



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 CO₂ fluxes in these regions, where water availability limits vascular plant growth and development. The effect of biocrusts on CO₂ 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 CO₂ 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, CO₂ 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 CO₂ 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

CO₂ 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 CO₂ 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 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 $11.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ under optimal conditions, which is very similar to the rates of some higher plants (Lange, 2003).

In drylands, daily and seasonal CO_2 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, CO_2 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 CO_2 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 CO_2 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 CO_2 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 CO_2 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 CO_2 fluxes in biologically crusted soils and the main factors that govern their variability. This goal was achieved by: (i) *in situ* CO_2 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 CO_2 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 CO_2 fluxes on both annual and daily time scales (iv) estimating daily CO_2 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 CO_2 fluxes from biocrusts, so that CO_2 fluxes would be negligible during dry periods and significantly increase during wet soil periods. We also hypothesized that gross photosynthesis, and thus net CO_2 uptake, would be higher in well-developed biocrusts than 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 (N37°01' W2°27', 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 south-east, 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 calcareous 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 Rey, 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, high-intensity and associated with thunderstorms, but there are also low-intensity 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

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