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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 higher in lichens; under watering, it was not different from the control but decreased under rain exclusion.

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 reactivate 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 of the multiple ecological functions they perform. 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 effects 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 provides 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 and 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 °C 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 the 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 3 years of continuous drought was also recorded. We studied five crust types hypothetically representative of successional stages (according to Lázaro 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 °C, which can reach 45 °C in summer and −5.5 °C 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 crust 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 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 cartilaginea* 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 included the following three 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, 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 and a new record was taken 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 3 years of experimentation: two annual (winter and summer) and some additional ones after heavy rainfall events. Because biocrust 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 only a few cover categories, the error can be assumed to be acceptable. We could not monitor the chlorophyll to avoid disturbing the small plots through successive sampling, 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 the surface horizon (about 4 mm). We distinguished physical crust, incipient and mature cyanobacteria, mosses and the main lichen species. A hard grid of 11 × 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 on the same 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 species and crust types that appeared in at least 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 using the data from the nearest rain gauge based on the regression between the two 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 6 h.

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 were 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 3-year experiment, treatment and crust type significantly affected the cover of all the components, except for moss (Table 1).

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 and dark respiration), and results of GLM analyses for chlorophyll *a* fluorescence

Cover	Crust	Treatment	Time	Time × Treatment	Crust × Treatment	Time × Crust × Treatment
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*	

Note: * indicates the significant effects (p-value < .05).

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.

