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Short Communication

Non-rainfall water inputs: A key water source for biocrust carbon fixation

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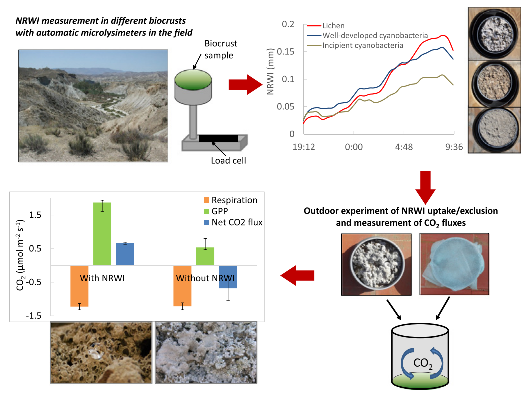
HIGHLIGHTS

- NRWI was measured with automated microlysimeters in different biocrust types.
- NRWI deposition increased with greater biocrust development.
- The effect of NRWI on biocrust CO_2 fluxes depended on the main NRWI source.
- Dew mainly stimulated biocrust photosynthesis, resulting in a net CO_2 uptake.

GRAPHICAL ABSTRACT



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ABSTRACT

Links between water and carbon (C) cycles in drylands are strongly regulated by biocrusts. These widespread communities in the intershrub spaces of drylands are able to use non-rainfall water inputs (NRWI) (fog, dewfall and water vapour) to become active and fix carbon dioxide (CO_2), converting biocrusts into the main soil C contributors during periods in which vegetation remains inactive. In this study, we first evaluated the influence of biocrust type on NRWI uptake using automated microlysimeters, and second, we performed an outdoor experiment to examine how NRWI affected C exchange (photosynthesis and respiration) in biocrusts. NRWI uptake increased from incipient cyanobacteria to well-developed cyanobacteria and lichen biocrusts. NRWI triggered biocrust activity but with contrasting effects on CO_2 fluxes depending on the main NRWI source. Fog mainly stimulated respiration of biocrust-covered soils, reaching net CO_2 emissions of 0.68 μmol m^{-2} s^{-1}, while dew had a greater effect stimulating biocrust photosynthesis and resulted in net CO_2 uptake of 0.66 μmol m^{-2} s^{-1}. These findings demonstrate the key role that NRWI play in biocrust activity and the soil C balance in drylands.

1. Introduction

Water is essential for the functioning of living organisms and ecosystems. Most terrestrial organisms depend on water availability, mainly supplied by rainfall, for their metabolic activity. In drylands, where rainfall is scarce, other water sources such as fog, dewfall and water vapour adsorption, also known as non-rainfall water inputs (NRWI), acquire special relevance in the maintenance of biotic communities and ecosystem processes (Wang et al., 2017). For example, NRWI is the primary water source for endolith and biocrust communities in the hyperarid Atacama desert (Wierzchos et al., 2012; Lehnert et al., 2018; Jung et al., 2020) as well as for activation of fungal communities and soil

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microbial respiration responsible for litter decomposition in the Namib desert (Jacobson et al., 2015; Evans et al., 2020). These water sources are also fundamental for the functioning of a widespread soil community in drylands: biological soil crusts or biocrusts. They are associations of various living organisms comprising cyanobacteria, algae, microfungi, lichen and mosses that occupy the interplant spaces in most drylands around the world (Weber et al., 2016; Rodríguez-Caballero et al., 2018). Biocrusts communities are dominated by poikilohydric organisms that remain dormant during dry periods but become active as soon as moisture from either rainfall or small water amounts from NRWI become available (Lange et al., 1994, 2006). Because of their physiological activity upon wetting, biocrusts influence carbon (C) exchange in soils (Su et al., 2012; Miralles et al., 2018; Kheirfam, 2020) and numerous soil biogeochemical processes, modifying soil properties and affecting water processes and NRWI uptake (Fischer et al., 2012; Chamizo et al., 2016; Cantón et al., 2020; Eldridge et al., 2020). Biocrusts affect NRWI deposition by modifying the albedo, surface temperature, surface roughness and organic matter and fine particles content (Fischer et al., 2012; Rodríguez-Caballero et al., 2012; Rutherford et al., 2017). As all these variables change with biocrust cover and composition, it can be expected that different biocrust types have different effects on NRWI deposition. For example, previous studies have shown greater NRWI deposition in biocrusts compared to bare soils and that later-successional biocrusts composed of lichens and mosses capture water from NRWI more efficiently than less developed cyanobacteria biocrusts (Liu et al., 2006; Ouyang et al., 2017; Li et al., 2021). NRWI might also play an important role in biocrust C uptake (Ouyang and Hu, 2017), leading to a positive feedback mechanism between biocrusts development and water capture. However, the role of NRWI in biocrust C fixation might depend on NRWI amount and the main NRWI source. For instance, a minimum water amount is needed to achieve net C gain in biocrusts (known as "minimum water compensation point") (Lange et al., 1997). On the other hand, photosynthetic activity of some biocrust constituents can be stimulated by water vapour alone while others require liquid water in the form of fog or dew for their activation (Rosentreter et al., 2016; Jung et al., 2019).

