Biocrusts positively affect the soil water balance in semiarid ecosystems

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Abstract

Biocrusts play crucial roles in hydrological processes by controlling soil water availability and regulating water redistribution from source to sink areas. Most studies have examined the influence of biocrusts on isolated components of the soil water balance, but few have addressed this matter from an integrated point of view, involving their influence on all components together. Such integration is crucial to elucidate the overall effects of biocrusts on the soil water balance. The aim of this study was to review the role of biocrusts in the soil water balance, by examining their influence on infiltration, evaporation and soil moisture at plot scale, in two contrasting ecosystems of SE Spain. Our results show that biocrust infiltration was higher in flat soils with sandy loam texture than in steep soils with silty loam texture. The influence of biocrusts on infiltration depended on rainfall intensity. Biocrusts increased infiltration with respect to biocrust-removed soils during low intensity rainfalls, but showed similar or even lower infiltration than biocrust-removed soils during high intensity events. As a result of the increase in infiltration and a decrease in evaporation during wet cold periods, biocrusts increased soil moisture when compared to biocrust-removed soils. However, during warm periods, biocrusts and biocrust-removed soils lost water very quickly, thus resulting in similar water losses and moisture content under both types of surfaces. We conclude that biocrusts increase water input by increasing infiltration and soil moisture, and reduce water output by reducing soil evaporation, thus eventually enhancing the available water to plants.

KEY WORDS: biological soil crust, physical soil crust, infiltration, moisture, evaporation, available water capacity, review.

INTRODUCTION

Arid and semiarid areas throughout the world are characterised by sparse and patchy distribution of vegetation embedded in an open matrix. In these ecosystems, water availability is the most limiting factor for ecosystem functioning (Reynolds *et al*., 2004), and water redistribution from source to sinks areas plays a vital role in maintaining plant productivity. During episodic rainfall events, runoff is generated in the non-vegetated areas and redistributed to adjacent vegetation, which acts as surface obstruction for water, sediments and nutrients (Ludwig *et al*., 2005; Puigdefábregas, 2005; Cantón *et al*., 2011). Hence, functioning of vegetation is strongly conditioned by the hydrological response of interplant areas (Cantón *et al*., 2011). These interplant areas, though apparently "absent of life", are not bare but commonly colonised by complex communities of various living organisms such as cyanobacteria, algae, microfungi, lichen, mosses and other microorganisms known as biological soil crusts or biocrusts, which dramatically modify soil functions at the surface. Biocrusts are widely distributed in arid and semiarid areas where they can cover more than 70% of the interplant soil surface (Belnap, 2006). Biocrusts represent a crucial link between atmospheric and soil processes and become an essential element in understanding hydrological, geomorphologic, biological and ecological processes (Maestre *et al*., 2011). Biocrusts modify the hydrological response of soils where they appear and thereby, control the transfer of water, nutrients and sediments from "bare" to vegetated areas (Belnap *et al*., 2005; Ludwig *et al*., 2005).

Despite their recognized importance, the role of biocrusts in hydrological processes, as compared to soils devoid of them, is not fully understood. Direct factors such as crust cover and composition and their indirect effects on soil properties such as soil roughness, stability, porosity and hydrophobicity and interactions among them, regulate water movement and retention in soils which ultimately determine their role in hydrological processes. On the one hand, biocrusts can increase infiltration and thereby decrease runoff by enhancing surface roughness (Rodríguez-Caballero *et al*., 2012) and soil porosity (Menon *et al*., 2011), but on the other hand they can decrease infiltration and increase runoff due to the hydrophobicity of some species (Tighe *et al*., 2012) and clogging of soil pores as a consequence of cyanobacteria swelling when wet (Malam Issa *et al*., 2009; Fischer *et al*., 2010; Rodríguez-Caballero *et al*., 2015a). High water retention capacity and subsequent pore clogging in biocrusts lead to lower evaporation and increased soil moisture versus bare surfaces (Colica *et al*., 2014), but alternatively, biocrusts may increase the amount of water available to be evaporated, thus increasing evaporation rates (Chamizo *et al*., 2013a). Biocrusts may also increase evaporation and reduce soil moisture by darkening the soil surface and increasing soil temperatures (Kidron and Tal, 2012). Due to the complex effects of biocrusts on hydrological processes, understanding their final role in the soil water balance is an issue yet to be sorted out.

Moreover, the influence of biocrusts on soil hydrology can be strongly conditioned by the community that dominates the crust. Later successional biocrusts composed mainly of lichens and mosses are likely to have a different role in hydrological processes than early successional biocrusts mainly composed of cyanobacteria. For instance, more developed biocrusts confer greater roughness to the soil surface and have the ability to absorb large amounts of water, thereby, increasing infiltration (Belnap *et al*., 2013; Chamizo *et al*., 2012a) and soil water content (Chamizo *et al*., 2013b; Berdugo *et al*., 2014; Colica *et al*., 2014) but, on the other hand, their higher biomass can cause pore clogging and reduce soil permeability, thus reducing water movement to deeper soil layers (Xiao *et al*., 2011; Fischer *et al*., 2012; Zhao and Xu, 2013). These complex interactions among biocrust attributes make advisable the study of a variety of crust types or biocrust developmental stages to achieve more accurate knowledge of how biocrusts can affect hydrological processes.

In addition to the biocrust type and its effects on soil properties, factors related to site characteristics are essential to understand biocrust influence on hydrological processes. The soil type and especially soil texture determines to a large extent the influence of biocrusts on soil hydrology. In soils with more than 80% sand, the presence of biocrusts increases water retention of top soils but also seals the surface, limiting downward movement of water through the sand and increasing runoff. In soils with less than 80% sand, the presence of biocrusts increases the formation of soil aggregates and consequently porosity, thus enhancing infiltration compared to bare soils (reviewed in Warren, 2003). Concerning the temporal variability of hydrological processes, recent studies point to the importance of antecedent moisture and the type of rainfall (Wang *et al*., 2007; Li *et al*., 2010; Chamizo *et al*., 2012b; Wu *et al*., 2012; Rodríguez-Caballero *et al*., 2013) in the role of biocrusts in hydrological processes. Most studies on infiltration-runoff in biocrusts have either consisted of point measurements with infiltrometers, which do not account for the effect of key biocrust properties such as surface roughness on runoff generation, or have consisted of runoff assessments based on rainfall simulation experiments which, however, do not account for the variability in rainfall intensity that characterises natural rain events. Investigation of how biocrusts affect infiltration-runoff processes under different types of rain event, with varying intensity and amount, may help explain the contradicting results found in the literature.

