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Soil CO₂ exchange controlled by the interaction of biocrust successional stage and environmental variables in two semiarid ecosystems



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ABSTRACT

Biocrusts are a critical biological community that represents one of the most important photosynthetic biomass pools in dryland regions. Thus, they play an important role in CO_2 fluxes in these regions, where water availability limits vascular plant growth and development. The effect of biocrusts on CO_2 fluxes was expected to be controlled by the interplay of several environmental factors, as well as biocrust developmental stage and coverage. To test this hypothesis, we performed an *in situ* study during which we measured net CO_2 fluxes and dark respiration over biocrusted soils at different successional stages in two semiarid ecosystems, where biocrusts are one of the main surface components. In addition, CO_2 flux was measured in annual plants, which were an abundant interplant cover in one of the study sites during the measurement period. Field campaigns were conducted from early morning to dusk on selected days with different environmental conditions over the year. Gross photosynthesis was calculated from net CO_2 flux and dark respiration.

Biocrusts showed contrasting responses in CO₂ exchange depending on environmental conditions during the day and the year and depending on biocrust developmental stage. CO2 flux in biocrusts was highly correlated with soil moisture, but also with photosynthetically active radiation and temperature. During dry soil periods, soils colonized by biocrusts had net CO₂ fluxes close to zero, but after precipitation events (light or heavy) all the biocrust types began to photosynthesize. When the rainfall was right after an extended drought, the respiration by biocrusts themselves and underlying soil exceeded the biocrust gross photosynthesis, and consequently soils colonized by biocrusts behaved as CO₂ sources. On the contrary, consecutive precipitation events and mild temperatures caused soil colonization by biocrusts to behave as CO₂ sinks. Annual plants were measured during their senescence and acted as CO₂ sources during all measurement campaigns. The time of day when the biocrusts showed net CO₂ fixation depended on the interplay of humidity just above them, air temperature and photosynthetically active radiation. The biocrust type also significantly influenced CO₂ fluxes in both semiarid ecosystems. In general, during wet periods, late successional biocrusts (i.e. lichens and mosses) had higher gross photosynthesis than early successional biocrusts (developed and incipient cyanobacteria crusts). Nevertheless, dark respiration from late successional biocrusts and underlying soils was also higher than from early successional biocrusts, so both biocrust types had similar net CO₂ fluxes. These results highlight the importance of considering the whole soil profile under biocrusts with their associated microbial communities as well as the temporal variability of CO₂ fluxes in soils covered by biocrusts in carbon balance studies in semiarid regions.

1. Introduction

 CO_2 exchange between the soil and the atmosphere and its controlling mechanisms have been less studied in drylands than in other ecosystems, such as the humid tropics or Arctic regions (Wohlfahrt et al., 2008; Schulze et al., 2009; Schimel, 2010). The traditionally low importance attributed to the global C-cycle in these areas may be due to the perception that such ecosystems, composed of scarce and patchy vegetation along with bare soil surfaces, may have negligible net CO_2 fixation rates compared to other biomes. However, in these ecosystems,

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a relevant fraction of their soil (up to 70%) is colonized by a complex community of cyanobacteria, bacteria, green algae, microfungi, lichens and bryophytes (Weber et al., 2016) known as biocrusts. These biological communities are considered one of the main sources of soil organic carbon (SOC) in drylands (Belnap et al., 2003; Housman et al., 2006; Mager, 2010; Mager and Thomas, 2011; Miralles et al., 2012a, 2013; Gypser et al., 2015), and they are play an important role in the global C-cycle (Rodríguez-Caballero et al., 2018). Biocrusts have an important photosynthetic potential, as they are able to achieve net photosynthesis rates of 11.5 µmol CO₂ m⁻²s⁻¹ under optimal conditions, which is very similar to the rates of some higher plants (Lange, 2003).

In drylands, daily and seasonal CO₂ exchange patterns of biocrust communities and the underlying soil layer show wide variability (Wilske et al., 2008; Pintado et al., 2010; Ladrón de Guevara et al., 2014), because they are strongly influenced by the interplay of several factors, such as temperature, CO2 concentration, radiation and specially, water availability (Lange et al., 2001; Housman et al., 2006; Grote et al., 2010; Su et al., 2012; Li et al., 2012; Feng et al., 2014). Biocrusts are poikilohydric organisms able to rapidly respond to erratic rainfall of less than 1 mm, and some species even to dew, fog and high air humidity (Lange et al., 2001; Burgheimer et al., 2006; Wilske et al., 2008; Büdel et al., 2013; Huang et al., 2014). Once wetted, biocrusts recover from metabolic dormancy immediately, losing C by respiration, which can be much higher (for example, in lichens one to three times higher) than their stabilized rates, depending on previous water content and the length of dry spells (Smith and Molesworth, 1973; Kappen and Valladares, 1999; Alpert and Oliver, 2002; Grote et al., 2010). If the biocrust remains hydrated long enough to overcome this initial loss, they are able to fix C. Therefore, not only length and intensity of rainfall, but also water inputs from other sources, such as fog and dew and other environmental variables, as well as antecedent soil moisture conditions, affect the length of the hydration period and are important variables for biocrust CO2 exchange (Grote et al., 2010; Evans and Lange, 2003; Lange, 2003; Kidron et al., 2009, 2015).

Biocrust development stage and type and abundance of the species present in it are also essential ecological factors affecting CO₂ flux variability. Later-stage biocrusts usually have higher photosynthetic rates (Zaady et al., 2000; Su et al., 2011; Kidron et al., 2015), but even within successional groups, the relationships between CO₂ exchange and environmental variables may differ between species. For example, the C fixation that lichen-dominated biocrusts can achieve at any given moisture level and hydration period depends on many factors intrinsic to the species, such as structure, colour, or thermal properties of the lichens (Lange et al., 1994). Moreover, biocrusts are able to develop strategies that enable them to adapt to microniches with specific environmental conditions through species-specific mechanisms (Miralles et al., 2012b, 2017). This allows, for example, that the seasonal temperature ranges during which net photosynthetic optima occur vary from one population of the same species to another (Brown and Kershaw, 1984). In addition, soil characteristics could have an important effect on biocrust gas exchange and water content relationships, since the lichen-substrate interface, for instance, plays an important role in the water use strategy of these organisms (Souza-Egipsy et al., 2002)