Although some studies show that NRWI is able to trigger biocrust activity during early morning hours and stimulate C uptake (Lange et al., 1994, 2006), the direct effect of NRWI on biocrust C fluxes by explicitly excluding NRWI interception, has not been evaluated so far. The objective of this study was two-fold: i) to examine whether biocrust type affects NRWI uptake; ii) to evaluate the ability of NRWI to trigger biocrust photosynthetic and respiratory activity and whether this response depends on the main NRWI source. In this paper, we aimed to test the following two hypotheses: i) the effect of biocrusts on NRWI uptake depends on biocrust type or composition; ii) NRWI is able to trigger biocrust activity with different effects on C dynamics depending on the predominant NRWI source.

2. Material and methods

2.1. NRWI deposition measurement in different biocrust types under field conditions

NRWI deposition was measured in different biocrust types under field conditions at the El Cautivo experimental site. The site is a badlands catchment within the Tabernas desert, SE Spain (N37°00′37″, W2°26′ 30). Soils are scarcely developed, with low organic C content (0.6%), and a silty loam texture (Chamizo et al., 2016). Mean annual temperature is 18.5 °C, mean annual rainfall is 235 mm, and mean annual potential evapotranspiration is 1666 mm, indicating a strong annual water deficit. Dew can represent up to 12% of the total rainfall in the area (Moro et al., 2007). Most non-vegetated areas are covered by biocrusts, which occupy up to 50% of the soil's surface (Rodríguez-Caballero et al., 2019). According to crust colour, morphology and composition (mainly presence of mid-late successional lichen species), three biocrust types, from lower to higher development, were identified at this site: i) incipient light cyanobacterial biocrust; ii) well-developed dark cyanobacteria biocrust; and iii) *Diploschistes diacapsis*-dominated lichen biocrust (L). Nine PVC collars (15 cm diameter and 9 cm depth) were driven into biocrust covered soil (3 on each biocrust type) and then extracted and sealed on the bottom with a PVC base. NRWI were measured on these samples using automated microlysimeters. The automated microlysimeter consisted of a 3 kg rated capacity single-point aluminium load cell (model 1022, 0.013 m × 0.0026 m × 0.0022 m, Vishay Tedea-Huntleigh, Switzerland) connected to a PVC plate by a rod, which was also protected by a PVC tube. In the field, the collected soil samples were placed over the PVC plate so that their surface was at the ground level. Data were recorded at 15 s intervals and stored as 15-min averages in a datalogger (CR1000, Campbell Scientific, Logan, UT, USA). The load cell gives a mV signal so that we performed a calibration of the load cell by adding small loads from lower to higher weight up to 2 kg, to transform voltage to weight. A more detailed description of the automated microlysimeters can be found in Uclés et al. (2013, 2015). Dew was considered when changes in mass of the microlysimeters were positive and soil temperature was below the dew point temperature, and the rest of water input was assumed to be water vapour adsorption. Measurements were recorded between mid-October and December 2012. Some data were lost due to instrument malfunctioning, so that a total of 49 days were recorded.