Given that biocrusts cover a large extent of the non-vegetated areas in many arid and semiarid ecosystems and considering water as the main limiting factor of these ecosystems, issue of how they affect hydrological processes is a relevant question of interest. So far, studies have examined the influence of biocrusts on isolated components of the water balance. However, this approach provides a biased view of the global role that biocrusts play in soil hydrology. Addressing the role of biocrusts in the water balance from an integrated perspective, by jointly analysing their effect on infiltration-runoff, evaporation and soil moisture, can provide a better understanding of how these soil communities affect soil water availability in arid and semiarid areas. In this study, we therefore explore the role of biocrusts in the major soil water balance components (infiltration-runoff, evaporation, and soil moisture) considering a gradient of crust types, including physical crusts or bare soils and biocrusts at different stages of development, in two different ecosystems characterised by contrasting soil texture. Our main objectives were to examine how the presence and developmental stage of biocrust affects: i) infiltration-runoff at the plot scale under simulated and natural rainfall; ii) soil evaporation; and iii) soil moisture dynamics, as a result of their influence on both water infiltration and evaporation. Our ultimate goal is to verify whether biocrusts have a positive or negative role in the soil water balance and eventually, whether their presence enhances the amount of water available.

STUDY AREA AND METHODS

Study sites and characterization of soil crusts

Two sites representing key spatial distributions of biocrusts in semiarid ecosystems were chosen in Almeria province (SE Spain): a) El Cautivo, in the Tabernas desert, with crusts (physical and biological) covering around 80% of the soil surface and located on fine-textured soils; and b) Las Amoladeras, with crusts (mainly biocrusts) representing almost a third of the soil cover and on coarse-textured soils. At both sites, the interplant soil not covered by biocrusts is usually physically crusted.

i) El Cautivo (N37º00´37”, W2º26´30”) site is located in the Tabernas basin, partially surrounded by the Betic cordillera. The Tabernas basin is mainly filled with Neogene marine sediments (Kleverlaan, 1989), consisting of gypsum-calcareous mudstones and calcaric sandstones. Badlands have developed on the gypsum-calcareous mudstones from the Tortonian age, where the overlying sandstone has been dissected. The climate is semiarid thermo-Mediterranean, with long, dry summers and most rainfall falling in winter (31% to 55%), the rest being distributed between spring and autumn. The average annual precipitation is 235 mm and the mean annual temperature is 17.8ºC, making this area among the driest in Europe. Annual potential evapotranspiration is around 1500 mm, indicating a considerable annual water deficit (Cantón *et al*., 2003). The main soil types are Epileptic and Endoleptic Leptosols, Calcaric Regosols and Eutric Gypsisols (FAO, 1998), and soil texture is silty loam (30% sand, 59% silt, 11% clay). The landscape is characterized by narrow valleys mostly running in a NW-

SE direction, clearly asymmetrical in slope gradient and plant cover. The SW-facing slopes are steeper (slope gradients from 30º to 77º) than the NE slopes (10º to 40º), with little soil development and are practically devoid of vegetation (Cantón *et al*., 2004a). On these SW-facing slopes, low soil stability and higher water stress restricts the establishment of biocrusts and vascular vegetation, and the soil surface is mainly covered by physical crusts, except in some areas where it is covered by incipient biocrusts and isolated shrubs. In contrast, NE-facing slopes are densely covered by lichens and scattered annual and perennial plants in the upper part, with decreasing lichen cover and increasing perennial vegetation cover down towards sediments. In the sediments, soils are covered by annual and perennial plants with biocrusts appearing in the interplant spaces. The following crust types, from lesser to higher development, were identified at this site (Fig. 1a): 1) a physical soil crust (P) formed by raindrop impact, which appears in the soils uncovered by vegetation or biocrusts; 2) a light-coloured early-successional cyanobacteria biocrust (referred to hereafter as "light cyanobacteria" or LC); 3) a dark-coloured late-successional cyanobacteria biocrust (referred to hereafter as "dark cyanobacteria" or "cyanobacteria" or DC), which also contained numerous pioneer lichens such as *Placynthium nigrum*, *Collema sp.*, *Endocarpon pusillum, Catapyrenium rufescens* and *Fulgensia sp.*; and 4) a light-coloured lichen biocrust (L), mainly composed of *Diploschistes diacapasis* (crustose) and *Squamarina lentigera* (squamulose), with considerable cyanobacterial cover. Other less frequent lichen species were *Buellia zoharyi* and *B. Epigea, Lepraria crassissima, Acarospora nodulosa, Toninia sedifolia* and *Psora decipiens*.

ii) Las Amoladeras (N36º48´34", W2º16´6") is located in Cabo de Gata-Níjar Natural Park, approximately 22 km east of the city of Almería and 1 km north from the Mediterranean Sea. It is an exposed, dissected caliche area in the distal, flat part of an alluvial fan system south of the Alhamilla range. The climate is also semiarid, with mean annual rainfall of 200 mm and a mean annual temperature of 18°C. Annual potential evapotranspiration is around 1390 mm (Rey *et al*., 2011). Soils are thin, saturated in carbonates, and have moderate rock fragment content. They are classified as Calcaric Leptosols and Haplic Calcisols (FAO, 1998) and soil texture is sandy loam (61% sand, 29% silt, 10% clay). Trampling by grazing sheep and goats is frequent. Vegetation consists of grasses and scattered shrubs which cover around 30% of the area. Annual plants develop among the perennial grasses and shrubs and cover from 10 to 25% of the soil surface depending on the amount of annual rainfall. Biocrusts occupy the open areas in between the shrubs and represent up to 30% of the whole soil surface. The rest of the area is occupied by caliche outcrops and rock fragments, with very few interplant patches occupied by bare soil. The most representative crust types identified in this area were biocrusts (Fig. 1b): 1) dark-coloured late-successional cyanobacterial biocrust (DC), 2) light-coloured lichen crust (L), and 3) dark-coloured late-successional moss-dominated biocrust (M). Lichens and mosses represented later stages of biocrust development than cyanobacteria. The species composition of the cyanobacteria and lichen biocrusts was similar to that of the same biocrust types at El Cautivo.