Although there are far fewer studies examining the CO_2 exchange from biologically crusted soils than from higher plants under field conditions, it has been demonstrated that biocrusts have an important influence on soil CO_2 fluxes (Thomas et al., 2008; Wilske et al., 2008; Castillo-Monroy et al., 2011; Zhao et al., 2014; Wu et al., 2015). However, the role of biologically crusted soils as possible C sinks/ sources is still uncertain, and more thorough field research on the environmental variables controlling the CO_2 flux in different biocrust types and areas is a priority. Moreover, photosynthetic performance of different biocrust constituents has traditionally been studied under controlled laboratory conditions for a clearer understanding of its relationships with environmental variables (eg., Lange et al., 1992, 1997; 1998; Del Prado et al., 2001) and removing the underlying soil for better discrimination of its gas exchange by subsoil heterotrophic respiration. However, in recent years, a holistic approach has required integrating their gas exchange activity with the fluxes of the whole soil profile for a better understanding of soil C balances in drylands and their implications in the global C-cycle. Therefore, we have studied the role of biocrusts in CO2 patterns at different successional stages and their underlying soils in two different semiarid areas under natural field conditions. The main goal was to gain more knowledge of CO₂ fluxes in biologically crusted soils and the main factors that govern their variability. This goal was achieved by: (i) in situ CO₂ flux monitoring of biologically crusted soils with different biocrust successional stages in two semiarid areas, with different soils and hydrological properties, but similar biocrust communities, on representative days throughout the year under different environmental conditions; (ii) comparing CO₂ fluxes of the different surface types in the two semiarid areas and within each area; (iii) elucidating the main environmental and ecological factors explaining variability in the CO₂ fluxes on both annual and daily time scales (iv) estimating daily CO₂ fluxes from different biocrust types on representative days throughout the year under different environmental conditions in both semiarid areas. We hypothesized that soil moisture would be the main factor controlling CO₂ fluxes from biocrusts, so that CO₂ fluxes would be negligible during dry periods and significantly increase during wet soil periods. We also hypothesized that gross photosynthesis, and thus net CO₂ uptake, would be higher in well-developed biocrusts that in poorly-developed biocrusts.

2. Material and methods

2.1. Study sites

Two semiarid ecosystems located in the province of Almería (SE Spain) were selected (El Cautivo and Las Amoladeras; Supplementary Fig. 1). Both ecosystems are characterized by abundant biocrust coverage and are representative of semiarid Mediterranean ecosystems, but they showed different soil properties and topography.

2.1.1. El Cautivo

El Cautivo is located in the Tabernas Desert (N37º01' W2º27', elevation: 345 m.a.s.l), and it is one of the most extensive badlands in Spain. This basin is located in the interior of the Betic System, delimited by the Filabres Range to the north, the Alhamilla Range to the southeast, the Gádor Range to the south and the Sierra Nevada Range to the west. The altitude within the study site ranges from 240 to 385 m.a.s.l. The main geological materials in the catchment are calcaric-gypsiferous mudstone and calcareous sandstones (Cantón et al., 2003). A stepped landscape of multiple-age badlands has resulted from episodic uplifting and dissection during the Quaternary (Alexander et al., 2008). Soils are loamy silts, the silt being the dominant soil fraction (ranged from $540\,g\,kg^{-1}$ to $638\,g\,kg^{-1})$ and followed by sand (from $139\,g\,kg^{-1}$ to 326 g kg^{-1}) and clay (from 134 g kg^{-1} to 223 g kg^{-1}). Soil pH ranges from 7.3 to 7.8, calcium carbonate from 226 g kg^{-1} to 265 g kg^{-1} and total soil organic carbon from 4.9 to 9.0 g kg^{-1} (Chamizo et al., 2012). The climate is semiarid Thermo-Mediterranean (Lázaro and Rev, 1991) with long summers and severe water deficits, with a mean annual rainfall of 235 mm (mostly in winter) and mean annual temperature of 18 °C (with an absolute maximum of 45 °C and absolute minimum of -5.5 °C; Lázaro et al., 2000). Rainfall events are usually short, highintensity and associated with thunderstorms, but there are also lowintensity rainfall events lasting several hours. The landscape consists of asymmetric NW-SE valleys. The NE-facing slope gradients are about 30° with incipient soils (Endoleptic Regosols) near the top, densely covered (over 70% of the soil surface) with lichens (mostly Diploschistes diacapsis (Ach.) Lumbsch, Squamarina lentigera (Web.) Poelt., Lepraria crassissima (Hue.) Lettau and Fulgensia fulgida (Nyl.) Szatala). There are

also cyanobacteria and mosses, although in much lower proportions. Soils developed on the pediment, with gentle slope gradients, are relatively thick (Haplic Calcisols) and covered by very scattered annual (9% of the soil surface) and perennial plants (36% of the surface, dominated by *Macrochloa tenacissima* (L.) Kunth, *Helianthemum almeriense* Pau, *Hammada articulate* (Moq.) O. Bolós & Vigo, *Artemisia barrelieri* Besser, and *Salsola genistoides* Poiret), while biocrusts cover the 34% of the pediment. The SW-facing slopes are steeper (up to 70°) with very poor soil development (Epileptic Regosols), sparsely covered by lichens and perennial plants (*S. genistoides*) representing less than 5% of the soil surface, and by less than 2% annual plants (*Moricandia foetida* Bourgeau ex Cosson) (Cantón et al., 2004).

2.1.2. Las Amoladeras

Las Amoladeras, is a coastal habitat in the Cabo de Gata Natural Park (N36º50'1" W2º15'8", elevation: 90 m.a.s.l.), representative of flat coastal-steppe ecosystems, and characterized by a semiarid climate with long hot summers and random precipitation patterns with severe interannual variation. The mean annual rainfall is 200 mm, falling mainly in winter, and the mean annual temperature is 18 °C (Aranda and Oyonarte, 2005). Vegetation cover is sparse (30% of the total surface), including perennial plants mainly dominated by Macrochloa tenacissima (L.) Kunth and annual plants. Biocrusts, mainly lichens (D. diacapsis), cyanobacteria and mosses cover the 30% of the soil surface in open areas among scattered plants, followed by frequent stone cover (13%), rock outcrops (14%) and shallow soils. Lithic Calcaric Leptosols and Haplic Calcisols are the dominant soils. Soil texture is sandy loam, being the most abundant soil fraction the sand (ranging from $588\,g\,kg^{-1}$ to $628\,g\,kg^{-1}$), followed by the silt (from $263\,g\,kg^{-1}$ to 294 g kg⁻¹) and clay (from 109 g kg⁻¹ to 118 g kg⁻¹). Soil pH is basic with values ranging from 7.7 to 7.9, calcium carbonate ranged from 128 g kg^{-1} to 141 g kg^{-1} and total organic carbon range from 12.1 to 13.8 g kg^{-1} (Chamizo et al., 2012).

2.2. Experimental design: in situ measurements of CO_2 fluxes on different soil covers

For this study, we selected the most common biocrust types representing ecological successional stages at the two different study areas, characterized by similar climate conditions but different soils and topography. The biocrusts selected, in order of successional and growth stages were: bare soils with very incipient cyanobacterial colonization < cyanobacteria < D. diacapsis and S. lentigera lichens at El Cautivo; and incipient cyanobacterial < cyanobacteria-dominated < lichen-dominated (D. diacapsis) < moss-dominated at Las Amoladeras. Mosses were not selected at El Cautivo because of their limited cover at that site. Only D. diacapsis was selected in Las Amoladeras because it was the most representative lichen species there. At Las Amoladeras, annual plants, mainly dominated by Stipa capensis Thunb., were also included as an additional surface type. This was done because of their representativeness in the area during the experimental setup (more than 30% of coverage) and the possibility of measuring their CO₂ fluxes with the same method as the biocrusts. Annual plants were not selected at El Cautivo because of their sparse coverage, especially after the drought in the previous two years (unpublished data).

