, *23*, 1639–1658,

Büdel B, Williams WJ and Reichenberger H (2018): Annual net primary productivity of a cyanobacteria-dominated biological soil crust in the Gulf Savannah, Queensland, Australia, Biogeosciences, **15**, 491–505, Chamizo S, Cantón Y, Miralles I and Domingo F (2012) Biological soil crust development affects physicochemical characteristics of soil surface in semiarid ecosystems. Soil Biology & Biochemistry **49**, 96-105.

Chamizo S, Rodríguez-Caballero E, Cantón Y, Asensio C and Domingo F (2015) Penetration resistance of biological soil crusts and its dynamics after crust removal: Relationships with runoff and soil detachment. Catena, **126,** 164-172

Chamizo S, Belnap J, Eldridge DJ, Canton Y, Malam Isa O 2016 The role of biocrusts in arid land hydrology. In Weber B et al (Eds) Biological soil crusts: An organizing principle in drylands. Springer, Ecological Studies 226, 321-346.

Chamizo S, Rodríguez-Caballero E, Román JR and Cantón Y (2017) Effects of biocrust on soil erosion and organic carbon losses under natural rainfall. Catena **148**, 117-125.

Del Prado R and Sancho LG (2007) Dew as a key factor for the distribution pattern of the lichen species Teloschistes lacunosus in the Tabernas Desert (Spain). Flora **202(5)**, 417-428.

Dojani S, Büdel B, Deutschewitz K and Weber B (2011) Rapid succession of Biological Soil Crusts after experimental disturbance in the Succulent Karoo, South Africa. Applied Soil Ecology **48(3)**, 263-269.

Drahorad SL, Steckenmesser D, Henningsen PF, Lichner L and Rodný M (2013) Ongoing succession of biological soil crusts increases water repellency – a case study on Arenosols in Sekule, Slovakia. Biologia **68/6**, 1089—1093

Farrar JF (1976) Ecological physiology of the lichen H*ypogymnia physodes*. New Phytologist **77(1)**, 105-113.

Geng Y, Zhou P, Wang Z, Peng C, Li G and Li D (2024). The roles of rare and abundant microbial species in the primary succession of biological soil crusts are differentiated in metal tailings ponds with different states. Journal of Hazardous Materials, **472**, 134577

GIMP Development Team (2023) GIMP (Version 2.10.34) [Software].

Green TGA, Sancho LG and Pintado A (2011) Ecophysiology of Desiccation/Rehydration Cycles in Mosses and Lichens. In Plant Desiccation Tolerance, (eds. U. Lüttge, E. Beck, D. Bartels), pp. 89-120. Berlin: Springer.

Harel Y, Ohad I and Kaplan A (2004) Activation of Photosynthesis and Resistance to Photoinhibition in Cyanobacteria within Biological Desert Crust. Plant Physiology **136(2)**, 3070-3079.

Heber U and Lüttge U (2011) Lichens and Bryophytes: Light Stress and Photoinhibition in Desiccation/Rehydration Cycles – Mechanisms of Photoprotection. In Plant Desiccation Tolerance, (eds. U. Lüttge, E. Beck, D. Bartels), pp. 121-137. Berlin: Springer. Hoekstra FA and Golovina EA (2002) The role of amphiphiles. Comparative Biochemistry and Physiology. Part A, Molecular & Integrative Physiology **131(3)**, 527-533.

Hoekstra FA, Golovina EA and Buitink J (2001) Mechanisms of plant desiccation tolerance. Trends In Plant Science **6(9)**, 431-438.

IPCC (2023) Summary for Policymakers. In: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland, pp. 1-34

Johnson SL, Kuske CR, Carney TD, Housman DC, Gallegos-Graves LV and Belnap J (2012) Increased temperature and altered summer precipitation have differential effects on biological soil crusts in a dryland ecosystem. Global Change Biology **18(8)**, 2583-2593.

Kappen L and Valladares F (2007) Opportunistic Growth and Desiccation Tolerance: The Ecological Success of Poikilohydrous Autotrophs. In Functional Plant Ecology, (eds. F. Pugnaire, F. Valladares), pp. 7-66. Florida: CRC Press.

Kidron GJ, Vonshak A, Dor I, Barinova S, Abeliovich A (2010) Properties and spatial distribution of microbiotic crusts in the Negev Desert, Israel. Catena, **82**, 92-101

Kidron GJ, Ying W, Starinsky A, Herzberg M (2017) Drought effect on biocrust resilience: High-speed winds result in crust burial and crust rupture and flaking. STOTEN, **579**, 848-859

Kidron GJ (2019). Biocrust research: A critical view on eight common hydrological-related paradigms and dubious theses. Ecohydrology, **12**, e2061.