2.2. Influence of NRWI deposition on CO_2 exchange in biocrusts

We performed an outdoor experiment to examine the potential of NRWI to stimulate biocrust activity on the biocrust dominated by *D. diacapsis*, which was selected as the focal type because it showed the highest NRWI uptake during the microlysimeter monitoring experiment. Initially, an attempt was made to conduct the CO_2 exchange measurements in situ in the field, but after several unsuccessful attempts due to the absence of NRWI events, samples were collected from the field and transported to the University of Almeria campus, located at 30 km from the field site and exhibiting similar climatic conditions. Six PVC collars (10 cm diameter and 5 cm depth) containing the *D. diacapsis* lichen biocrust and the underlying soil were extracted, sealed on the bottom with a PVC base and carefully transported to the Almeria University, where they were placed outdoors. An automated microlysimeter containing the *D. diacapsis* lichen biocrust was also set up above the soil surface in an area adjacent to the samples (less than 1 m) to register NRWI amount. We assumed that registered NRWI amount at the outdoor experiment could be higher than in the field experiment due to microlysimeter placement above the soil level (not inserted into the soil) and its possible faster cooling. However, the main purpose of this experiment was not to quantify NRWI deposition in the biocrust but to assess whether NRWI uptake was able to trigger or not biocrust activity. To explore this, samples were divided into two sets, each one comprising three samples. First, we measured CO_2 fluxes in the two sets of samples after one night with low NRWI deposition (event 1, <0.10 mm) and after another night in which an important NRWI event (mainly fog) occurred (event 2, 0.45 mm). After this, we excluded NRWI deposition from the second sample set (set 2) by covering the PVC collars during night with a thin polypropylene cloth (Xuanying Crafts Co., Ltd., Wenzhou, Zhejiang), which allowed heat and gas exchange but avoided water passing. Further, we measured CO_2 fluxes in the two sets, exposed (set 1) and excluded from NRWI uptake (set 2), after two NRWI events, one in which the main water source was fog (event 3, 0.45 mm) and another in which the dominant source was dew (event 4, 0.40 mm). For NRWI exclusion, samples were covered in the late evening, and CO_2 fluxes were measured in the early morning of the following day, after checking the occurrence of NRWI during night. The cloth was removed from the collars of the second sample set and after allowing soil adaption to light for 15 min, CO_2 fluxes were measured in all samples. Net CO_2 exchange (μmol m^{-2} s^{-1}) was measured with an infrared gas analyzer (IRGA) (LI-6400, Lincoln, NE, USA) attached to a custom-designed transparent methacrylate chamber with a volume of 668 cm^3 (Ladrón De Guevara et al., 2015). Values were recorded once the CO_2 and H_2O values of the sample and reference IRGAs were stabilized. CO_2 readings of the sample and reference IRGAs were matched (i.e. the sample IRGA was adjusted to match the reference) before each individual measurement to minimise possible biases in the measurements, especially when the ΔCO_2 value is small. Positive values indicate net CO_2 uptake while negative values indicate net CO_2 emissions. Dark respiration (DR, μmol m^{-2} s^{-1}) was measured with an opaque chamber attached to an IRGA EGM-4 (PP systems, Hitchin, UK). This device operates as closed dynamic systems, so that the flux was determined from the initial slope of CO_2 molar fraction versus time using a quadratic regression. Each respiration measurement lasted for 120 s and was corrected for atmospheric pressure and the chamber air temperature. On each sample, we measured first net CO_2 flux and immediately after, dark respiration. Gross photosynthesis (GPP, μmol m^{-2} s^{-1}) was obtained as the sum of the net photosynthesis and dark respiration. See Miralles et al. (2018) for further details about the measurement protocol. Measurements lasted until mid-morning, the time at which NRWI effect was no longer noticeable.

2.3. Statistical analyses

CO_2 flux variables were checked for normality and the effect of NRWI event and treatment (set 1/set 2) on Net CO_2 exchange, DR and GPP was analysed using a General Linear Model (GLM). After this, significant differences in CO_2 fluxes between the two biocrust sets at the different measurement times during the four NRWI events were analysed using a *t*-test. Significance was established at $p < 0.05$. Statistical analyses were performed using STATISTICA 8.0 (StatSoft, Inc., Tulsa, OK, USA).