Runoff measurements

i) Rainfall simulations. The influence of biocrusts on infiltration was examined at both study sites under a high-intensity simulated rainfall, due to the importance of intense events from the perspective of runoff and sediment yield (Cantón et al., 2011). Four circular 0.25 m^2-microplots bounded by steel rings were delimited on soils covered by each crust type (physical soil crust, light cyanobacteria, dark cyanobacteria and lichen biocrusts at El Cautivo, and dark cyanobacteria, lichen and moss biocrusts at Las Amoladeras). A rainfall simulation of 1 hour-duration with a constant intensity of 50 mm h^{-1} (5 year return period) was conducted over each microplot. We used the rainfall simulator designed by Calvo-Cases et al. (1988), which possess a sprinkler nozzle (Hardi4680-10E) that rains over a 1-m^2 area and generates drops with a mean time-specific kinetic energy of 638 J m^{-2} h^{-1} (Iserloh *et al*., 2013). Runoff volume was recorded at different intervals during the duration of the experiment. Infiltration amount in the different crust types was determined as the difference between applied rainfall and total runoff after the 1-hour simulated rainfall.

ii) Natural rainfall. As the influence of biocrusts on infiltration may vary with type of rainfall and considering that most rainfalls in arid and semiarid areas are low in amount and intensity, runoff was monitored in soils covered by biocrusts and biocrust-removed soils under natural rains. Due to the limited occurrence of runoff events at Las Amoladeras, as consequence of its flat topography and coarser soil texture, runoff monitoring during natural rainfall was only conducted at the El Cautivo badlands site, where the occurrence of runoff events is more frequent. Runoff yield was measured in 10 open plots of around 1-m^2 area, during the hydrological year 2009-2010 (September 2009-August 2010). We selected plots of the two most widely represented biocrust types in the area: dark cyanobacteria (~70% cyanobacteria plot cover) and lichen biocrusts (~40% lichen plot cover and the rest colonised by cyanobacteria ~30% and bare soil), and soils where the top crust (0.5 cm thickness) was removed in 2007 and mainly consisted of physical crusts with very incipient colonization by cyanobacteria. Three plots were selected of each undisturbed biocrust type and 4 plots of biocrust-removed soils. All plots were set up on the same type of soil and had similar slope (10-15º) and aspect (NW). Plots were bounded at the bottom by a steel sheet with a hole in the centre to drain runoff water to a 20-l deposit container. Runoff volume was measured in these plots after each rainfall event that was heavy enough to produce runoff. Rainfall amount was recorded by a tipping-bucket gauge with a 0.20-mm resolution located next to the plots. The contributing area to each plot was estimated from a 1 cm-resolution digital elevation model built up from height points of the plot surface recorded with a Leica ScanStation 2 terrestrial laser scanner (Leica Geosystems AG, Heerbrugg, Switzerland) using the D-8 algorithm (O'Callagan and Mark, 1984). Infiltration amount after each rainfall event as well as annual infiltration during the monitored year were determined for each plot. A more extensive description of the plots and the field instrumentation in the study site can be found in Chamizo *et al*. (2012b) and Rodríguez-Caballero *et al*. (2012, 2013).

Evaporation measurements

In late spring, soil evaporation was measured in the different biocrust types identified at El Cautivo (physical crust, light cyanobacteria, dark cyanobacteria and lichen biocrusts), using PVC micro-lysimeters (5 cm-radius and 5 cm-height). The micro-lysimeters were inserted into the soil one month before the evaporation measurements were conducted to allow their stabilization. Three micro-lysimeters were inserted into each crust type. To investigate whether the biocrust had any effect on evaporation, three additional replicates of each biocrust type were selected and the crust was removed once the micro-lysimeters had been extracted from the soil. Prior to the extraction of the micro-lysimeters, soil was irrigated to saturation down to at least 10 cm depth. Then, the micro-lysimeters were carefully removed from the soil and sealed at the bottom with a PVC sheet and placed in the field. Mass losses from saturation to dry soil were determined by manually weighting the micro-lysimeters every day on a calibrated balance with a precision of 0.1 g.

Soil moisture monitoring

During the study period (September 2009-August 2010), soil moisture was monitored in soils covered by the most representative crust types at both study sites: dark cyanobacteria and lichen biocrusts, and soil where the biocrust was removed. Soil moisture was continuously monitored with ECH_2O moisture sensors inserted horizontally at 3 and 10 cm depths (EC-5 and 10HS, respectively, Decagon Devices, Inc., Pullman, Washington, USA), and data were stored every 10 min in Decagon's Em50 loggers. Raw data were converted to volumetric water content (VWC, m^3 m^{-3}) using the standard calibration equations developed by Decagon for the ECH_2O sensors. Daily averages were determined from the 10-min soil moisture records. From the moisture probe data, we calculated soil water loss (%), as the difference between the maximum VWC after rainfall and the minimum VWC after soil drying, under the biocrust types and biocrust-removed soil during periods of soil drying. In addition, available water capacity (in mm) in the upper 5 cm under the biocrust types and biocrust-removed soil was determined as the difference between water retention at field capacity and water retention at the wilting point. Field capacity was determined from the 10-min records after several rainfall events in which maximum VWC was reached and selecting values once drainage had decreased and VWC reached a steady-state, with a rate of change less than 0.001 m^3 m^{-3} hr^{-1} (Cantón *et al*., 2010). The wilting point was obtained from previous laboratory determinations with a Richard´s pressure membrane conducted on samples of the different crust types at both study sites (see Chamizo *et al*., 2012c).

Statistical analysis

Significant differences in infiltration and evaporation among crust types were analysed using one-way ANOVAs and the post-hoc LSD test. Significance was established at $p<0.05$. STATISTICA 8.0 (StatSoft, Inc., Tulsa, Oklahoma, USA) was used to perform the analyses.