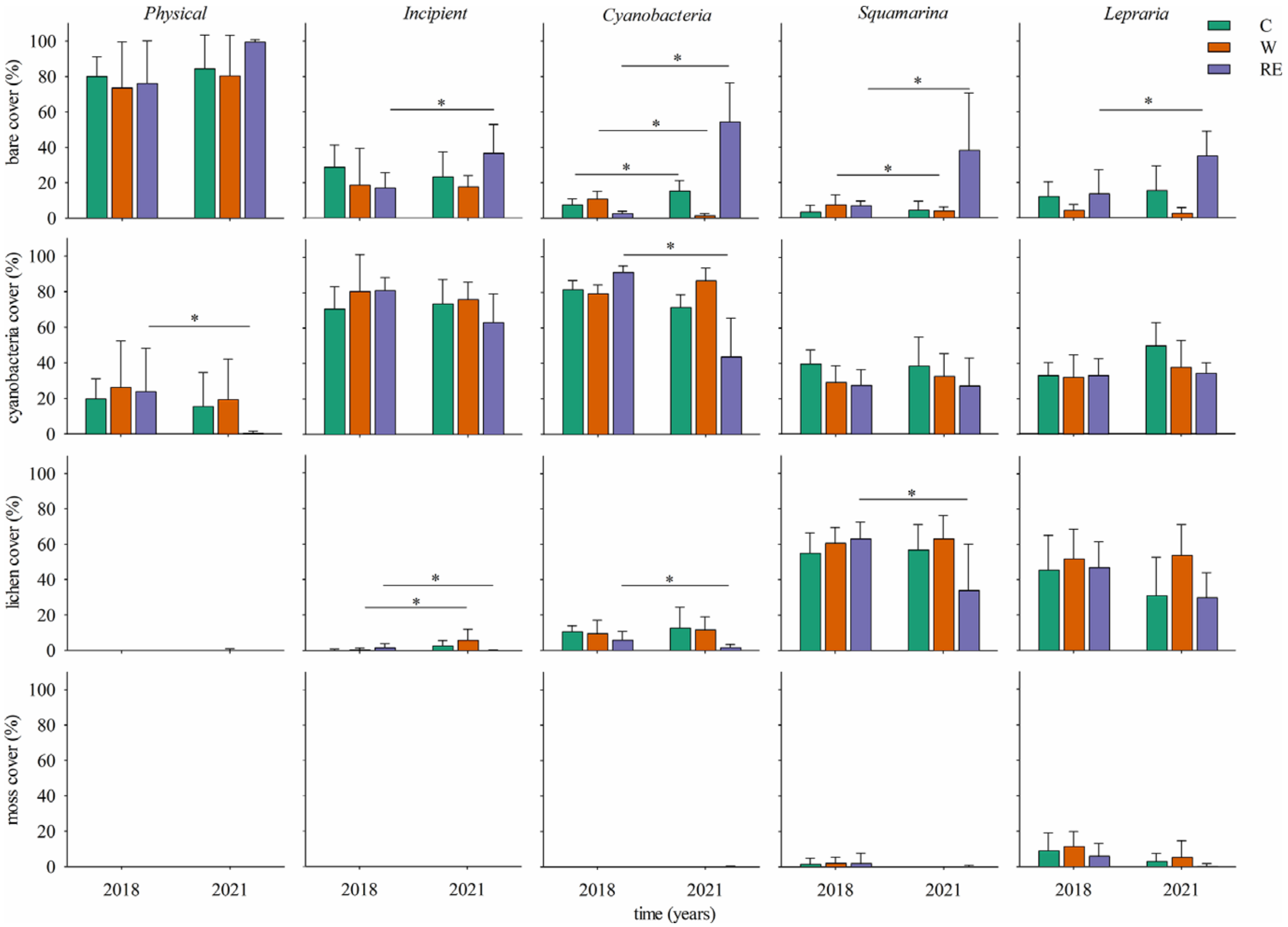

Figure 1. Cover of bare soil, cyanobacteria, lichens and mosses of each treatment, at the beginning (2018) and at the end (2021) of the experiment in each of the crust types (Physical, Incipient, Cyanobacteria, Squamarina and Lepraria). The bars represent the averages and error bars represent the average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

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 the Squamarina crust (where it decreased by 29%; however, its decline in the 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 and 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 3 years (Figures 2 and 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 3 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 was significantly higher than that 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, with different effects depending on 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 Cyanobacterial 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 the 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 with 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