3. Results and discussion

During the field experiment, 33 dewfall events were registered, of which 33% were lower than 0.05 mm, 27% were between 0.05 and 0.10 mm, 15% were between 0.10 and 0.15 mm, 12% were between 0.15 and 0.20 mm, and 12% were higher than 0.20 mm. Total dewfall deposition during the measured period ranged from 2.84 mm in the incipient biocrust to 3.21 mm in the lichen biocrust. Average daily dewfall deposition was 0.08 mm in the incipient cyanobacterial biocrust and 0.09 mm in the well-developed cyanobacteria and lichen biocrusts. Fig. 1 shows NRWI deposition by the crust types during two events in which dewfall was the predominant water input, one recorded in autumn (October 16th) and another recorded in winter (December 26th). In autumn, incipient cyanobacteria showed the lowest accumulated NRWI during night (0.08 mm), then followed by well-developed cyanobacteria (0.10 mm) and lichen biocrust (0.12 mm) (Fig. 1a). Accumulated NRWI reached a peak at 7:00 solar hour time (GMT + 0, 1 h before sunrise), after which it decreased due to water loss by evaporation. NRWI accumulation was higher during the event registered in winter but the same pattern was observed among crust types (Fig. 1b). NRWI accumulation was lower in incipient cyanobacteria (0.11 mm) and increased in well-developed cyanobacteria (0.16 mm) and lichen biocrust (0.18 mm). Accumulated NRWI reached a peak at 8:30 solar hour (GMT + 0), coinciding with sunrise.

Our results coincide with previous studies that have also found that NRWI accumulation in biocrusts is the greatest before sunrise (Ouyang et al., 2017) or that NRWI deposition increases with biocrust development (Liu et al., 2006; Zhang et al., 2009; Ouyang et al., 2017; Li et al., 2021). The higher NRWI uptake in the most developed biocrusts, the lichen biocrust, can be attributed to biocrust effects on different variables that influence NRWI deposition. Thickness and biomass of photosynthetic organisms, which increase with biocrust development, have been reported as the main factors affecting NRWI deposition in biocrusts (Ouyang et al., 2017). Lower albedo (Rutherford et al., 2017) and the effect of crust thickness regulating soil temperature and enhancing the difference between surface and subsurface temperature (Ouyang et al., 2017) can also explain higher NRWI deposition in lichen biocrusts compared to less developed cyanobacterial biocrusts. Lichens also increase surface roughness and thereby surface area for water absorption (Rodríguez-Caballero et al., 2012), and organic matter and exopolysaccharide content (Chamizo et al., 2013) thus having a higher ability to retain water from NRWI. Besides, the peculiar morphology of *D. diacapsis*, which usually presents a low degree of attachment to the soil surface, thus facilitating water in the lichen's medulla to be retained by the thallus, could also enhance NRWI uptake (Souza-Egipsy et al., 2002; Raggio et al., 2021).

The recorded NRWI amounts exceeded the lower moisture compensation point reported in literature for different biocrust lichens (0.05–0.08 mm for *Diploschistes diacapsis*, Lange et al., 1997), suggesting that these water sources could have a crucial role in soil C gain by biocrusts. This was corroborated by the results obtained in the second experiment, in which we found significant differences in CO_2 fluxes in the biocrusts exposed to and excluded from NRWI interception.