RESULTS

Biocrust influence on infiltration

The influence of biocrusts on infiltration depended on the crust type, but also on other factors such as the site characteristics and the type of rainfall, mainly rainfall intensity. During the intense simulated rainfall (Fig. 2), infiltration showed contrasting results between sites and was lower at El Cautivo, where values ranged from 9 to 33 mm h^{-1}, than at Las Amoladeras, where values ranged from 17 to 48 mm h^{-1}, attributed to differences in topography and soil properties between both sites. At each site, infiltration significantly differed among crust types and generally increased with biocrust development, but there were some exceptions to this general pattern. At El Cautivo, infiltration increased with cyanobacteria cover, from physical crusts to light cyanobacteria to dark cyanobacteria. However, the most developed crust - the lichen biocrust - showed lower infiltration than cyanobacteria biocrusts and similar infiltration to physical crusts (Fig. 2a). By contrast, a different response was found at Las Amoladeras, where lichens exhibited numerous discontinuities due to frequent livestock trampling and thereby, these biocrust types showed higher infiltration than cyanobacteria. The highest infiltration at this site was recorded in the most developed moss biocrusts, which showed 1.5 and 2.2 times higher infiltration than lichen and cyanobacteria, respectively (Fig. 2b).

Similar behaviour to that observed during the simulated rain was found during the high intensity rains recorded in the monitored hydrological year (2009-2010). This year was atypically rainy and the annual rainfall greatly exceeded the mean annual rainfall of the area. Annual rainfall was 405 mm at El Cautivo and 535 mm at Las Amoladeras. Half of the events that generated runoff exceeded 35 mm, while the rest were less than 25 mm. For more than two thirds of the events, the maximum 5-min rainfall intensity did not exceed 20 mm h^{-1}. Figure 3 shows total infiltration after several rainfalls of different amounts (19.4, 57.8, 37.2, 19.8 and 11.9 mm for events 1 to 5) and intensities (maximum 5-min rainfall, I_5max of 8.9, 12.4, 15.5, 27.9 and 29.7 mm h^{-1} for events 1 to 5), at El Cautivo. During high intensity events, with I_5max of 27.9 and 29.7 mm h^{-1} (Fig. 3, see rains 4 and 5), no significant difference was found in infiltration among the surface types and both cyanobacteria and lichen biocrusts showed similar infiltration to biocrust-removed soils. Thus, as was observed under simulated rain, the most developed lichen biocrusts exhibited low infiltration values during intense events.

However, this pattern changed when infiltration was analysed under low intensity rainfall. After several rainfalls of different amount (Fig. 3, see events 1, 2 and 3 with rainfall amounts of 19.4, 57.8 and 37.2 mm, respectively) with I_5max less than 20 mm h^{-1} (8.9, 12.4 and 15.5 mm h^{-1}, respectively), it was found that biocrust-removed soils generated significantly lower infiltration than the undisturbed biocrust types. Within biocrusts, lichens exhibited slightly higher infiltration than cyanobacteria biocrusts, but differences were not significant.

These differences in the hydrological behaviour of the crusts depending on rainfall intensity were also observed at annual scale. Table 1 shows annual infiltration during the studied hydrological year in the biocrust types and biocrust-removed soil. The lowest infiltration was recorded in the biocrust-removed soil, whereas cyanobacteria biocrusts showed slightly higher annual infiltration than lichen biocrusts. However, these differences were not significant. Nonetheless, significant differences were observed when characterization of low and high intensity rainfalls was taken into account. Annual infiltration during low intensity rains was higher in lichens than cyanobacteria and both biocrust types showed significantly higher infiltration than biocrust-removed soils. On the contrary, annual infiltration during high intensity rains was slightly higher in cyanobacteria than in lichens and biocrust-removed soil, but differences were not significant.

Biocrust influence on soil evaporation

Biocrusts affected evaporation at both soil depths, but this effect depended on soil properties and the ambient conditions during the evaporation process. During periods of soil drying under warm ambient conditions, the crust types and biocrust-removed soils showed similar evaporation. However, during wet soil periods and mild ambient temperatures, biocrusts decreased evaporation compared to biocrust-removed soils.

Table 2 shows water loss from the crust types and biocrust-removed soils, measured with the micro-lysimeters, after the complete drying cycle, from saturation to dry soil. All crust types lost water very quickly due to the high ambient temperatures reached during the period of the experiment (diurnal temperatures up to 30ºC), and the crust types dried out after only 5 days since soil saturation. Gravimetric water content of the samples decreased from 21% under saturation to 1% when soil was dry. From saturation to dry soil, mean water loss in the biocrusts and biocrust-removed soils was 12.2 ± 2.0 and 11.5 ± 2.0 mm, respectively. No significant differences were found in total evaporation losses either among crust types (physical and biocrusts in different development stages) or between the biocrust types and the respective biocrust-removed soil.

However, the moisture probe data showed a different pattern in water losses of the biocrust types and biocrust-removed soil during periods of soil drying in the wet season. Fig. 4 illustrates volumetric water loss (%) after a January rainfall that amounted 39 and 35 mm, at El Cautivo and Las Amoladeras, respectively. After 19 days of soil drying, water losses in soils covered by biocrusts were much lower than those recorded in soils devoid of them, at both study sites.

The effect of biocrust removal on evaporation varied depending on the study site and soil depth. At El Cautivo, biocrust removal mainly increased surface evaporation, but had less effect at depth. Water loss at 3 cm was 1.7 times higher in biocrust-removed soil than in soils covered by biocrusts, while both showed similar water losses at 10 cm. At Las Amoladeras, biocrust removal caused an important increase in evaporation at both 3 and 10 cm soil depths. Soil water loss at 3 cm was up to 3.2 times higher in biocrust-removed soil than in undisturbed biocrusts, while at 10 cm, soil devoid of biocrusts showed 2.9 times higher water losses than soils covered by biocrusts.

Biocrust influence on soil moisture

Similar to the pattern found in water losses, the influence of biocrusts on soil moisture content depended on the period of the year. During summer, when soil moisture content was low, all surface types showed similar moisture content. At both sites, average moisture content at 3 cm was very low (2% and 1% under the biocrusts and biocrust-removed soil, respectively). At El Cautivo, average moisture content at 10 cm was slightly higher in biocrust-removed soil than in the undisturbed biocrusts (7%, 4% and 5%, in biocrust-removed soil, lichen and cyanobacteria, respectively), whereas at Las Amoladeras, average moisture content at 10 cm was slightly higher in lichen (8%) and cyanobacteria (9%) than in biocrust-removed soil (6%).