Four experimental plots (replicas) were selected for each surface types mentioned above in each study area, resulting in a total of 20 plots at Las Amoladeras (differentiating incipient cyanobacteria, well developed cyanobacteria, *D. diacapsis* lichens, moss and annual plants) and 16 plots at El Cautivo (differentiating incipient cyanobacteria, well developed cyanobacteria and two different lichens species, *S. lentigera* and *D. Diacapsis*). Each experimental plot was delimited with 5-cm high by 10-cm diameter PVC soil-borne collars (80 cm²) randomly distributed on homogenous areas covering over 80% of each surface type. The collars were inserted in the soil, leaving 2–3 cm above ground, one

month before starting measurements. All experimental plots were installed over the same hillslope covering a maximum 100 m² surface area at El Cautivo and 150 m^2 at Las Amoladeras. The soil CO₂ fluxes throughout the soil column, including the biocrusts and annual plants living on its surface, and the entire soil microbial community associated with them, were measured in situ. Net CO₂ flux or net photosynthesis (NP) and dark respiration (DR) were measured in eight field campaigns (four at El Cautivo and four at Las Amoladeras) carried out under different environmental conditions (Supplementary Tables 1 and 2): i) In summer, after a long drought and high temperatures ("Summer campaign": carried out in 07/26/2012 at El Cautivo and in 08/01/2012 at Las Amoladeras), ii) after the first heavy rainfall event following the summer drought ("Fall campaign": carried out in 10/01/2012 at El Cautivo and in 10/02/2012 at Las Amoladeras), iii) after frequent rainfall events and mild temperatures in the wet season ("Winter campaign"; carried out in 11/16/2012 at El Cautivo and in 02/21/ 2013 at Las Amoladeras), iv) after light rainfalls and high temperatures in spring ("Spring campaign"; carried out in 05/20/2013 at El Cautivo and in 05/15/2013 at Las Amoladeras). During each field campaign, either NP and DR were measured in the field several times during daylight hours (from sunrise to sunset). Each measurement period lasted about 2 h (measurement time period, MTP) to ensure homogeneous environmental conditions within periods. Supplementary Table 2 shows all MTPs with their times and variability in environmental parameters during the day at both study sites. First, NP was measured in the plot exposed to direct sunlight using a Licor LI-6400 (Lincoln, NE, USA) infrared gas analyser (IRGA) system connected to a custom-made transparent chamber with the same diameter as the collar and a volume of 668 cm³ (for more information about chamber specifications and measurement protocol, see Maestre et al., 2013; Ladrón de Guevara et al., 2014, 2015). CO₂ sample and reference IRGA readings were matched before each individual measurement, as this is very important for accurate measurement when CO₂ is expected to be low (LI-COR, 2012). NP was recorded when CO_2 was stabilized in both sample and reference IRGAs. Positive NP indicates net CO₂ fixation while negative NP shows net CO₂ emission to the atmosphere. DR was measured for the same samples using a PP Systems EGM-4 IRGA with the measurement time set for 120 s and data stored every 5 s.

Before starting to measure, specific LI-6400 and EGM-4 comparison testing was performed to check the fit between measurements by the two devices and find an equation for converting respiration rates measured with the EGM-4 to equivalent LI-6400 measurements. This was done by taking consecutive measurements with both devices on biocrust samples with different soil water content for two days. First, the custom transparent chamber attached to the LI-6400 was covered with a cloth and the respiration rate in the sample was measured, and immediately afterwards, the respiration rate was measured over the same sample with the EGM-4. The CO₂ flux measurements of both devices were adjusted to linear regression ($R^2 = 0.90$) and the equation found was applied to all the respiration records to acquire the final sample CO2 effluxes (DRcorrected). As both devices measured the gas exchange of the whole soil profile, the respiration of autotrophic and heterotrophic components was present in both cases, and gross photosynthesis (GP) could be calculated by the formula $GP = NP + DR_{corrected}$. The photosynthetic rates were calculated by surface area as μ mol CO₂ m⁻²s⁻¹. Based on these data, the daily CO₂ fluxes for the period between sunrise and sunset were estimated by trapezoidal integration, dividing the time elapsed between two short consecutive measurements of each sample into two periods. The first measurement was multiplied by the first period, and the second by the second period. The products of all time periods were added up to find the daily NP, GP and DR.

2.3. Microclimatic parameters and monitoring of key environmental variables

Air temperature (T_{BC}) and relative humidity (RH_{BC}) over the surface types were continuously monitored during gas exchange measurements using automated sensors (DS1923 Hygrochron Temperature/Humidity Logger iButton, Embedded Data Systems, USA) placed right over each surface type and close to the experimental plots. Then the T_{BC} and RH_{BC} during each MTP were averaged. Soil moisture was continuously monitored at a depth of 3 cm and subsurface temperature at a depth of 1 cm in two representative plots of each surface type using automated ECH₂O probes (EC-5 and ECT, respectively, Decagon Devices, Inc., Pullman, Washington). Photosynthetically active radiation (PAR) was measured with a LICOR external quantum sensor (LICOR 9901-013, Lincoln, NE, USA) placed next to the transparent chamber for a reference close to the sample surfaces, and an E-type thermocouple in contact with these surfaces was used to record their temperatures. These variables (PAR and surface temperature) were recorded for every measurement, at the same time as NP.

The antecedent water input characteristics were studied for 30 days before the gas exchange measurements. Continuous temperature and RH (Vaisala HMP 35C, Campbell Scientific, Logan, UT, USA) from weather stations in the study areas, as well as soil temperature (0–1 cm), were used to discriminate the water input source (rainfall, fog or dew) recorded with an accuracy of 0.2 mm by gauges located near the experimental plots (less than 20 m). Previous studies have found that in drylands, dew and fog are relevant sources of non-rainfall water inputs for biocrust photosynthetic activity during the early morning hours in the absence of rain (Lange et al., 1992, 2006; Veste et al., 2001). In this study, small night-time water pulses were considered fog events when RH was over 97%, as the sensors had an accuracy of 3% with RH over 90%, and dew when soil surface temperature was similar to (\pm 0.5 °C) or below dew point (calculated with RH and T data).