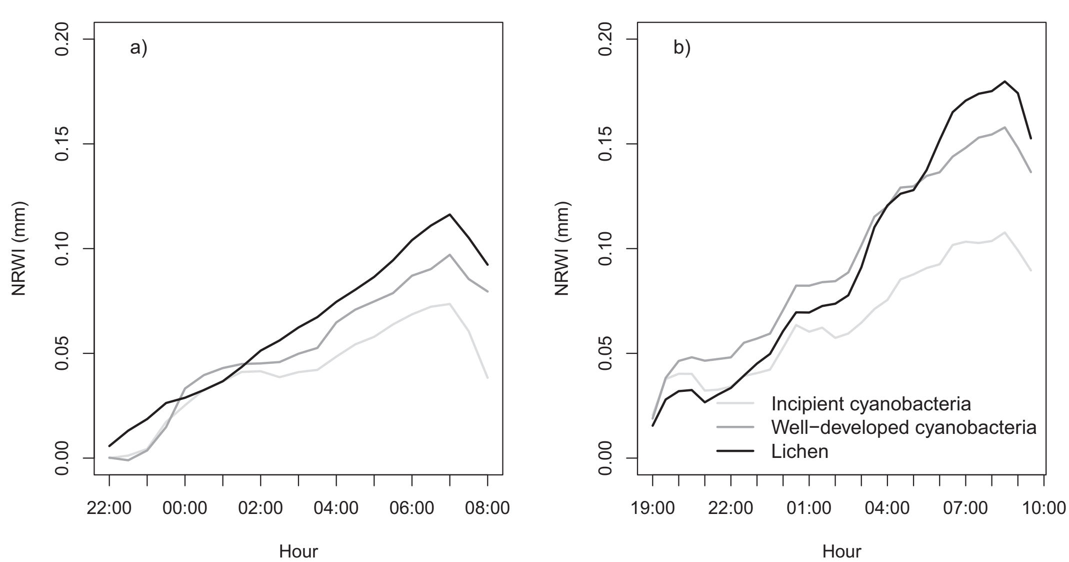

Fig. 1. Mean NRWI accumulation measured in the field in the biocrust types during an event occurring in autumn (a) and winter (b). Maximum standard deviation for the crust types was 0.01 mm in the autumn event and 0.03 mm in the winter event.

According to the GLM, there was a significant interaction of NRWI event and treatment on net CO_2 flux ($p < 0.001$), DR ($p = 0.014$) and GPP ($p < 0.001$), meaning that the two sets of samples showed different responses (net CO_2 flux, GPP and DR) to the different NRWI events. Net CO_2 exchange and GPP significantly differed between samples with and without NRWI in the dew event ($p < 0.001$), while DR significantly differed in the samples with and without NRWI in the fog event ($p < 0.01$).

Under low NRWI amount (Fig. 2, event 1, <0.10 mm, mean air temperature was 9.1 ± 1.2° and PAR ranged from 58 to 314 μmol photons m^{-2} s^{-1}), all samples (set 1 and 2) showed low CO_2 fluxes. Net CO_2 exchange ranged from −0.15 (in the early morning) to −0.51 μmol m^{-2} s^{-1} (late morning), indicating a net CO_2 emission to the atmosphere. After the NRWI event (0.46 mm) in which the main source was fog (Fig. 2, event 2, mean air temperature was 11.8 ± 0.6° and PAR ranged from 55 to 118 μmol photons m^{-2} s^{-1}), though photosynthesis was also activated, DR was the dominant process and CO_2 emissions (biocrust+underlying soil) surpassed biocrust CO_2 fixation, resulting in a net soil CO_2 release. A similar behaviour was observed after the fog event (0.45 mm) occurred under warmer conditions (mean air temperature was 20.7 ± 1.4° and PAR ranged from 329 to 644 μmol photons m^{-2} s^{-1}) in which the set 1 was exposed to NRWI interception and set 2 was excluded from it (Fig. 2, event 3). DR was higher in the samples receiving NRWI, which also showed a higher net CO_2 emission (net CO_2 exchange up to −0.68 μmol m^{-2} s^{-1}) than samples excluded from NRWI. It could be noted that the samples excluded from NRWI showed a low but positive C balance during the earliest hour, which could have been caused by small water uptake after removing the cloth and brief stimulation of lichen photosynthetic activity. A different behaviour was found after one night in which dew was the dominant NRWI source (0.40 mm). In this event (Fig. 2, event 4, mean air temperature was 11.4 ± 0.7° and PAR ranged from 72 to 389 μmol photons m^{-2} s^{-1}), CO_2 fluxes were measured in the biocrusts exposed to (set 1) and excluded (set 2) from NRWI uptake. In the early morning (8:00 s.h., GMT + 0), DR was similar in the two sets but photosynthesis was significantly higher in the biocrusts receiving NRWI. As a result, a net C gain was found in the biocrusts with NRWI (net CO_2 exchange up to 0.66 μmol m^{-2} s^{-1}), while a net CO_2 emission was found in the biocrusts excluded from NRWI. With time, as temperature and radiation increased, DR increased, resulting in a neutral CO_2 balance in the biocrusts with NRWI uptake, while biocrusts excluded from NRWI still showed a net CO_2 emission. During the last measure (9:00 s.h., GMT + 0), DR exceeded photosynthesis in biocrusts with and without NRWI uptake, resulting in a net CO_2 emission in both. Our results agree with previous findings that show an increase in both DR and positive net photosynthesis in lichen biocrusts after nocturnal NRWI hydration, lasting only for a short time (2 h) until desiccation (Lange et al., 2006). Minimum water content reported to maintain C balance was between 0.04 and 0.26 mm (Lange et al., 1997, 2006) and