Kidron GJ and Xiao B (2024) A false paradigm? Do biocrust types necessarily reflect ‘successional stages’? Ecohydrology, **17**(1), e2610.

Knapp AK, Fay PA, Blair JM, Collins SL, Smith MD, Carlisle JD, Harper CW, Danner BT, Lett MS and McCarron JK (2002) Rainfall Variability, Carbon Cycling, and Plant Species Diversity in a Mesic Grassland. Science **297**, 2202-2205.

Kranner I (2002) Glutathione status correlates with different degrees of desiccation tolerance in three lichens. New Phytologist **154(2)**, 451-460.

Kranner I, Zorn M, Turk B, Wornik S, Beckett RP and Batič F (2003) Biochemical traits of lichens differing in relative desiccation tolerance. New Phytologist **160(1)**, 167-176.

Kranner I, Beckett R, Hochman A and Nash TH (2008) Desiccation-Tolerance in Lichens: A Review. The Bryologist **111(4)**, 576-593.

Ladrón de Guevara M, Lázaro R, Quero JL, Chamizo S and Domingo F (2015) Easy-to-make portable chamber for in situ CO_2 exchange measurements on biological soil crusts. Photosynthetica **53(1)**, 72-84.

Ladrón de Guevara M, Lázaro R, Quero JL, Ochoa V, Gozalo B, Berdugo M, Uclés O, Escolar C and Maestre FT (2014) Simulated climate change reduced the capacity of lichen-dominated biocrusts to act as carbon sinks in two semi-arid Mediterranean ecosystems. Biodiversity And Conservation **23(7)**, 1787-1807.

Lange OL (1980) Moisture Content and CO2 Exchange of Lichens. I. Influence of Temperature on Moisture-Dependent Net Photosynthesis and Dark Respiration in Ramalina maciformis. Oecologia (Berl.) **45**, 82-87

Lázaro R (2004) Implications of precipitation on vegetation of water-limited lands. In Recent Research Development in Environmental Biology, (ed. S.G. Pandalai), pp. 553-591. Kerala: Research Signpost.

Lázaro R, Cantón Y, Solé-Benet A, Bevan J, Alexander R, Sancho L and Puigdefábregas J (2008) The influence of competition between lichen colonization and erosion on the evolution of soil surfaces in the Tabernas badlands (SE Spain) and its landscape effects. Geomorphology **102(2)**, 252-266.

Lázaro R, Rodriguez-Tamayo ML, Ordiales R, Puigdefábregas J (2004) El Clima. In Subdesiertos de Almería: Naturaleza de cine, (eds. J. Moya, J. Cabello, MI Cerillo, ML Rodriguez-Tamayo), pp. 63-79. Andalucia: Junta de Andalucia.

Lázaro R, Gascón C and Rubio C (2023) Runoff and soil loss in biocrusts and physical crusts from the Tabernas Desert (southeast Spain) according to rainfall intensity. Frontiers in Microbiology **14**, 1171096.

Lázaro R, Rodrigo F, Gutiérrez L, Domingo F and Puigdefábregas J (2001) Analysis of a 30-year rainfall record (1967–1997) in semi–arid SE Spain for implications on vegetation. Journal Of Arid Environments **48(3)**, 373-395.

Li X, Hui R, Zhang P and Song N (2021) Divergent responses of moss- and lichen-dominated biocrusts to warming and increased drought in arid desert regions. Agricultural And Forest Meteorology **303**, 108387.

Lopez-Canfin C, Lázaro R and Sánchez-Cañete EP (2022a). Disparate responses of soil-atmosphere CO_2 exchange to biophysical and geochemical factors over a biocrust ecological succession in the Tabernas Desert. Geoderma, **425**, 116067.

Lopez-Canfin C, Lázaro R and Sánchez-Cañete EP (2022b) Water vapor adsorption by dry soils: A potential link between the water and carbon cycles. Science of the Total Environment, **824**, 153746.

Maestre FT, Eldridge DJ, Soliveres S, Kéfi S, Delgado-Baquerizo M, Bowker MA, García-Palacios P, Gaitán J, Gallardo A, Lázaro R and Berdugo M (2016) Structure and Functioning of Dryland Ecosystems in a Changing World. Annual Review Of Ecology, Evolution, And Systematics **47(1)**, 215-237.

