



Effects of rainfall manipulations on carbon exchange of cyanobacteria and moss-dominated biological soil crusts

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ARTICLE INFO

Keywords:

Biocrusts
Water addition
Semi-arid region
Carbon balance

ABSTRACT

Biological soil crusts (biocrusts) are a vital biotic component of dryland ecosystems that impact global nitrogen (N) and carbon (C) cycling. Water availability is the main controller of physiological function of biocrusts in these ecosystems, yet few studies have compared the carbon balance of different biocrusts responding to different water treatments. In this study, we explored the effects of water availability on carbon exchanges of different biocrusts by measuring *in situ* net CO₂ fluxes in cyanobacteria and moss-dominated biocrusts under four water treatments (2 mm, 5 mm, 10 mm, and 20 mm) in a fenced grassland on the Loess Plateau, China. Our results indicate that water availability played a vital role in carbon balance of the biocrusts. Under higher water additions, both cyanobacteria and moss-dominated biocrusts fixed carbon but lower water additions did not always lead to net carbon gains, especially for the moss-dominated crusts. Importantly, our data indicate the existence of water thresholds for net carbon fixation of both cyanobacteria and moss-dominated biocrusts, below which carbon loss occurs. This implies that higher water availability would benefit moss growth, while lower water availability results in suitable circumstance for the growth of cyanobacteria.

1. Introduction

Biological soil crusts (hereafter termed biocrusts) are complex communities of cyanobacteria, lichens, mosses, fungi, and other bacteria (Belnap and Lange, 2003; Johnson et al., 2012). These crusts occupy about 40% of the Earth's terrestrial area (Safriel et al., 2005). Globally, biocrusts fix over 2.6 Pg of atmospheric CO₂ per year (Elbert et al., 2012) and can regulate the temporal dynamics of soil CO₂ efflux and carbon cycling in dryland ecosystems (Wilske et al., 2008, 2009; Castillo-Monroy et al., 2011b), mostly by influencing water runoff-infiltration rates (Chamizo et al., 2011; Zaady et al., 2013), affecting N fixation (Elbert et al., 2012), and modulating the activity of soil enzymes (Bowker et al., 2011; Miralles et al., 2013). These findings illustrate the importance of biocrusts in dryland ecosystems and highlight the need to account for biocrusts when assessing carbon balance in drylands.

Carbon fixation by biocrusts is an important source of organic C in

dryland soils (Billings et al., 2003; Wohlfahrt et al., 2008; Elbert et al., 2009; Mager and Thomas, 2011) and this process depends on the physiological activities of biocrusts, which are, in turn, regulated by water availability. Biocrust organisms are physiologically active only when wet and, once wetted, metabolic functions begin almost immediately (Belnap et al., 2001; Grote et al., 2010). In addition, the duration of water supply can affect biocrust carbon balance because, following a rainfall event, biocrusts usually initially exhibit net carbon loss due to the increased respiration required for ramping up photosynthetic machinery and later exhibit net carbon uptake as long as water availability continues to be sufficient (Coe et al., 2012). Thus, variations in the magnitude and temporal patterns of rainfall in drylands under climate change (Solomon, 2007; Singh and Kumar, 2015) would impact biocrust metabolism, including carbon fixation (Coe et al., 2012; Grote et al., 2010; Reed et al., 2012). Since the carbon balance of biocrusts is a substantial component of the C cycling of dryland ecosystems (Castillo-Monroy et al., 2011b), clarifying how

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their carbon balance responds to changes in water availability is critical for understanding how biocrusts may be altered under a changing climate.

Apart from the impacts of water availability, community composition of biocrusts can also influence their carbon fixation (Housman et al., 2006; Yu et al., 2012; Pietrasiak et al., 2013). Biocrusts with abundant lichens and mosses are capable of higher photosynthetic rates (Lange, 2003). Conversely, cyanobacteria-dominated crusts generally have low carbon fixation rates due to their relatively low biomass and chlorophyll contents (Garcia-Pichel and Belnap, 1996), as well as the limited penetration of light into the crust (Lange, 2003; Housman et al., 2006). Additionally, when water availability is extremely low, small additions of water, even dew, can activate cyanobacteria (Lange et al., 1997, 1998; Strong et al., 2013), while mosses require more water before achieving net carbon gains (Coe et al., 2012; Reed et al., 2012). Thus, assessing the responses of different biocrust species to changes in water availability is necessary for projecting carbon dynamics of drylands ecosystems.

Although ecologists have a rudimentary understanding of the effects of rainfall change on carbon balance of biocrusts (e.g. Coe et al., 2012), direct *in situ* experimental evidence of the impacts of water availability is still lacking. We sought to address this gap via water manipulations in drylands on China's Loess Plateau. Known for its serious soil erosion, the Loess Plateau occupies a total area of 628,000 km² in northern China and is mainly characterized by arid and semiarid climate. Biocrusts cover more than 70% of soil surface in this area. To assess how carbon fixation of biocrusts responds to variation of water, we measured *in situ* net CO₂ fluxes in cyanobacteria and moss-dominated biocrusts under four water treatments (equivalent to precipitation inputs of 2 mm, 5 mm, 10 mm, and 20 mm) in a fenced grassland. We hypothesized that carbon fixation of cyanobacteria and moss-dominated would respond differentially to water availability and that the water threshold for net carbon fixation of cyanobacteria-dominated biocrusts is lower than that for moss-dominated biocrusts.