2.4. Data analysis

Two different analyses were carried out for all variables (NP, GP and DR) for each type of data: 1) point-in-time measurements clustered in MTPs and 2) daily gas exchange estimates. As the biocrust communities at the selected sites had some differences, we also analyzed the two data types: 1) By area separately selecting all covers and 2) Both areas together selecting only the covers in common to both. General linear mixed models (LMMs) with repeated measures were used for each analysis. The factors were MTP, measurement campaign, surface type and study site (see Tables 1 and 2), and their interactions were included as fixed effects. Inclusion of the plots as a random effect improved the models. MTPs were numbered as a continuous temporal factor in all measurement campaigns. The models were run using restricted maximum likelihood (REML) to choose the best variance/covariance structure according to Akaike's Information Criterion (AIC). The absence of variance heterogeneity and temporal autocorrelations was checked by Pearson standardized residuals versus fitted value plots and autocorrelation function (ACF) plots, respectively. The normal distribution of the Pearson standardized residuals was verified by QOplots. To reduce the influence of microenvironmental changes in the plots within each MTP, the effect of including environmental covariates in the models (PAR, surface temperature, soil moisture, RH_{BC} and T_B) as fixed terms was tested by running the models with maximum likelihood (ML) and selecting the best variance/covariance structures by the protocol explained. A forward stepwise procedure was carried out to select only significant (p value < 0.05) covariates that improved the models by reducing their AIC values. As the combination of covariates did not improve the models more than their individual effects, a correlation test was unnecessary. In each model selected, Fisher's least significant difference (LSD) post-hoc test was applied to the most complex interactions of the factors that showed significant differences for all pairwise comparisons. The individual relationships between environmental variables (RH_{BC} , T_{BC} , soil moisture, PAR) and CO_2 fluxes were also explored. To do this the Pearson's correlation coefficient between each environmental variable and GP, DR, and NP was estimated in each study site and for: 1) all surface types together and 2) for each of the surface types separately. Statistical analyses were performed in R (ver. 3.1.2) using Infostat software (ver. 2014, Di Rienzo et al., 2014).

3. Results

3.1. Rainfall, dew and fog pulses before CO₂ flux-measurements

Field summer campaigns were characterized by hot and very dry conditions resulting from the absence of any water input during the 30 days before measurement at both study sites (Supplementary Tables 1 and 2). The first rainfall after the long dry summer occurred at the end of September, when an important rainfall event took place a few days before the fall field campaigns at both study sites. During these events, 25 mm fell at El Cautivo and 15 mm at Las Amoladeras, increasing soil moisture content up to 16.5% and 10.4%, respectively. There was no fog recorded at El Cautivo in the days prior to the fall field campaign, but 3 dew events (0.60 mm) were estimated in this site (Supplementary Table 1). Winter campaign at El Cautivo was characterized by several light and medium-size rainfalls, as well as 3 dew events, whereas a heavy rainfall event of 32 mm was recorded one day before the winter field campaign at Las Amoladeras. Prior to this rainfall, there were two small rains of 0.2 mm and few events of fog and dew (1.6 mm in total). Therefore, this period was characterized by high soil water content and mild soil temperature in both study areas (Supplementary Table 1). Before spring field campaigns, some light to medium-size rainfalls were recorded at both study sites, but soil water content was moderate in comparison to that measured during fall and winter field campaigns (6.6% at El Cautivo and 10.2% at Las Amoladeras) due to relatively high temperatures.

3.2. Short-term in situ CO₂ fluxes at El Cautivo and Las Amoladeras

General linear mixed models for each study site and when both study areas were compared showed that all the factors (MTP, site, surface type and PAR) and their interactions significantly influenced CO₂ fluxes. From the different factors analyzed, MTP, which integrates the combined effect of several environmental variables throughout the day (e.g., surface moisture, RH_{BC}, T_{BC} and PAR) and surface type were the most important factors influencing NP, GP and DR (Table 1). The study site also exerted a significant effect on CO₂ fluxes (Table 1). In general, CO₂ fluxes showed the highest number of significant correlations with soil moisture and RH_{BC}, followed by T_{BC} and PAR in both study areas (Supplementary Table 3).

At El Cautivo, there were no significant differences in NP or DR in the biocrust types during the summer campaign. The CO₂ fluxes were almost negligible for all surface types with only very small CO₂ effluxes to the atmosphere (Figs. 1 and 2). However, biocrusts within this study site were especially metabolically active in fall and winter field campaigns conducted after rainfalls. During the fall campaign, biocrusts showed GP peaks in the late morning, being especially high in D. diacapsis, and noon (Supplementary Fig. 2). Nevertheless, DR was higher than GP in all biocrust types at El Cautivo, resulting in a negative NP throughout the day (indicating net CO₂ emission to the atmosphere), except in D. diacapsis in the late morning, which showed NP close to zero (Figs. 1 and 2). During the winter campaign, when soil moisture was the highest, all biocrust types showed a positive NP flux (indicating net CO₂ fixation) in the early morning, but it decreased during the day, as the soil became dry (Fig. 1). When the different biocrust types are compared, we found that D. diacapsis had significantly higher GP and DR fluxes than cyanobacterial crust types in the early morning, but

Table 1

Results of the MIXED model analysis evaluating the gas exchange of different cover types and times during each campaign in two semi-arid areas. P-values below 0.05 are in bold; those between 0.05 and 0.10 are in italics.

| MTP measurements | Net photosynthesis | | | Gross photosynthesis | | | Dark respiration | | | | |
|-----------------------------------------------|--------------------|---------|---------|----------------------|---------|---------|------------------|---------|---------|--|--|
| | El Cautivo | | | | | | | | | | |
| | DF | F-value | p-value | DF | F-value | p-value | DF | F-value | p-value | | |
| МТР | 18 | 13.24 | < 0.001 | 18, 216 | 35.67 | < 0.001 | 18, 215 | 45.30 | < 0.001 | | |
| Surface type | 3 | 3.82 | 0.01 | 3, 12 | 1.64 | 0.23 | 3, 12 | 8.11 | 0.00 | | |
| T _{BC} | - | - | - | - | - | - | 1, 215 | 4.73 | 0.03 | | |
| MTP \times Surface type | 54 | 2.12 | 0.00 | 54, 216 | 2.28 | < 0.001 | 54, 215 | 2.43 | < 0.001 | | |
| Las Amoladeras | | | | | | | | | | | |
| MTP | 16, 228 | 65.15 | < 0.001 | 16 | 37.16 | < 0.001 | 16, 232 | 96.91 | < 0.001 | | |
| Surface type | 4, 15 | 14.09 | < 0.001 | 4 | 11.63 | < 0.001 | 4, 15 | 43.40 | < 0.001 | | |
| PAR | 1, 228 | 9.82 | 0.00 | - | | - | - | - | - | | |
| MTP \times Surface type | 64, 228 | 6.87 | < 0.001 | 64 | 1.98 | < 0.001 | 64, 232 | 12.77 | < 0.001 | | |
| Comparison between areas | | | | | | | | | | | |
| MTP | 16 | 41.66 | < 0.001 | 16, 283 | 59.91 | < 0.001 | 16, 284 | 83.45 | < 0.001 | | |
| Study site | 1 | 2.99 | 0.09 | 1, 18 | 9.44 | 0.00 | 1, 18 | 16.82 | 0.00 | | |
| Surface type | 2 | 2.18 | 0.51 | 2, 18 | 21.25 | < 0.001 | 2, 18 | 21.58 | < 0.001 | | |
| PAR | - | - | - | 1, 283 | 4.46 | 0.04 | - | - | - | | |
| MTP \times Study site | 16 | 5.37 | < 0.001 | 16, 283 | 5.84 | < 0.001 | 16, 284 | 6.53 | < 0.001 | | |
| MTP \times Surface type | 32 | 3.91 | < 0.001 | 32, 283 | 3.90 | < 0.001 | 32, 284 | 8.26 | < 0.001 | | |
| Study site \times Surface type | 2 | 3.66 | 0.03 | 2, 18 | 4.06 | 0.04 | 2, 18 | 4.50 | 0.03 | | |
| MTP \times Study site \times Surface type | 32 | 2.31 | 0.00 | 32, 283 | 3.05 | < 0.001 | 32, 284 | 5.03 | < 0.001 | | |