Maestre FT, Escolar C, De Guevara ML, Quero JL, Lázaro R, Delgado-Baquerizo M, Ochoa V, Berdugo M, Gozalo B and Gallardo A (2013) Changes in biocrust cover drive carbon cycle responses to climate change in drylands. Global Change Biology **19(12)**, 3835-3847.

McHugh TA, Morrissey EM, Reed SC, Hungate BA and Schwartz E (2015) Water from air: an overlooked source of moisture in arid and semiarid regions. Scientific Reports **5(1), 13767**.

Miralles I, Lázaro R, Sánchez-Marañón M, Soriano M and Ortega R (2020) Biocrust cover and successional stages influence soil bacterial composition and diversity in semiarid ecosystems. Science Of The Total Environment **709**, 134654.

Miranda JD, Padilla FM, Lázaro R, Pugnaire FI (2009) Do changes in rainfall patterns affect semiarid annual plant communities? Journal of Vegetation Science **20**, 269-276.

Munzi S, Varela Z and Paoli L (2019) Is the length of the drying period critical for photosynthesis reactivation in lichen and moss components of biological soil crusts? Journal Of Arid Environments **166**, 86-90.

Oliver MJ and Goffinet B (2008) Biochemical and molecular mechanisms of desiccation tolerance in bryophytes. In Bryophyte Biology, (ed. A.J. Shaw), pp. 269-298. Cambridge: Cambridge University Press.

Pintado A, Sancho LG, Green TGA, Blanquer JM and Lázaro R (2005) Functional ecology of the biological soil crust in semiarid SE Spain: sun and shade populations of *Diploschistes diacapsis* (Ach.) Lumbsch. Lichenologist, **37(5),** 425-432

Proctor MCF, Oliver MJ, Wood AJ, Alpert P, Stark LR, Cleavitt NL and Mishler BD (2007) Desiccation-tolerance in bryophytes: A review. The Bryologist **110**, 595-621.

Raggio J, Pintado A, Vivas M, Sancho LG, Büdel B, Colesie C, Weber B, Schroeter B, Lázaro R and Green TGA (2014) Continuous chlorophyll fluorescence, gas exchange and microclimate monitoring in a natural soil crust habitat in Tabernas badlands, Almería, Spain: progressing towards a model to understand productivity. Biodiversity And Conservation **23(7)**, 1809-1826.

Reed SC, Coe KK, Sparks JP, Housman DC, Zelikova TJ and Belnap J (2012) Changes to dryland rainfall result in rapid moss mortality and altered soil fertility. Nature Climate Change **2(10)**, 752-755.

Rodríguez-Caballero E, Cantón Y, Chamizo S, Lázaro R and Escudero A (2013) Soil Loss and Runoff in Semiarid Ecosystems: A Complex Interaction Between Biological Soil Crusts, Micro-topography, and Hydrological Drivers. Ecosystems **16(4)**, 529-546.

Roncero-Ramos, B.; Muñoz-Martín, M.A.; Chamizo, S.; Fernández-Valvuena, L.; Mendoza, D.; Perona, E.; Cantón, Y.; Mateo, P. Polyphasic evaluation of key cyanobacteria in biocrusts from the most arid region in Europe. *Peer J.* **2019**, *7*, e6169.

Rubio C and Lázaro R (2023) Patterns in biocrust recovery over time in semiarid southeast Spain. Frontiers In Microbiology **14**, 1184065.

Rubio C and Lazaro R (2024) Surface instability driven by wetting-drying cycles hinders the colonization by biocrusts in Tabernas Desert. Biologia https://doi.org/10.1007/s11756-024-01792-5.

Weber B, Bowker M, Zhang Y and Belnap J (2016) Natural Recovery of Biological Soil Crusts After Disturbance. In Biological Soil Crusts: An Organizing Principle in Drylands, (eds. B. Weber, B. Büdel, J. Belnap), pp. 479-498. Switzerland: Springer.

Williams WJ, Büdel B, Reichenberger H and Rose N (2014) Cyanobacteria in the Australian northern savannah detect the difference between intermittent dry season and wet season rain. Biodiversity And Conservation **23(7)**, 1827-1844.

Zhang Y, Gao M, Yu C, Zhang H, Yan N, Wu Q, Song Y and Li X (2022) Soil nutrients, enzyme activities, and microbial communities differ among biocrust types and soil layers in a degraded karst ecosystem. Catena, **212**, 106057.