During cold wet periods, soils covered by biocrusts showed greater moisture at depths of 3 cm and 10 cm than where the biocrust was lacking. Within the biocrust types, lichens showed higher moisture than cyanobacteria at both study sites (Fig. 5). At El Cautivo, average soil moisture content during winter in lichen, cyanobacteria and biocrust-removed soil was, respectively, 24%, 18% and 15% at 3 cm, and 29%, 28% and 24% at 10 cm. At this site, the decrease in soil moisture after biocrust removal was higher at 3 cm than at 10 cm soil depth (Figs. 5a and 5b). At 3 cm, removal of lichen and cyanobacteria biocrusts caused a decrease in soil moisture up to 12% and 7%, respectively (Fig. 5a), whereas at 10 cm, moisture decreased up to 8% when both biocrust types were removed (Fig. 5b). At Las Amoladeras, average soil moisture content during winter in lichen, cyanobacteria and biocrust-removed soil was, respectively, 31%, 24% and 23% at 3 cm, and 35%, 33% and 27% at 10 cm. Moisture content at 3 cm decreased up to 13% and 6% when lichen and cyanobacteria were removed, respectively (Fig. 5c), whereas at 10 cm, moisture decreased up to 13% and 10% after removal of lichen and cyanobacteria biocrusts (Fig. 5d).

This greater soil moisture content promoted by the presence of biocrusts reflected an increase in the available water capacity. Figure 6 shows available water under the biocrust types and biocrust-removed soil during the study period; at both sites this increased as crust development increased: biocrust-removed soil< cyanobacteria biocrust< lichen biocrust. In addition to the amount of available water, the percentage of days with available water in the soil during the hydrological year also increased with crust development. The percentage of days with available water in the soil was 39%, 38% and 27% in lichen, cyanobacteria and biocrust-removed soil, respectively, at El Cautivo, and 56%, 57% and 46%, respectively, at Las Amoladeras. As can also be seen in Fig. 6, biocrusts maintained available water in the underlying soil during the whole wet soil period, from 15th December to 27th April, while fewer days were accounted for in the biocrust-removed soil during this wet period (71% of days at El Cautivo and 88% of days at Las Amoladeras).

DISCUSSION

Interaction of factors controlling biocrust effect on soil hydrology

Water retention in soils is strongly influenced by soil surface properties such as microtopography (Kidron, 2007; Rodríguez-Caballero *et al*., 2012), carbohydrate content (Rossi *et al*., 2012), porosity (Menon *et al*., 2011; Felde *et al*., 2014) and hydrophobicity (Tighe *et al*., 2012), all of which are affected by the presence of biocrusts. Hence, biocrusts have a great influence on all components of the soil water balance, by regulating water inputs and losses in soils and thus influencing the soil water budget (Belnap, 2006). Most studies have explored the effect of biocrusts on isolated components of the water balance such as infiltration or runoff (Li *et al*., 2010; Chamizo *et al*., 2012a,b; Kidron *et al*., 2012; Rodríguez-Caballero *et al*., 2012, 2013), evaporation and soil moisture (Xiao *et al*., 2010; Yu *et al*., 2010; Kidron and Tal, 2012; Chamizo *et al*., 2013a,b), but a broad approach involving their influence on all these components together, which is crucial to certainly understand their overall effect on soil hydrology, has rarely been shown in the literature. This study addresses this topic by examining jointly the influence of biocrusts on infiltration, evaporation and soil moisture, under field conditions and taking into account the temporal variability of these processes.

As expected, the type and development of biocrusts affected hydrological processes, but other factors associated with site characteristics had key influences in modifying the role of biocrusts on these processes, such as topography and underlying soil texture, as well as rainfall properties and ambient conditions during the year. We found that, under intense simulated rainfall, infiltration was higher in biocrusts on flat sandy loam soils at Las Amoladeras (alluvial fan system) than on steep silty loam soils at El Cautivo (badlands system). In general, infiltration increased with higher biocrust development, in terms of higher cyanobacteria and moss cover (Fig. 2), coinciding with previous studies that have also shown increased infiltration with greater biocrust development (Xiao *et al*., 2011; Belnap *et al*., 2013). However, there were some differences between study areas. At El Cautivo, infiltration was lower in physical crusts and light cyanobacteria biocrusts due to their low roughness (Chamizo et al., 2012a) and the low porosity of the underlying soil (Miralles-Mellado et al., 2011), thus reducing hydraulic conductivity and increasing runoff (Neave and Rayburg, 2007). Dark cyanobacteria biocrusts, due to their greater biomass and surface roughness, showed the highest infiltration. Nonetheless, and according to previous studies that have also reported lower infiltration in soils covered by lichens compared to cyanobacteria or moss biocrusts (Eldridge *et al*., 2010), especially during high intense events (Rodríguez-Caballero *et al*., 2013), well-developed biocrusts dominated by crustose and squamulose lichens showed low infiltration during very intense rains (Fig. 2a). This is attributed to three main causes: i) hydrophobicity of lichen species (Tighe *et al*., 2012), ii) the existence of an air layer between the lichen thallus and the soil, which disconnects infiltration flow though soil (Souza-Egipsy *et al*., 2002; Miralles-Mellado *et al*., 2011; Rodríguez-Caballero *et al*., 2013), and iii) higher polysaccharide content compared to cyanobacteria or moss biocrusts (Chamizo *et al*., 2013a) and consequently, higher ability to clog soil pores due to polysaccharide swelling. At Las Amoladeras, livestock trampling due to frequent grazing breaks down lichens and generates numerous surface cracks that increase the possibility for water infiltration (Chamizo *et al*., 2012a). At this site, lichen biocrusts showed greater infiltration than cyanobacteria (Fig. 2b) during intense simulated rainfall, while mosses showed the highest infiltration due to their high infiltration capacity (Almog and Yair, 2007) and high water retention capacity (Chamizo *et al*., 2012c). Although lichen biocrusts and physical crusts showed similar runoff during intense events, which are the major sediment sources on these areas (Cantón *et al*., 2011), it is unquestionable that biocrusts play a role in soil stability and the prevention of erosion. For instance, during intense events, bare soils covered by physical crusts have been reported to increase sediment yield by up to 60 times compared to well-developed biocrusts (Chamizo *et al*., 2012a).