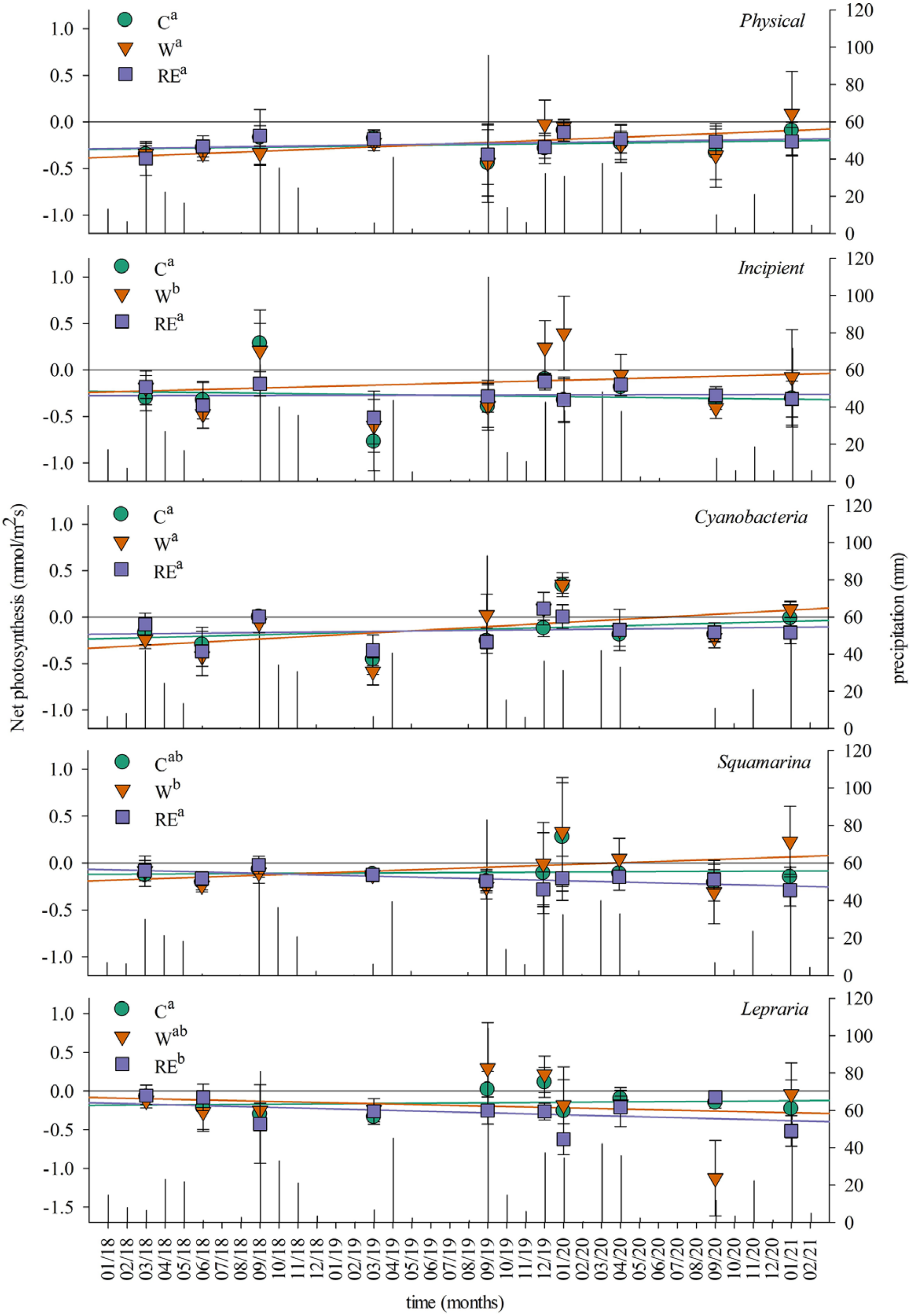

Figure 2. Evolution of net photosynthesis (with regression lines) per treatment and crust type in relation to the rainfall from the climate station representative of each crust type. Symbols represent the averages, and error bars represent the average ± 95% confidence level. In the legend of each graph 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).