Zelikova TJ, Housman DC, Grote EE, Neher DA and Belnap J (2012) Warming and increased precipitation frequency on the Colorado Plateau: implications for biological soil crusts and soil processes. Plant And Soil **355(1-2)**, 265-282.

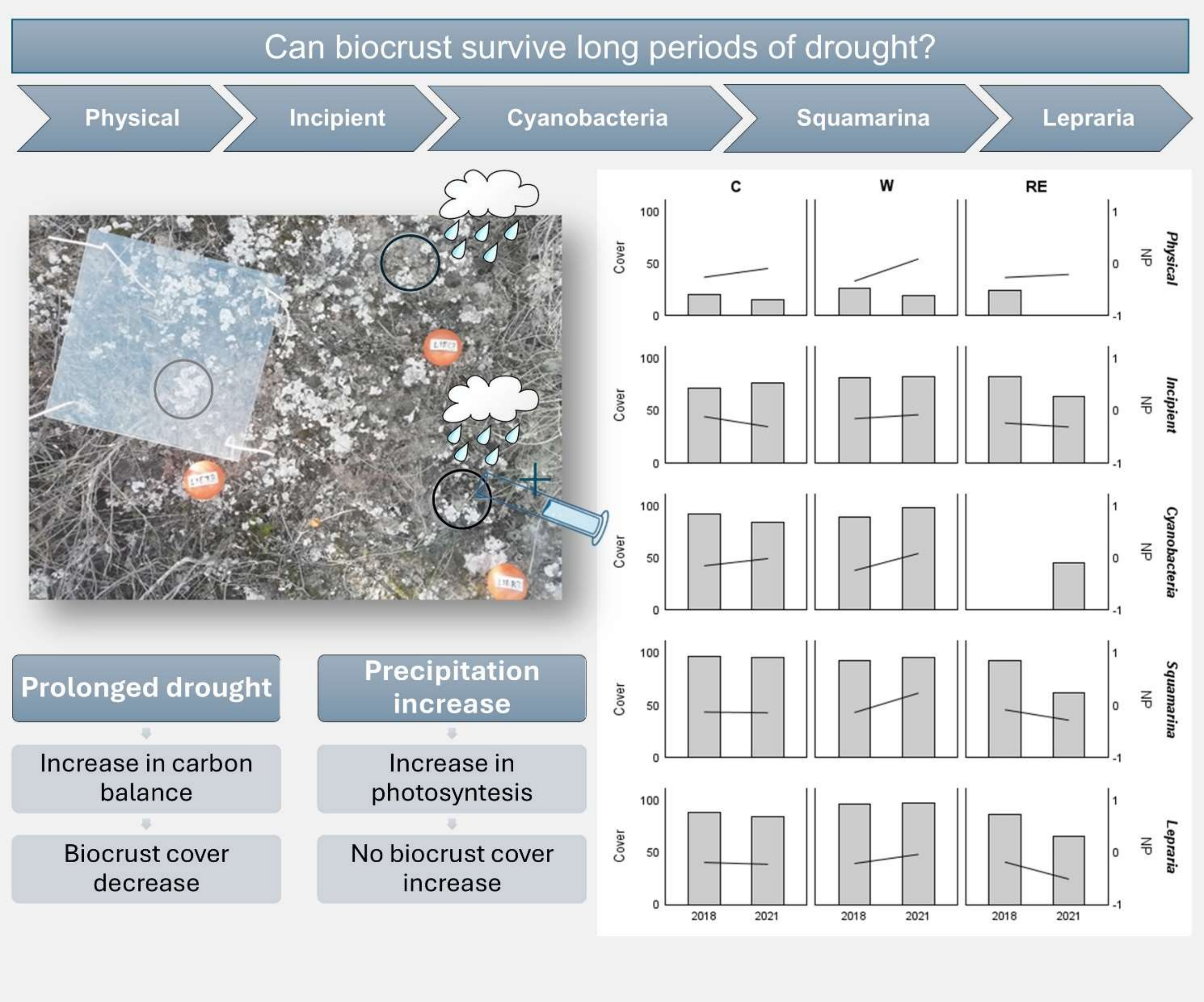
Zhuang B, Zhang Y, Zhao J, Wu N, Chen R and Zhang J (2009) Microalgal species variation at different successional stages in biological soil crusts of the Gurbantunggut Desert, Northwestern China. Biology and Fertility of Soils, **45**, 539–547.