Measurement time period (MTP), photosynthetically active radiation (PAR), relative air humidity (RH_{BC}) and air temperature (T_{BC}) over biocrusts.

well-developed cyanobacteria had significantly higher GP than *D. diacapsis* at noon (cyanobacterial crusts were the only biocrust type with a positive C balance at this period; Fig. 2). During the spring campaign at El Cautivo, DR rates were higher than GP in all biocrust types throughout the day (Fig. 2), resulting in slightly negative NP. Differences between biocrust types were not significant, except in DR at the early morning, when the lichen *D. diacapsis* had higher rates than all the other biocrust types (Fig. 2).

A similar pattern to El Cautivo was found in CO_2 fluxes at Las Amoladeras during the different field campaigns. During the summer campaign, CO_2 fluxes were very low and close to zero in all biocrust types and annual plants throughout the day at Las Amoladeras. Moreover, there were no significant differences in CO_2 fluxes among surface types within MTPs or in each surface type throughout the day (Figs. 3 and 4). During the fall campaign, which was conducted after the first rainfall event after summer drought, all covers showed the largest CO₂ emissions as consequence of the high values of DR exceeding the GP values (Figs. 3 and 4). Moreover, whereas GP peaks from lichens, moss and annual plants were recorded in the late morning, the maximum DR peaks from all covers types occurred at late morning and early afternoon (Supplementary Fig. 2). Annual plants showed the highest negative NP and DR values throughout the fall campaign (Fig. 4). During the winter field campaign at Las Amoladeras, all biocrust types showed the highest GP rates resulting in positive NP fluxes (Figs. 3 and 4). Mosses and lichens had higher GP rates than cyanobacteria, reaching their maximum at noon (Supplementary Fig. 2). However, they also showed higher DR rates than either developed or incipient cyanobacteria, which resulted in a higher net CO₂ fixation rate on cyanobacteria (Figs. 3 and 4). Annual plants had the highest DR rates, surpassing their GP rates and causing the most negative NP flux throughout the entire field campaign (Figs. 3 and 4). During the spring campaign at Las Amoladeras GP and DR rates from all

Table 2

Results of the MIXED model analysis evaluating the daily gas exchange estimates of different cover types during each campaign in two semi-arid areas. P-values below 0.05 are in bold; those between 0.05 and 0.10 are in italics.

| Daily activity estimates | Net photosynthesis | | | Gross photosynthesis | | | Dark respiration | | |
|----------------------------------------------------|--------------------|---------|---------|----------------------|---------|---------|------------------|---------|---------|
| | El Cautivo | | | | | | | | |
| | DF | F-value | p-value | DF | F-value | p-value | DF | F-value | p-value |
| Campaign | 3 | 27.19 | < 0.001 | 3 | 68.93 | < 0.001 | 3 | 44.31 | < 0.001 |
| Surface type | 3 | 2.22 | 0.10 | 3 | 1.49 | 0.23 | 3 | 0.97 | 0.41 |
| T _{BC} | - | - | - | - | - | - | 1 | 5.04 | 0.03 |
| Campaign \times Surface type | 9 | 1.13 | 0.36 | 9 | 1.67 | 0.12 | 9 | 1.02 | 0.44 |
| Las Amoladeras | | | | | | | | | |
| Campaign | 3 | 146.78 | < 0.001 | 3 | 34.55 | < 0.001 | 3 | 101.06 | < 0.001 |
| Surface type | 4 | 8.66 | < 0.001 | 4 | 20.29 | < 0.001 | 4 | 11.34 | < 0.001 |
| Campaign \times Surface type | 12 | 22.75 | < 0.001 | 12 | 3.8 | < 0.001 | 12 | 9.61 | < 0.001 |
| Comparison between areas | | | | | | | | | |
| Campaign | 3, 53 | 117.76 | < 0.001 | 3 | 90.56 | < 0.001 | 3, 53 | 97.46 | < 0.001 |
| Study site | 1, 18 | 4.18 | 0.06 | 1 | 8.1 | 0.01 | 1, 18 | 33.46 | < 0.001 |
| Surface type | 2, 18 | 0.83 | 0.45 | 2 | 14.03 | < 0.001 | 2, 18 | 5.71 | 0.01 |
| Campaign \times Study site | 3, 53 | 11.58 | < 0.001 | 3 | 2.87 | 0.04 | 3, 53 | 5.11 | 0.00 |
| Campaign \times Surface type | 6, 53 | 4.31 | 0.00 | 6 | 3.41 | 0.01 | 6, 53 | 4.77 | 0.00 |
| Study site \times Surface type | 2, 18 | 1.2 | 0.32 | 2 | 2.55 | 0.09 | 2, 18 | 3.24 | 0.06 |
| Campaign \times Study site \times Surface type | 6, 53 | 1.11 | 0.36 | 6 | 2.29 | 0.04 | 6, 53 | 2.67 | 0.03 |

Relative air temperature over biocrusts (T_{BC}).



Fig. 1. Mean \pm SE (n = 4) Net photosynthetic activity (NP) in each measurement time period (MTP) at El Cautivo. Different capital letters indicate significant differences (p < 0.05.) between cover types within each MTP, whereas N.S.D. indicates no significant differences. Significant NP differences along the day within cover types are showed with lowercase letters. Significant NP differences between areas within cover types in common are indicated with arrows. Arrows pointing up and down indicate greater NP (or less negative) at El Cautivo and Las Amoladeras, respectively.

surface types showed intermediate values between summer and winter campaigns (Fig. 4), with a slight negative net CO_2 balance (Fig. 3).

3.3. Daily estimations of biocrust CO₂ fluxes

At El Cautivo, LMM analysis of daily gas exchange estimations showed that measurement campaign (factor integrating the variations in environmental conditions during the year) was the only factor that significantly influenced the NP, DR and GP fluxes (Table 2). Nevertheless, the most significantly influential factor in CO₂ fluxes (NP, DR, GP) at Las Amoladeras site was the measurement campaign, followed by surface type and their interaction (Table 2). When the two study areas were compared in the LMM analysis, only the measurement campaign factor and its interaction with surface type and site separately significantly influenced NP fluxes, whereas all factors (campaign, site, surface type and their interactions) significantly influenced GP and DR fluxes (Table 2). The measurement campaign had the highest F-value, indicating that it had the most weight in the significant differences in the NP, GP and DR. Nevertheless, the second factor with the greatest weight influencing DR was site, also showing the considerable importance of site characteristics in this variable and the surface type was the second factor with the greatest weight influencing GP (Table 2).