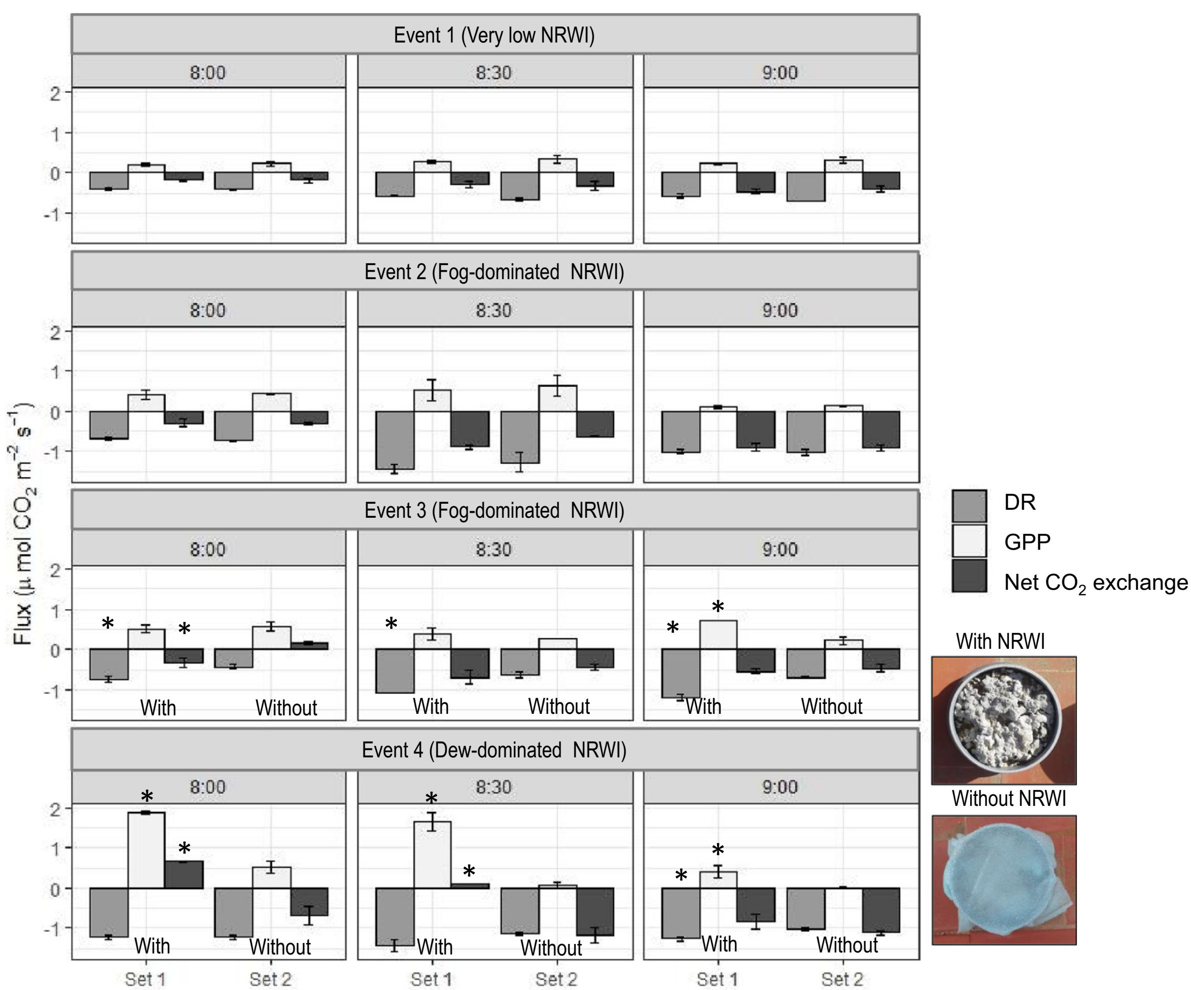

Fig. 2. CO_2 fluxes measured in the lichen biocrust during four NRWI events at outdoor conditions: event 1, one night with very low NRWI amount; event 2, NRWI with fog as predominant water source; event 3, NRWI with fog as predominant water source; event 4, NRWI with dew as predominant water source. In events 1 and 2, both sets of samples received NRWI. In events 3 and 4, set 1 received NRWI, while set 2 was excluded from NRWI interception. Negative values of net CO_2 uptake indicate net CO_2 emissions, while positive values indicate net CO_2 uptake. The asterisk indicates significant differences ($p < 0.05$) between the samples exposed to and excluded from NRWI deposition.

0.17 mm (Ouyang et al., 2017). According to our results, estimated C gain due to biocrust activation by dew-dominated NRWI uptake during the measured event was 121 mg C m^{-2} day^{-1}. While fog has been found to be a relevant water source for biocrusts in some hyperarid coastal deserts such as the Namib (Lange et al., 1994, 2006) or the Atacama desert (Jung et al., 2019, 2020) where it can account for up to 1.4 mm day^{-1} (Lehnert et al., 2018), fog has been found to be a minor NRWI component in our study area, where water vapour adsorption and dewfall are the main NRWI sources for biocrusts (Uclés et al., 2016). The higher occurrence of these events in our study site and the observed C gain due to biocrust activation by dewfall in the current experiment let us think that these NRWI events can be responsable for an important fraction of the annual C fixed by biocrusts in our study site.

In the coming decades, NRWI amount and/or duration might decrease in Mediterranean drylands due to predicted increase in temperature and consequent evaporation as consequence of global warming (Tomaszkiewicz et al., 2016), thus affecting biocrust compensation point and reducing the net C balance of biocrusts (Ladrón De Guevara et al., 2014). Moreover, impacts of climate change and