Table with caption

Table 1. F-values in the results of GLMM analyses for cover of biocrust principal components (bare soil, cyanobacteria, lichens and mosses) and metabolism rates (net photosynthesis, dark respiration), and results of GLM analyses for Chlorophyll a fluorescence. * indicates the significant effects (p-value < .05).

	Crust	Treatment	Time	Time x Treatment	Crust x Treatment	Time x Crust x Treatment
Cover						
Bare	112.88*	32.37*	14.61*	43.57*	5.81*	6.00*
Cyanobacteria	50.03*	5.67*	6.76*	6.03*	1.33	1.76
Lichen	141.36*	9.88*	0.81	14.41*	3.21*	2.80*
Moss	1.12	0.16	4.34*	0.30	0.58	0.53
Metabolism						
Net photosynthesis	14.45*	7.58*	22.73*	8.42*	2.43*	4.08*
Dark respiration	52.56*	76.26*	46.41*	5.61*	5.59*	5.23*
Chlorophyll *a* fluorescence	230.057*	186.788*			123.924*	

Graphic Abstract



Can biocrust survive long periods of drought?

Physical → Incipient → Cyanobacteria → Squamarina → Lepraria

Prolonged drought

Increase in carbon balance

Biocrust cover decrease

Precipitation increase

Increase in photosyntesis

No biocrust cover increase

Figure captions

Figure 1. Cover of bare soil, cyanobacteria, lichens and mosses of each treatment, at the beginning (2018) and at the end (2021) of the experiment in each of the crust types (Physical, Incipient, Cyanobacteria, Squamarina and Lepraria). The bars represent the averages, and error bars represent the average ± 95% confidence level. * indicates significant differences (p < .05) based on the Bonferroni test.