Fig. 5 showed daily estimations of NP, GP and DR at El Cautivo and Las Amoladeras. During the summer campaign at El Cautivo, the daily GP, DR and NP estimations were close to zero since biocrusts were metabolically inactive during this long drought (Fig. 5). Daily NP, DR and GP differed significantly among campaigns in this site (Fig. 5). The highest estimated daily DR fluxes from all biocrusts were during the fall campaign followed by the winter field campaign coinciding with the rainy periods and greater soil moisture, but the highest daily GP estimations were during the winter campaign, followed by fall and spring campaigns. The estimated daily NP at El Cautivo showed a negative balance with CO_2 effluxes to atmosphere from all biocrust types during the fall and spring campaigns, being slightly higher in the fall campaign right after the first rainfall after a long drought (Fig. 5). On the contrary, the winter campaign was the only season with a positive balance in the estimated daily NP in all surface types except in incipient cyanobacteria.

The patterns in daily soil CO_2 fluxes measured during the different field campaigns at Las Amoladeras were similar to El Cautivo, although in general the estimated daily GP and DR from the biocrusts were significantly higher at Las Amoladeras (Fig. 5). Similar to El Cautivo, during the summer campaign, estimated daily GP, DR and NP were close to zero (Fig. 5). During the fall campaign, *D. diacapsis* and developed cyanobacterial biocrusts showed higher daily DR at Las Amoladeras than at El Cautivo. These values were higher than observed GP rates at both study sites, thus resulting in higher net CO_2 emissions (negative NP flux) (Fig. 5). During the winter campaign at Las Amoladeras, and similar to that observed at El Cautivo, GP was also the highest, but significant differences were found between sites (Fig. 5). This increase in GP was able to offset CO_2 emissions through respiration, thus resulting in positive NP. However, this only occurred on *D*.



Fig. 2. Mean \pm SE (n = 4) Gross photosynthetic activity (GP) and dark respiration (DR) in each measurement time period (MTP) at El Cautivo. Different capital letters indicate significant differences (p < 0.05.) between cover types within each MTP, whereas N.S.D. indicates no significant differences. Significant NP differences along the day within cover types are showed with lowercase letters. Arrows pointing up and down indicate greater GP and DR, respectively, in comparison with Las Amoladeras rates.

diacapsis and developed cyanobacteria, whereas mosses and incipient cyanobacteria showed NP fluxes close to zero, and annual plants had a clearly negative CO_2 balance (Fig. 5) with the highest emission rates despite the fact that they had the second highest daily GP in this campaign. This was due to its high daily DR (~5 g CO_2 m⁻²), by far the highest recorded in all campaigns.

4. Discussion

4.1. Effect of environmental variables and site on CO₂ fluxes from biocrusts

In our analysis, environmental variability during the day (MTP factor) and year (measurement campaign factor) had the greatest weight in explaining the CO₂ flux dynamics (GP, DR and NP) at both El Cautivo and Las Amoladeras, and also when the two study areas were compared (Tables 1 and 2). This is because under natural conditions, biocrusts interact simultaneously with several environmental variables (soil moisture, non-rainfall water inputs such as dew and fog, air humidity, temperature and PAR), greatly increasing the complexity of predicting CO₂ flux patterns. Other authors have already pointed out that CO₂ exchange in biocrusts is strongly influenced by environmental variables such as seasonality, temperature, light, and especially moisture (Thomas and Hoon, 2010; Castillo-Monroy et al., 2011; Zelikova et al., 2012; Coe et al., 2012; Su et al., 2013; Feng et al., 2014; Cao et al., 2015; Wu et al., 2015). Of all the different environmental factors, precipitation patterns, including rainfall event size and precipitation history, rainfall seasonality and dew are the most important drivers of CO₂ flux exchange in biocrusts (Kidron et al., 2015; Coe et al.,

2012; Wu et al., 2015). Our results also showed that biocrust CO₂ exchange is clearly marked by RH_{BC} and soil moisture, as corroborated by the highly significant correlations between these variables and CO₂ fluxes in all biocrust types at El Cautivo and Las Amoladeras (Supplementary Table 3). Thus, GP and DR fluxes were close to zero in summer when biocrusts and microorganisms in underlying soil were inactive (Wu et al., 2015). After the first heavy rainfalls following a long period of drought (fall campaigns), negative net CO₂ fluxes were recorded in the biocrusts at El Cautivo and Las Amoladeras as a result of higher DR rates surpassing GP (Figs. 1-4). This could be due to the increased energy cost of biocrust metabolic recovery following long desiccation under these environmental conditions. Thus, the higher respiratory losses after long dry periods would be more difficult to overcome by CO₂ fixation (Coe et al., 2012). Moreover, the first rainfalls could have infiltrated to deeper layers, activating the surviving populations of heterotrophic bacteria and fungi, which rapidly consumed the available organic carbon (dry organic matter accumulated after the long dry period), contributing to higher soil respiration (DR), and therefore, CO_2 emissions at both sites. Other authors have also observed significant CO₂ emissions from biologically crusted soils after heavy rainfall events (Cable and Huxman, 2004; Thomas and Hoon, 2010; Thomas et al., 2008; Grote et al., 2010). After the net CO₂ emission peaks during the first rainfalls after a long dry period, positive NP was recorded on the biologically crusted soils during the winter campaigns in both study sites. These campaigns occurred after a longwet period (Supplementary Table 1) favorable for biocrust photosynthetic activity, during which biocrust photosynthetic system could be repaired. This may explain the high GP fluxes measured during



Fig. 3. Mean \pm SE (n = 4) Net photosynthetic activity (NP) in each daily measurement time interval (MTP) at Las Amoladeras. Different capital letters indicate significant differences (p < 0.05.) between cover types within each MTP, whereas N.S.D. indicates no significant differences. Significant NP differences along the day within cover types are showed with lowercase letters. Significant NP differences between areas within cover types in common are indicated with arrows. Arrows pointing up and down indicate greater NP (or less negative) at Las Amoladeras and El Cautivo, respectively.

winter campaign that overpassed biocrust and soil CO_2 loss by respiration, thus resulting in net C gain in soils covered by biocrusts (Figs. 1–4).

Once biocrusts were activated by sufficient soil moisture conditions (fall and winter field campaigns), the significant differences in biocrust CO_2 fluxes during the day were due to the interplay of other environmental variables such as temperature, air humidity and PAR which were also significantly correlated with CO_2 fluxes (NP, DR and GP) (Supplementary Table 3). Other authors have also found that the combination of these environmental variables modulates biocrust photosynthesis patterns when soil moisture is available (Huang et al., 2014; Weber et al., 2012). Therefore, environmental parameters such as temperature, water and light vary markedly, and it is difficult to analyse the effect of a single variable influencing biocrust photosynthesis patterns because, in the field, these changes are frequently synergistic (Feng et al., 2014).