2. Materials and methods

2.1. Field site description and experimental design

The field experiment was performed in a fenced, ungrazed grassland at the Semi-Arid Climate and Environment Observatory of Lanzhou University (SACOL), located at 35°57'N, 104°09'E (Gansu province, China) at an altitude of 1966 m above sea level. This region is characterized by a continental semiarid climate (mean annual air temperature is 6.7 °C and mean annual precipitation is about 382 mm). The soil is classified as a Sierozem, a calcareous soil that is characteristic of the Loess Plateau. The experimental site was a cultivated cropland before 1986 and has since been removed from long-term farming. The dominant plant species in this grassland are *Stipa bungeana*, *Artemisia frigida*, and *Tripolium vulgare*. Interplant spaces are dominated by cyanobacteria but patches of moss and lichens are also present. Biological soil crusts cover > 85% of the surface of the interplant space in this ecosystem.

In this study, 15 plots (three bare ground microsites, six cyanobacteria-dominated microsites, and six moss-dominated microsites) were randomly selected (Fig. 1). Each plot was 20 cm in diameter based on the measuring collars of the LI-8150 instrument. To avoid the influence of natural rainfall events, we chose October to conduct our experiment, a month in which the study site receives very little rain. The experiment started in early October 2013 and ended at the end of the month. First, plots with no plants and no bio-crust were chosen to serve as ambient controls (hereafter: bare soil). Second, microsites dominated by low cover of cyanobacteria were selected (hereafter: low C-BSCs). The third treatment consisted of microsites with high cyanobacteria cover (hereafter: high C-BSCs). The fourth and fifth treatments had low and high cover of mosses (hereafter: low M-BSCs and high M-

BSCs), respectively.

Due to limitation of gas flux equipment, we conducted the different water treatments sequentially, with subsequent water addition performed only after the effect of the previous one dissipated. Based on the local rainfall data (not shown), we selected 2 mm and 5 mm to represent low water treatments and 10 mm and 20 mm to simulate high water additions. Each experimental plot received four simulated water treatments in succession. To compare the differences between treatments, we performed same water treatment at the same time on all plots (avoiding climate variation); the sequence was 2 mm, 5 mm, 10 mm, and then 20 mm. When the CO₂ fluxes in the plot became similar with that at the beginning of the period, we assumed that the effects of rainfall events had been dissipated. We then proceeded to apply the next water treatment. The interval after low water treatments was one day while the interval for larger water treatments was five days. This approach may have introduced some uncertainty, as a small water treatment may not be as impactful after a large one and, likewise, a large water addition may not be as beneficial after a small one. However, our experiment was focused primarily on possible differences between different biocrusts and not on the effects of rainfall event size *per se*. Water treatments were simulated using distilled water and hand pump sprayers, with large watering events obtained by increasing the number of hand-pumped sprays. The sprayers provided a very light spray chosen to avoid damaging biota and bare ground. For the higher water treatments, the water was not sprayed all at once; spraying lasted for approx. 10 min to attempt to minimize loss of water to the surrounding area. To avoid measuring degassing (i.e. water displacement of soil pore space gas with high CO₂ concentration), water was added 1 h before CO₂ measurements (before sunrise on the measurement day).

2.2. Measurement protocols

2.2.1. Net CO₂ fluxes

Net CO₂ fluxes were measured from October 6 to 30, 2013 by employing a closed dynamic soil CO₂ flux system (LI-8100 automated soil CO₂ flux system, LI-COR Inc., Lincoln, Nebraska, USA) consisting of an infra-red gas analyser (IRGA) unit equipped with a 16-Port Multiplexer unit (LI-8150, LI-COR Inc.) connected to 16 long-term chambers (20 cm in diameter; system volume 4093 cm³; LI-8100-104c, LI-COR Inc.). The chambers have a transparent outer cover to allow passage of sunlight. Thus, measurements within the chambers reflect net system CO₂ flux. For each measurement microsite, one soil chamber collar (20 cm diameter × 10 cm high, constructed from cylindrical polyvinyl chloride pipe) was inserted approximately 4 cm into the soil and remained in place for the duration of the study. The automated system measured each chamber in turn once per hour using the following settings: (i) dead band (interval between the total closure of the chamber and the beginning of flux data consideration), 20 s; (ii) observation length (duration of a single measurement), 90 s; (iii) purge time (period of air forced ventilation after each measurement), 20 s; and (iv) observation delay (interval between two consecutive measurements), 20 s; a flow rate of approximately 1.5 dm³ per minute.

2.2.2. Soil temperature and moisture

Soil temperature and soil moisture were estimated simultaneously with net CO₂ fluxes. Soil temperature and moisture probes (Decagon Devices, Pullman, WA, USA) were attached to the chamber sensor interface in the long-term chambers, and were inserted 5 cm below the soil surface. All data were recorded automatically in the storage disk inside the LI-8100.

2.2.3. Net CO₂ fluxes of biocrusts

The measurements of biocrust microsites include both the biocrust biota living on the surface and the entire soil community under them. The status of heterotrophic microbes and plant root may be different between soils under biocrusts and bare soil. However, this difference

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