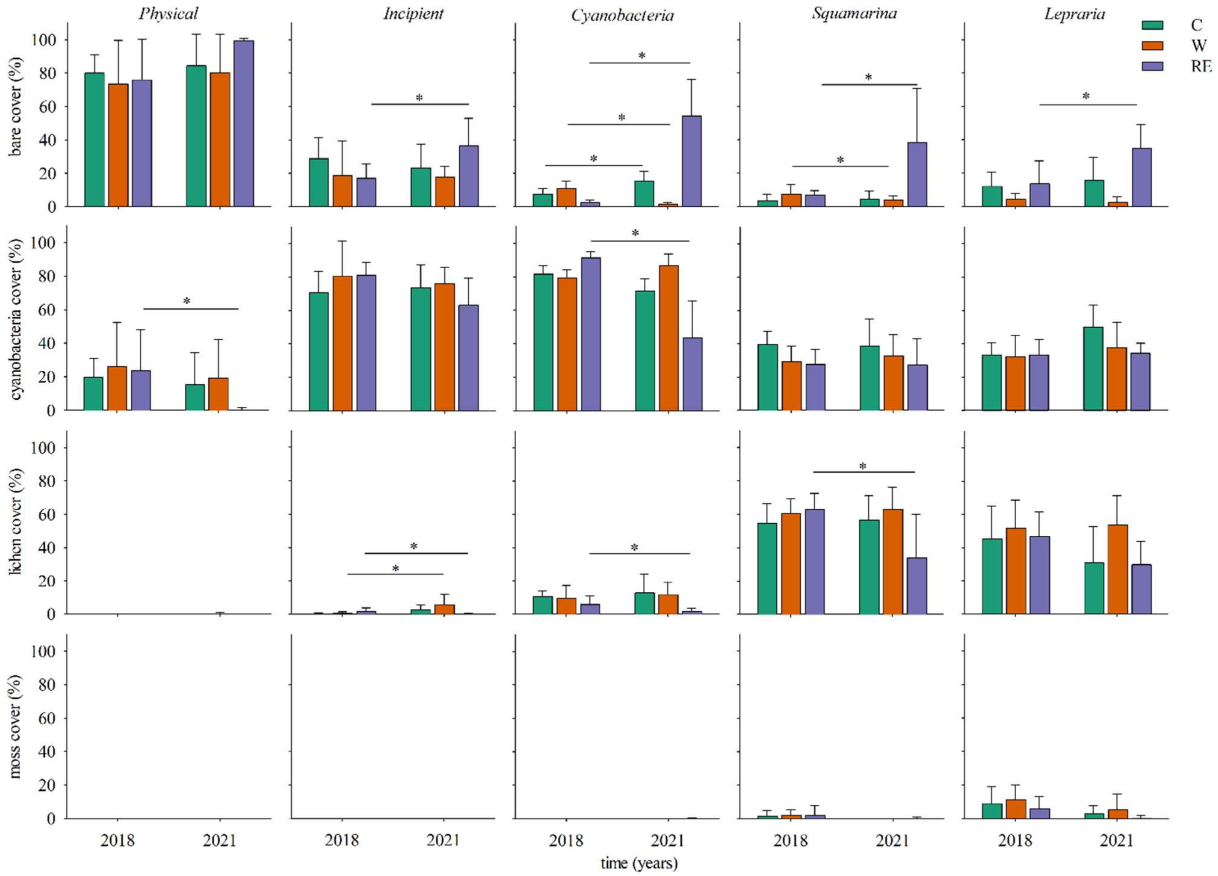


Figure 2. Evolution of net photosynthesis (with regression lines) per treatment and crust type in relation to the rainfall from the climate station representative of each crust type. Symbols represent the averages, and error bars represent the average ± 95% confidence level. In the legend of each graph at the upper left corner, C means control, W means watering treatment and RE means rain exclusion. The superscript letters in these treatment symbols indicate whether the differences between treatments are significant (two treatments are different if they do not share any letters)