Nevertheless, at both study sites the annual rainfall was low, and heavy or frequent rainfall events, which would allow sufficient minimum soil moisture content for both basic biocrust functions and photosynthesis, are usually very scarce, so the periods in which the biocrusts sequester carbon could be temporally limited and very conditioned to other sources of water in both ecosystems. Others authors have also shown that biocrusts forming lichens are photosynthetically active only for a short period during the year, mainly in winter (Del Prado and Sancho, 2007; Pintado et al., 2010; Maestre et al., 2013). The CO_2 exchange pattern found by Su et al. (2013) in the Gurbantunggut Desert (China) was similar to ours, where the biologically crusted soils exhibited either negligible CO_2 fluxes due to biocrust dormancy for most of the year, or carbon release after rainfall because respiration of biocrusts and soil microbial communities under biocrusts was greater than biocrust photosynthetic activity.

When both study areas were compared, the CO₂ fluxes registered at Las Amoladeras (Figs. 1-4) were generally higher than those found at El Cautivo, partially associated to the higher soil moisture content at the former site during most field campaigns (Supplementary Table 1), as it is a coastal ecosystem with generally higher non-rainfall inputs (Supplementary Table 1) favoring longer periods of biocrust biological activity (Lange et al., 1994; Pan et al., 2010). In addition, the differences in physical and chemical soil properties between El Cautivo and Las Amoladeras (Chamizo et al., 2012), inducing to different soil water redistribution and rainfall infiltration, also influence soil moisture and its duration (Kidron et al., 2015). Under moist soil conditions (fall and winter campaigns), DR in soil covered by most developed biocrusts at Las Amoladeras was higher than at El Cautivo, probably because of differences in the carbon pool and microbial abundance and activity between sites (Miralles et al., 2012a, 2013). In fact, soil underlying biocrusts at Las Amoladeras have a higher total organic carbon content than at El Cautivo (Chamizo et al., 2012), which would also lead to proliferation of microbial communities in the soil subsurface, enhancing biocrust and soil microorganism DR responses to favorable environmental conditions at this site. The generally higher soil temperatures, T_{BC} and soil moisture content at Las Amoladeras (Supplementary Tables 1 and 2) could also promote higher respiration activity of the biocrusts and soil subsurface at this site (Fig. 4). Nevertheless, although



Fig. 4. Mean \pm SE (n = 4) Gross photosynthetic activity (GP) and dark respiration (DR) in each measurement time period (MTP) at Las Amoladeras. Different capital letters indicate significant differences (p < 0.05.) between cover types within each MTP, whereas N.S.D. indicates no significant differences. Significant NP differences along the day within cover types are showed with lowercase letters. Arrows pointing up and down indicate greater GP and DR, respectively, in comparison with El Cautivo rates.

the most developed biocrusts (the lichen *D. diacapsis* and developed cyanobacteria) showed significant differences in DR between sites (Figs. 2 and 4), incipient cyanobacteria did not. This could be due to more developed biocrust contribute to increase the size and activity of soil microbial communities in the deeper layers than less developed biocrusts (Miralles et al., 2012c, 2012d), favoring a higher CO_2 emission in wet conditions. This result is consistent with the study by Castillo-Monroy et al. (2011), where they found that microsites with more biocrust cover had higher Q_{10} than bare soil.

LMM analyses evaluating the daily CO_2 exchange estimates during field campaigns in both biologically crusted semi-arid sites reasserted that environmental conditions were the most important driver for carbon sink/source behaviour in both ecosystems (Table 2), with patterns mainly associated with changes in soil moisture, temperature, light conditions and biocrust physiological status during the year. This corroborates the important role of the amount of rainfall and its distribution throughout the year in carbon sequestration in crusted drylands ecosystems.

4.2. Effect of surface type and biocrust successional stage on CO₂ fluxes

The most significant differences in CO_2 fluxes (NP, GP, DR) among biocrust types at El Cautivo and Las Amoladeras occurred under wet conditions (Figs. 1–4), when biocrust phototrophic organisms are active. Dominant species in biocrusts differ in their development and successional state, as well as physiological responses to the environment (Lange, 2003; Belnap et al., 2004; Grote et al., 2010; Sancho et al.,

2016) and therefore affect carbon fluxes differently. Some authors have shown that late successional biocrusts have the potential to fix more carbon due to the presence of more chlorophyll a concentration in both soil surface biomass and area (Yeager et al., 2004; Housman et al., 2006; Büdel et al., 2009; Castle et al., 2011; Zaady et al., 2014). However, net carbon sequestration in soils covered by biocrusts is the result of the difference between CO₂ fixation and CO₂ emissions by the biocrust and respiratory activity of the microbial community in the underlying soil. Our results show that under moist environmental conditions right after long dry periods (fall campaigns), developed biocrusts dominated by D. diacapsis had significantly higher GP rates than the rest of the biocrust types in the morning at both El Cautivo and Las Amoladeras (Figs. 2 and 4). In fact, this lichen was the only biocrust type with a slightly positive NP balance in the morning at El Cautivo, when its GP rates surpassed even its DR (Figs. 1 and 2). High chlorophyll content of this lichen compared to another North American one has been reported (Pintado et al., 2005), and therefore the photosynthetic activity of D. diacapsis at both study sites could be more effective than of other biocrusts under suitable light and temperature conditions. A positive relationship has been described between chlorophyll content and daylight wetness duration in soils covered by biocrusts (Kidron et al., 2009, 2010). In general, well-developed biocrusts are able to maintain surface moisture longer (Chamizo et al., 2013), thus prolonging the period of photosynthetic activity, and thereby increasing chlorophyll content and biocrust growth. Therefore, longer duration of surface wetness in the first millimeters in late successional biocrusts dominated by lichens could also explain its high GP rates in



Fig. 5. Mean \pm SE (n = 4) Daily estimations of net and gross photosynthetic activity (NP and GP, respectively) and dark respiration (DR) at Las Amoladeras and El Cautivo. Different capital letters indicate significant differences (p < 0.05.) between cover types within each field campaign, whereas N.S.D. indicates no significant differences. Significant NP differences along the day within cover types are showed with lowercase letters. As in lowercase letters, arrows below vertical lines indicate the results of daily estimation rates comparisons when cover types had not significant effects.

both study areas.