Despite the patterns observed among crust types under intense simulated rainfall, the numerous runoff events recorded during the studied hydrological year demonstrated that the influence of biocrusts on infiltration was strongly controlled by rainfall intensity. During low intensity rainfalls, both cyanobacteria and lichen biocrusts exhibited higher infiltration than biocrust-removed soils (Table 1, Fig. 3), these mainly consisting of physical crusts developed by raindrop impact with a very incipient colonization by pioneer cyanobacteria (runoff coefficients were up to 8 times higher in these soils than in the undisturbed biocrust-covered soils). The higher roughness of well-developed lichen biocrusts, in comparison to pioneer cyanobacteria crusts, decreases overland flow velocity and increases water residence time in surface micro-depressions and flow depth (Rodríguez-Caballero *et al*., 2012), which together with their ability to absorb high amounts of water (Chamizo *et al*., 2012c; Rodríguez-Caballero *et al*., 2015a) and larger porosity in soils occupied by lichens (Miralles-Mellado *et al*., 2011) enhance infiltration and decrease runoff with respect to biocrust-removed soils. In contrast, under high intensity rainfalls, water storage in soil microdepressions lasts for a short time, and infiltration of biocrusts approached that of biocrust-removed soils (Fig. 3; Rodríguez-Caballero *et al*., 2012). In a similar way, Kidron *et al*. (2012) reported that bare surfaces generated higher runoff than biocrusts during low intensity events, explained by the higher roughness promoted by biocrusts relative to bare soils, but that both biocrusts and bare surfaces showed similar runoff during high intensity rains. Other authors have found the influence of biocrusts on runoff varies with rainfall amount, showing biocrusts decrease infiltration only during low rainfall amounts (10 mm, Wang *et al*., 2007; or lower than 20 mm, Li *et al*., 2010), but have no effect during high rainfall amounts (60 mm, Wang *et al*., 2007; or higher than 20 mm; Li *et al*., 2010). However, these results were reported for biocrusts on sandy soils, whereas in our study site with soils having a loamy texture, biocrusts increased infiltration in most rainfalls, whether low or high magnitude (Fig. 3).

It is worth mentioning that, similar to the results found under simulated rainfall, lichens showed lower infiltration than cyanobacteria during intense natural events (Table 1, Fig. 3), although differences were not as marked as could be expected during a high intensity constant simulated rainfall. In this regard, application of structural equation models has recently shown the importance of taking into account the direct and indirect interactions among biocrust properties, rainfall properties and runoff yield to understand the complex effects of biocrusts on runoff response (Chamizo *et al*., 2012b; Rodríguez-Caballero *et al*., 2013).

After analysing their effects on the inputs of rainfall water in the soil, we also examined the effects of biocrusts on soil water losses to finally understand their overall effect on soil moisture content. The influence of biocrusts on water retention capacity and pore clogging caused evaporative losses to be lower in biocrust-covered soils than in biocrust-removed soils (Fig. 4), which agrees with previous studies that have also reported decreased evaporation in soils covered by biocrusts due to their effect in blocking soil pores (Verrecchia *et al*., 1995; Kidron *et al*., 1999). However, although biocrusts showed a significant effect in reducing evaporation during cold wet periods, no significant effect was found on evaporation during periods of soil drying under warm ambient conditions. During these periods, water is evaporated rapidly, shortening the duration of pore clogging in biocrusts and thus causing evaporative losses to be similar in soils with or without biocrusts. Other studies have shown an opposite pattern with increased evaporation through biocrusts in the early stages of evaporation (Wang *et al*., 2011), as a consequence of their high capacity to retain large amounts of water in the upper most layers of soils when compared to sandy soils (Zhang *et al*., 2007; Li *et al.*, 2009; Yu *et al*., 2010). Evaporation in biocrusts may also depend on rainfall amount. Li et al. (2010) found biocrusts reduced evaporation versus bare sands when rainfall was less than 10 mm but increased evaporation when rainfall reached 20 mm. Opposite to these results, we found biocrusts consistently reduced evaporation after the different rainfalls fallen during winter at both study sites (Fig. 4 and 5), independent of total rainfall amount or intensity.

The coupling between greater infiltration (Fig. 3) and decreased evaporation (Fig. 4) resulted in enhanced moisture content (Fig. 5) and available water capacity (Fig. 6) in soils covered by biocrusts versus biocrust-removed soils, and within biocrusts, greater moisture and available water capacity under more developed biocrusts. Our results agree with previous studies which have found higher moisture in soils covered by biocrusts than in uncrusted or bare soils (Gao *et al*., 2010; Yair *et al*., 2011; Chamizo *et al*., 2013b) and soils covered by physical crusts (Cantón *et al*., 2004b). Similarly, other studies have found good correlation between soil wetness duration and chlorophyll content, which is closely related to biocrust development (Kidron *et al*., 2010; Kidron and Vonshak, 2012). Nevertheless, despite these published studies, none of them had clearly demonstrated the effect of biocrusts on soil moisture as a result of their balanced effect on infiltration and evaporation.

We also found some differences in soil moisture content under biocrusts related to soil texture. Soil moisture and available water capacity were greater at Las Amoladeras than at El Cautivo, which we attribute to higher infiltration rates (Fig. 2, Chamizo *et al*., 2012a) and non-rainfall water inputs from frequent dew and fog events near the coast (Uclés *et al*., 2014), as well as lower potential evapotranspiration at the former site. Although a few studies, mostly on sandy soils, have shown that biocrusts increase moisture in upper soil layers (0-5 cm) but decrease moisture at depth (Almog and Yair, 2007; Gao *et al*., 2010; Yu *et al*., 2010; Kidron and Tal, 2012), at our sites with finer soil texture, biocrusts increased soil moisture at 3 and 10 cm depths in both silty and sandy loam textures (Fig. 5). Our belief is that the effect of biocrusts on soil moisture retention below this depth should be negligible and other factors such as plant roots could be the main drivers for soil moisture retention and evaporation at depth.