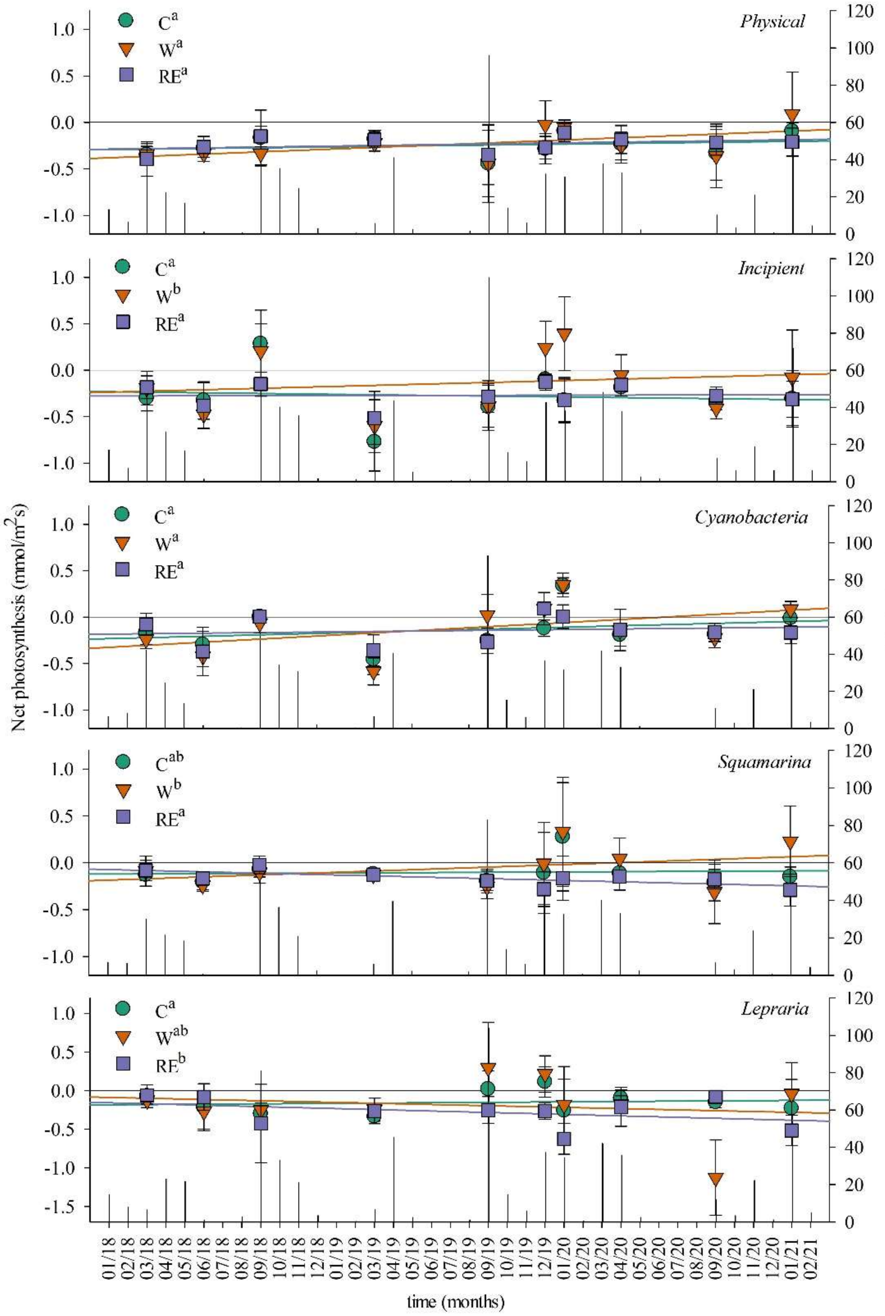
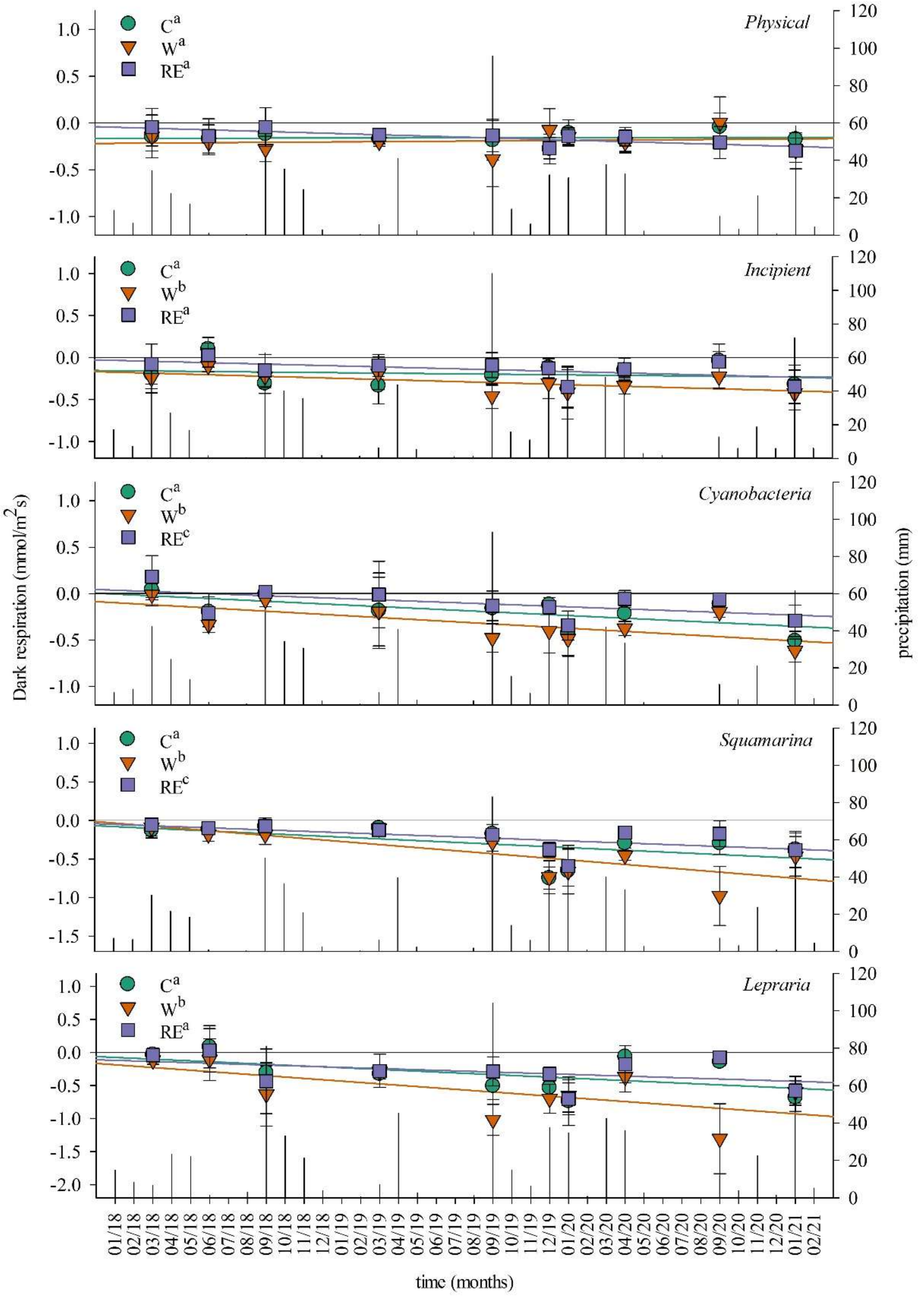
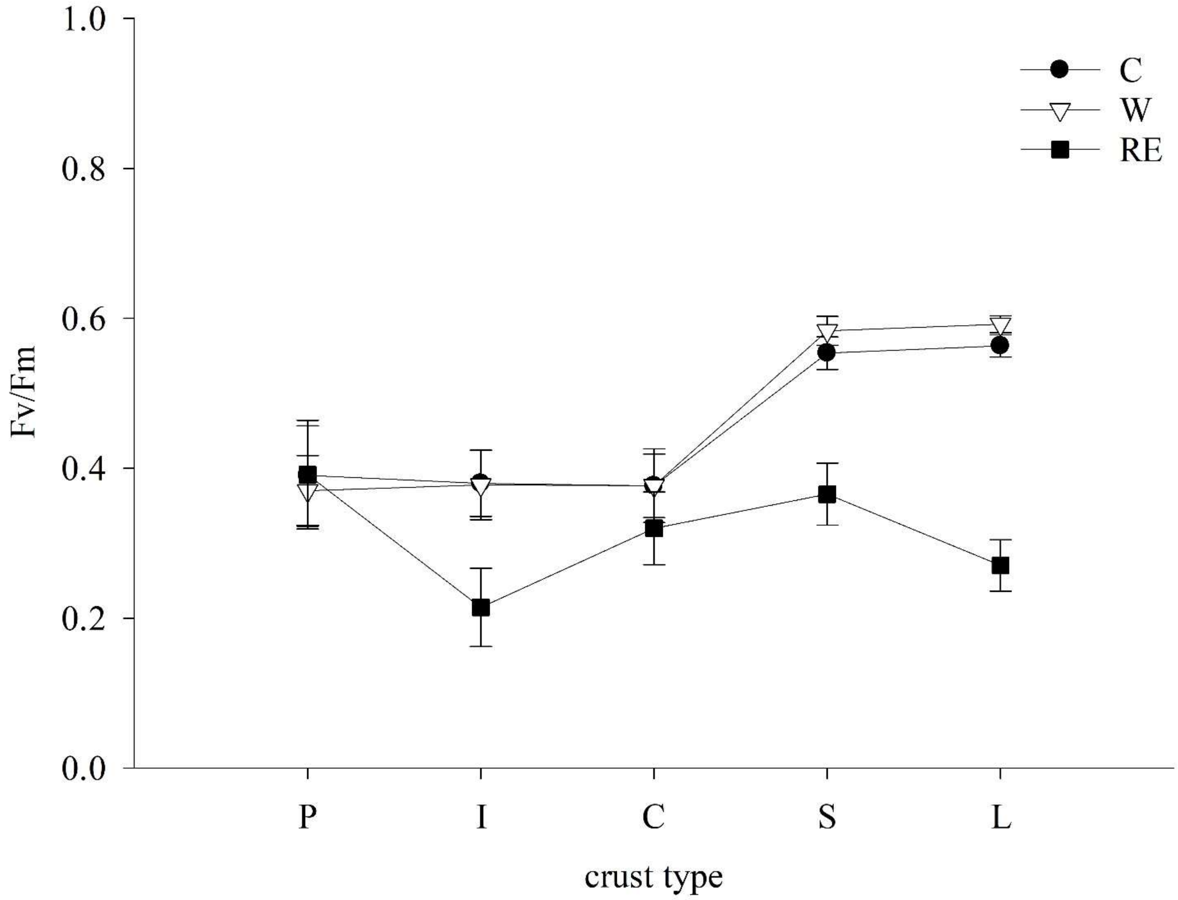


Figure 3 Evolution of dark respiration (with regression lines) per treatment and crust type in relation to the rainfall from the climate station representative of each crust type. Symbols represent the averages, and error bars represent the average ± 95% confidence level. In the legend of each graph at the upper left corner, C means control, W means watering treatment and RE means rain exclusion. The superscript letters in these treatment symbols indicate whether the differences between treatments are significant (two treatments are different if they do not share any letters)



604 **Figure 4**. Comparison of chlorophyll *a* fluorescence of each treatment in each crust type. Symbols represent the averages, and error bars represent the average ± 95% confidence level. P = Physical crust; I = Incipient crust; C = Cyanobacteria crust; S = Squamarina crust; L = Lepraria crust. In the legend at the upper right corner, C means control, W means watering treatment and RE means rain exclusion.



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