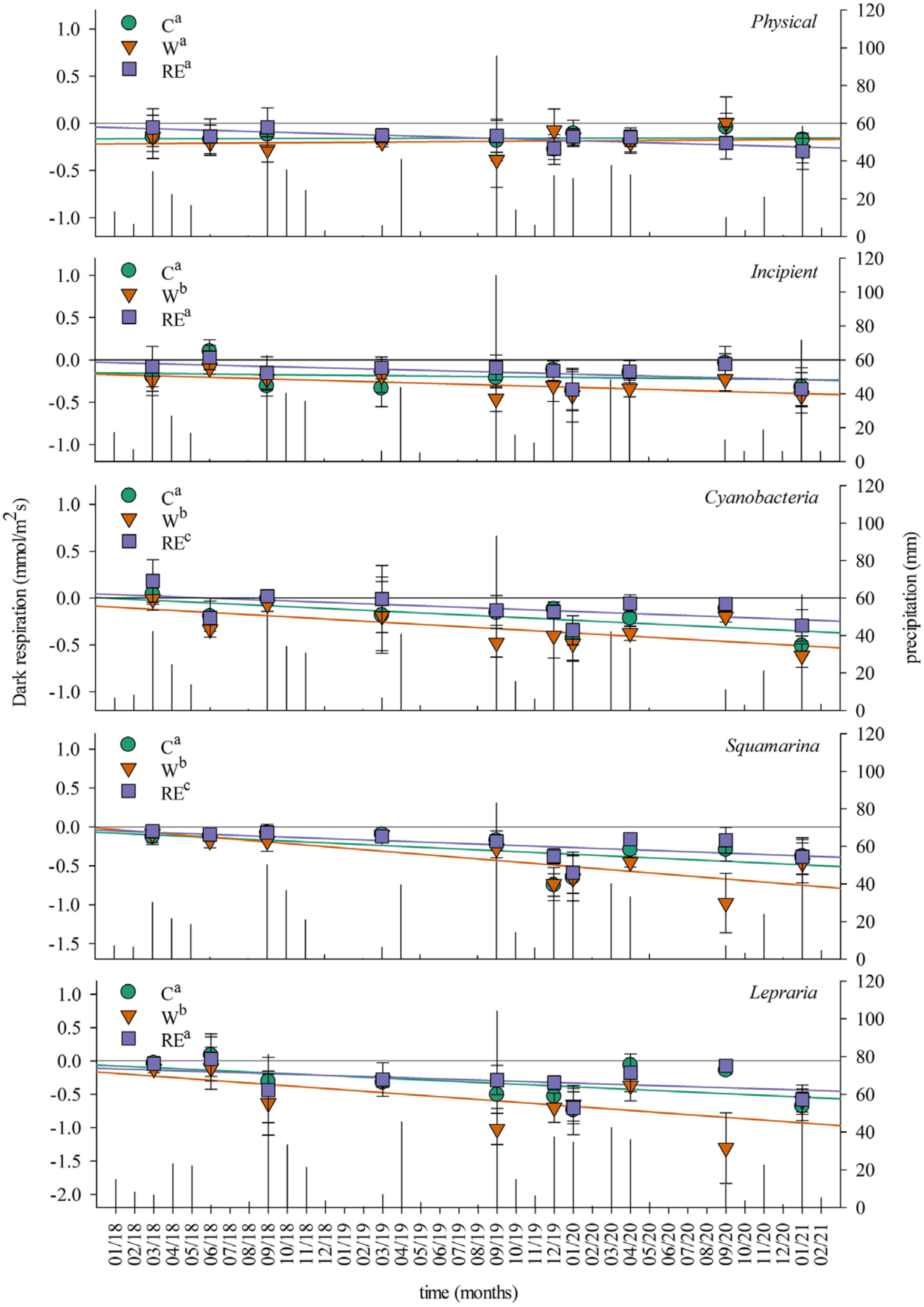

Figure 3. Evolution of dark respiration (with regression lines) per treatment and crust type in relation to the rainfall from the climate station representative of each crust type. Symbols represent the averages, and error bars represent the average ± 95% confidence level. In the legend of each graph 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).

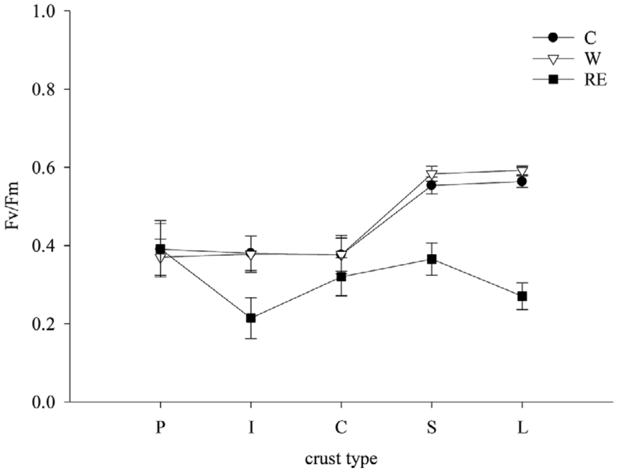

Figure 4. Comparison of chlorophyll *a* fluorescence of each treatment in each crust type. Symbols represent the averages and error bars represent the average ± 95% confidence level. P, Physical crust; I, Incipient crust; C, Cyanobacteria crust; S, Squamarina crust; L, Lepraria crust. In the legend at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

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 the desiccation tolerance of our main species, but many organisms are able to survive in a latent state for drought periods longer than 3 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 increase 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 consistent 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 3 months of carbon loss, likely due to the reestablishment of the structures of the organisms, prior to about a 4-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. (a) The experiment only lasted 3 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); (b) Since we selected the plots based on their representativeness, they had low bare-soil cover. Therefore, an increase in the 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 cyanobacterial 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 patterns 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 (Williams 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 the number of rain days 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 et 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 the Cyanobacterial 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 Cyanobacterial crusts. Rain exclusion caused a decreasing cover loss through the pothetical 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, higher 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 to various empirical findings, such as decreasing erodibility along succession (Lázaro et al., 2023), increasing water collection and retention (Chamizo et al., 2016) and growing nutrient accumulation (Zhang et 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 (Lázaro et al., 2023), they are at serious risk with the intensification of land use. Moreover, we have verified here that prolonged droughts indeed increase periods of negative carbon balance. On the other hand, a hypothetical substantial increase in natural precipitation would benefit vascular plants rather than biocrusts (Lázaro, 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 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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Data availability statement. The data that support the findings of this study are available from the corresponding author, R.L., upon reasonable request.

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Author contribution. 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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