Moreover, it should be noticed that, as most rainfall occurs in winter and biocrust effects on evaporation were only significant during wet periods (Table 2), this effect was only noticeable during wet soil periods (Fig 5). This is important as the period of biological activity in the Mediterranean climate occurs during the wet period rather than in the summer drought. Accordingly, it can be observed that during a rain event that occurred in June, although the maximum moisture peak at 3 cm increased from biocrust-removed soil to cyanobacteria to lichens, the soil moisture decline after rain was similar in all surface types and eventually resulted in similar moisture contents under both biocrusts and biocrust-removed soil (Fig. 5).

Implications for plant productivity and ecosystem functioning

The triggering of key ecological processes in arid and semiarid areas is strongly related to soil water availability, which is driven not only by rainfall properties, but also by the type of soil (Noy-Meir, 1973; Reynolds *et al*., 2004) and water redistribution from interplant soils to vegetation patches (Li *et al*., 2008). In this sense, the presence, cover and type of biocrust modifies the balance between the water that is retained and lost in soils, thereby finally conditioning the water available to plants and soil biota (Fig. 6). Biocrusts increase water inputs via infiltration and reduce soil water losses via evaporation, thus enhancing soil moisture content and eventually, available water capacity, versus bare soils. In addition, biocrusts are able to increase water inputs from non-rainfall sources such as dew, fog and water vapour adsorption, which are essential water sources in water-limited systems (Zhang *et al*., 2009).This greater available water in the upper soil layers of soils can be readily used by nearby vegetation, especially annual plants and vascular plants with shallow roots, for which access to deeper water sources can be quite limited. Although we found that biocrusts increased soil moisture to a depth of 10 cm in both silty and sandy loam soils, other authors have found on sandy soils that progressive biocrust development enhances the amount of available water in the top soil, but decreases available water in deep layers, thereby promoting the growth of herbaceous plants and shallow-rooted shrubs to the detriment of deep-rooted shrubs (Li *et al*., 2009, 2010). Such findings highlight the importance of taking into account soil texture to understand the contrasting effects of biocrusts on available soil water.

Greater available water is important for numerous biogeochemical processes occurring at the soil-atmosphere boundary, such as C and N fixation and leaching by biocrust organisms, which eventually affect soil microbial activity and vegetation performance in drylands (Collins *et al*., 2008). Loss of biocrusts due to frequent disturbances in arid and semiarid areas results in lower soil moisture in interplant spaces which can cause important changes in soil biogeochemical processes such as rates of C and N fixation, decomposition of organic compounds, mineralization of N, and soil microbe activity, all of which may lead to changes in the composition and structure of plant communities (Schwinning and Sala, 2004). Hence, disturbance of biocrusts would decrease water input and increase water output, leading to an overall negative effect on the local water balance.

Future challenges

Great controversy has been documented in the literature regarding the influence of biocrusts on hydrological processes. From this and other published studies, it is inferred that interactions among multiple factors - including biocrust properties, rainfall characteristics, soil type and land use - condition their hydrological behaviour and make it difficult to reach a general conclusion about their role in hydrological processes. In general, our results demonstrate that infiltration increases with greater biocrust development, but this effect is only observed during low intensity rainfalls. Well-developed biocrusts also decrease evaporation and enhance soil moisture content in the uppermost layers of the soil, especially during wet soil periods. The creation of a networked study to undertake similar measurements using similar methodologies in other areas around the world, with contrasting soil and climatic properties, would contribute to elucidate general patterns in the way the different factors analysed affect the hydrological response of crusts.

While this paper provides an initial approach to the effect of biocrusts on infiltration and runoff, as well as evaporation and soil moisture at a fine spatial scale (microplot/plot scale), further investigation is required to understand how biocrusts affect these processes at coarser spatial scales. Much of the existing controversy about the role of biocrusts as sinks or sources of runoff can be attributed to the lack of hydrological studies at coarser spatial scales such as hill-slope and catchment scales. Soil point measurements do not account for the temporal and spatial variability that characterise hydrological processes and usually neglect or dismiss the relevant influence of biocrust on soil properties like microtopography. In general, compared to vegetation, biocrusts are considered as sources of runoff and this runoff water and associated nutrients represent vital resources for the survival of nearby vegetation (Cantón *et al*., 2014; Rodríguez-Caballero *et al*., 2014a). Further studies should examine the effects of biocrusts on hydrological processes at coarser spatial scales, taking into account their temporal variability, and integrate the response of individual crust patches with other patch-scale components such as bare soil and vegetation. Results from all these studies should be incorporated into current hydrological (and erosion) models in order to improve their capabilities and usefulness as resource management tools in arid and semiarid areas (Rodríguez-Caballero *et al*., 2015b). Reliable cartography of biocrust distribution is a "must" toward achieving this goal. Distinctive spectral features of vegetation, bare soils and developmental stages of biocrust have shown the possibility of classifying these common ground covers in arid and semiarid areas from hyper spectral data (Weber *et al*., 2008; Chamizo *et al*., 2012d) and a recent study has demonstrated the possibility of accurately identifying and quantifying different biocrust types from hyper-spectral images (Weber *et al*., 2008; Rodríguez-Caballero *et al*., 2014b). Remote sensing data, thus, represent a promising means of studying biocrust distributions and of numerous ecosystem processes influenced by them at large spatial scales (Rodríguez-Caballero et al., 2015c).

Conclusions

Site characteristics, the type of biocrust and temporal variability associated with rainfall type, antecedent soil water content and ambient conditions all regulate the role of biocrusts in hydrological processes. In general, biocrusts increase infiltration versus biocrust-removed soils during low intensity rainfalls and, within them, more developed biocrusts such as lichens show higher infiltration than less developed biocrusts like cyanobacteria. However, during high intensity rainfalls, biocrust types and biocrust-removed soils show similar infiltration.

The influence of biocrusts on evaporation and soil moisture depend on the period of the year. During long wet cold periods, higher infiltration and lower evaporation due to higher water retention and pore clogging in biocrusts contribute to greater moisture in these than in soils devoid of them. However, during periods of soil drying under warm ambient conditions, soil water loss is fast in biocrusts and biocrust-removed soils and both show similar water losses, thus resulting in similar moisture content in biocrusts and biocrust-removed soils.

Our findings point to the importance of the presence and development of biocrust in increasing soil moisture and available water capacity, versus bare soils. In view of the reported effects of biocrusts on hydrological processes, we can affirm that biocrusts increase water input and reduce water output compared to bare soils, and that water input generally increases with greater biocrust development. Thus, the presence of biocrusts has a positive effect on the local water balance.