land use change are predicted to reduce global biocrust cover between 27 and 39% by 2070 and cause changes in biocrust composition by replacing well-developed biocrusts by less-developed ones (Rodríguez-Caballero et al., 2018). Both, combined reduction of NRWI and biocrust cover will affect water availability and C fluxes, with unpredictable consequences in dryland functioning that might potentially affect the global C balance in the mid-long term.

4. Conclusions

Biocrust affects NRWI deposition and consequently modify the local soil water balance. More developed biocrusts as those composed by lichens increase NRWI uptake compared to incipient cyanobacterial biocrusts. This study also confirms the crucial role of NRWI in biocrust activity and how different NRWI sources might have different effects on biocrust C fluxes. Our results suggest that NRWI whose main water source is dew could mainly stimulate biocrust photosynthetic activity, leading to a net CO_2 uptake. In contrast, NRWI whose main source is fog could mainly lead to net CO_2 emissions by activating respiration of biocrust constituents as well as underlying soil microorganisms. However, this behaviour should be further investigated during events of different environmental conditions and covering a wide range of biocrust types to accurately elucidate the role of these NRWI events on C fluxes in biocrust-covered soils. Therefore, in drylands where NRWI represents an important water input, a major role of biocrusts in C assimilation and affection of soil microbial activity and plant productivity can be expected.

CRediT authorship contribution statement

Sonia Chamizo: Investigation, Data curation, Writing – original draft, Visualization. **Emilio Rodríguez-Caballero:** Investigation, Data curation, Writing – review & editing, Visualization. **María José Moro:** Methodology, Writing – review & editing. **Yolanda Cantón:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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