After several rainfalls, when the soils had reached high moisture content (winter campaigns), GP was also significantly higher for D. diacapsis than the other biocrusts (S. lentigera and cyanobacteria) in the morning at El Cautivo, but this trend was reversed in the afternoon when cyanobacteria crusts had significantly higher GP rates (Supplementary Fig. 2 and Fig. 2). As several previous publications have pointed out (e.g., Lange et al., 1990; Moore, 1998; Lange, 2003), chlorolichens show greater C-fixing capacity in the morning, when the soil surface is normally wetter. But in line with the work by Housman et al. (2006), cyanobacteria have a greater ability to maintain photosynthetic activity during the day because they have more efficient mechanisms than chlorolichens to survive under more limited water availability conditions (Lange et al., 1998). For example, they produce a protective layer of exopolysaccharides that avoid desiccation (De Philippis and Vincenzini, 1998; Potts, 2001), and they are even able to migrate through the soil profile to protect themselves from severe desiccation on the soil surface and find water in the lower soil layers (García-Pichel and Pringault, 2001). In addition, cyanobacteria are also able to fix CO₂ under very harsh environmental conditions. They have low sensitivity to photoinhibition (Harel et al., 2004) and a more efficient CO₂ concentrating mechanism than green algae (Green et al., 1993; Badger et al., 2006; Price et al., 2008), which counteracts the increase of Rubisco oxygenase activity with temperature. Nevertheless, at Las Amoladeras, the D. diacapsis and mosses showed significantly higher GP rates than the rest of the surface types during the day (Supplementary Fig. 2 and Fig. 4). The higher soil moisture content at Las Amoladeras than at El Cautivo (Supplementary Tables 1 and 2) may have provided suitable environmental conditions for keeping up photosynthetic activity in both developed biocrusts until late morning.

However, under moist conditions (fall and winter campaigns), despite higher GP in well-developed crusts dominated by lichens and mosses, DR was also higher in these biocrusts compared to cyanobacterial crusts. In the case of D. diacapsis, its high DR rates could be partly due to its metabolism degrading polyphenols (Miralles et al., 2014; Delgado-Baquerizo et al., 2015). Moreover, it has been found that biocrusts dominated by D. diacapsis have a very high total labile-C content representing about 40% of its TOC, much higher than the labile-C content in early successional biocrusts dominated by cyanobacteria (Miralles et al., 2013). Therefore, soil organic carbon from this biocrust type is probably transferred to underlying soil microbial communities, favoring the growth of heterotrophs in underlying soils and enzymes that enable faster degradation of organic remains than in soils under cyanobacteria biocrusts (Miralles et al., 2012c, 2012d). Thus, these lichen biocrusts indirectly influence the respiration of the heterotrophic community of the soil column by increasing soil organic matter, thereby favoring soil respiration (Castillo-Monroy et al., 2011; Miralles et al., 2012d). The greater availability and duration of water content in the first centimeters of soil under the biocrusts (Kidron and Benenson, 2014) could also favor the organic matter mineralization and increase the DR rates under this biocrust type. Other authors have also found high respiration rates from soils below mosses, mainly caused by the presence of underground bacteria and fungi communities (García-Pichel et al., 2003; Weber et al., 2012). Like D. diacapsis, mosses release organic matter and nutrients into the underlying soils (Coxson, 1991; Melick and Seppelt, 1992), which probably also serve as effective fertilizer favoring the growth and development of soil heterotrophic communities (Conant et al., 2000; Weber et al., 2012).

 CO_2 patterns in annual plants differed from those of biocrusts, which is attributed to differences in their response to moisture pulses,

as well as the phenological cycle of annual plants. According to Karnieli (2003), whereas biocrusts turn green immediately after water pulses, more time is needed for annual plants to germinate and grow after the first rainfall event. Thus, just after the first effective rain of the hydrological year (fall campaign), when the soil surface was enriched with high organic matter content from the decomposition of annual plants germinated during previous seasons, annual plants showed a significantly more negative net CO₂ flux than any of the biocrust types in the field campaign (Fig. 3), because their DR rates were usually significantly higher than biocrusts and exceeded their GP rate (Fig. 4). Moreover, according to Karnieli (2003), annual plants are active for only a relatively short period, and after that, they dry out, incorporating new organic matter and litter into the soil surface. This may explain the low GP and high DR rates in annual plants measured during our following field campaigns (Fig. 4). The presence of a larger C pool in the soil underneath plants (Kieft et al., 1998; Cable et al., 2008; Qi et al., 2010) also encouraged greater proliferation of soil microorganisms that probably contributed to increasing DR in annual plant surfaces when activated by rainfall and soil moisture. In addition, annual plant DR also included the autotrophic respiration of the leaves, which contributed to the overall DR and was probably relevant during the growing season of these species. Previous studies have also pointed out higher CO2 effluxes from soil under plant cover than on interplant soil spaces in drylands (Maestre and Cortina, 2003; Cable et al., 2008; Qi et al., 2010; Muñoz-Rojas et al., 2016).

Our results show that photosynthesis of biocrusts overshadowed C lost by biocrusts and soil microbial communities under biocrusts, resulting in a C gain from all biocrust types only after long hydration with high available moisture as well as mild temperatures (winter field campaigns) at both El Cautivo and Las Amoladeras (Figs. 3 and 4). Nevertheless, all biocrust types had a low or insignificant net CO_2 flux most of the time during drought or with low soil moisture, or emitted CO_2 , especially following rainfalls after the long dry summer period (fall measurement campaigns) during which infiltration reached a substantial depth (subsequently wetting large heterotrophic communities) (Figs. 1 and 3). Therefore, a realistic estimate of the C-balance in ecosystems with crusted soils should not only take biocrusts into account, but also the microbial communities of the underlying soils, which significantly contribute to soil respiration.

5. Conclusions

Our study demonstrated that the C balance of biocrusts varies widely, depending on the interplay of several environmental variables (such as rainfall events, frequency of rainfall, soil moisture, air humidity, temperature, PAR and soil type) and biocrust successional stage. During periods of drought and high temperatures, both DR and GP fluxes were very low, resulting in almost negligible NP fluxes. However, when water was available again, they became active, first emitting large amounts of CO₂, and after recurrent short periods of water availability, promoting a neutral or a net C gain, while a net CO₂ release was generally found for other important ground covers such as annual plants.

When the biocrust was active, late successional biocrusts (i.e. lichens and mosses) had higher photosynthetic activity than early successional biocrusts (developed and incipient cyanobacteria crusts). Nevertheless, these late successional biocrusts and underlying soil also showed higher respiration rates than early successional stages. Therefore, although late successional biocrusts, such as the lichens and mosses, initially pointed to a better CO_2 sink potential than the cyanobacteria, there were no significant differences between the net CO_2 fluxes of these successional stages in either of the two semiarid ecosystems. These results highlight the importance of considering all contributions to C fluxes (both the biocrusts and the microorganisms throughout the soil profile) under real field conditions when modelling the C-balance of biologically crusted soils from drylands. The entire optimal range of environmental variables for net C gain in soils covered by biocrusts rarely occurs simultaneously in drylands, as these regions are characterized by their adverse environmental conditions. This significantly limits the CO_2 sink potential of biocrusts, making it sporadic, and causing them to act as either net or neutral CO_2 sources during most of the year. Thus, in order to characterize the role of biocrusts in dryland C balance correctly, fine-scale temporal measurements over different biocrust types and developmental stages are necessary. If not possible, field measurements should at least characterize their response during the first effective rainfalls of the year, as well as complete rainfall pulses and subsequent drying periods. Otherwise occasional measurements will not be representative of their real role in soil C fluxes.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx. doi.org/10.1016/j.soilbio.2018.05.020.

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