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Table 1. Annual infiltration during the hydrological year 2009-2010. The *p*-value is also shown. Different letters indicate significant differences among types of surfaces within each column.

	Annual infiltration (mm)		
	Total	Low intensity rains (I_5max<20 mm h^{-1})	High intensity rains (I_5max>20 mm h^{-1})
	p=0.197	p=0.050	p=0.116
Biocrust-removed soil	[a]316 ± 19	[b]227 ± 13	[a]82 ± 9
Dark cyanobacteria	[a]339 ± 12	[a]244 ± 6	[a]95 ± 7
Lichen	[a]333 ± 12	[a]249 ± 8	[a]84 ± 4

Table 2. Total soil water loss (mm) from saturation to dry soil in the micro-lysimeters (volume=393 cm^3) containing the different crust types and biocrust-removed soils. No significant difference in evaporation was found between the undisturbed crust types (p=0.787) or between each biocrust type and its respective biocrust-removed soil (light cyanobacteria, p=0.524; dark cyanobacteria, p=0.515; and lichen, p=0.900).

	Evaporation (mm)	
	Unaltered	Biocrust-removed
Physical crust	12.9 ± 0.7	
Light cyanobacteria biocrust	11.8 ± 2.0	10.2 ± 3.2
Dark cyanobacteria biocrust	13.0 ± 2.9	12.0 ± 2.6
Lichen biocrust	11.8 ± 1.3	11.9 ± 0.4

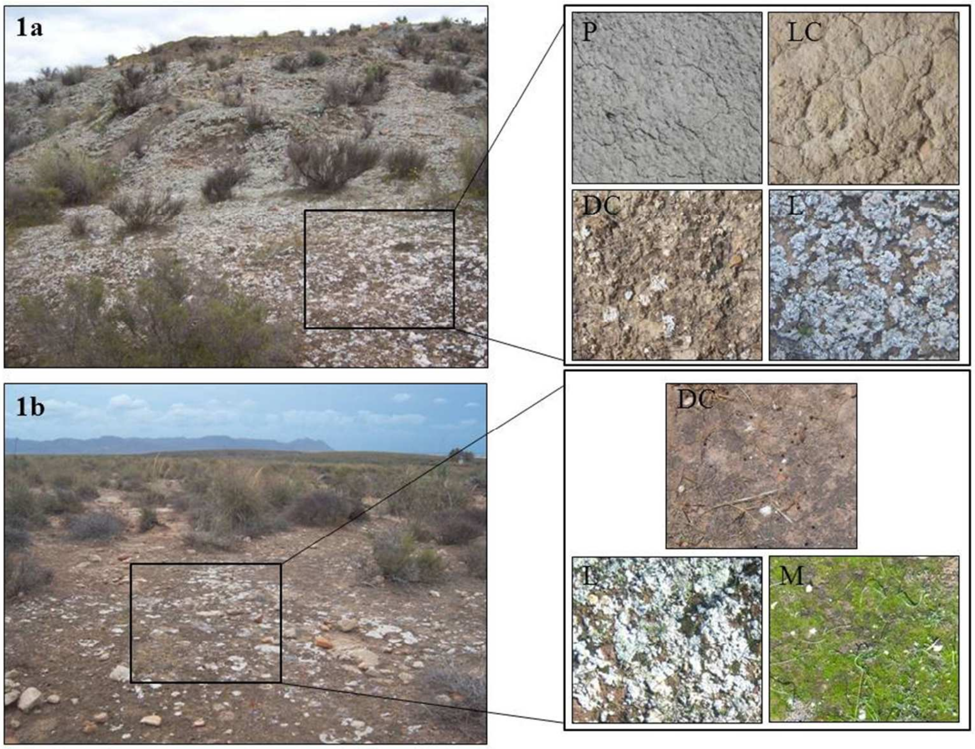


Figure 1. Crust types identified at each study site: a) El Cautivo (Tabernas Desert): P, physical soil crust; LC, light cyanobacteria crust; DC, dark cyanobacteria crust, L, lichen crust; and b) Las Amoladeras (Cabo de Gata-Níjar Natural Park): DC, dark cyanobacteria crust, L, lichen crust; M, moss crust.
254x190mm (96 x 96 DPI)

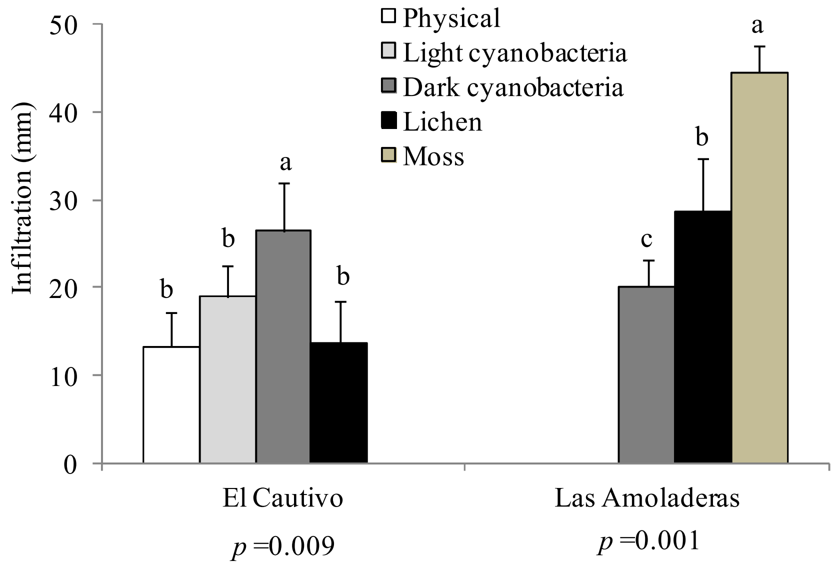


Figure 2. Total infiltration (mean±sd, n=4) in microplots (0.25 m^2) covered by different crust types after the 1h-rainfall simulation at a high constant intensity of 50 mm h^{-1}, at El Cautivo (silty loam texture) and Las Amoladeras (sandy loam texture). The *p*-value is indicated below the study site. The letters in the bars indicate significant differences among crust types at each site.

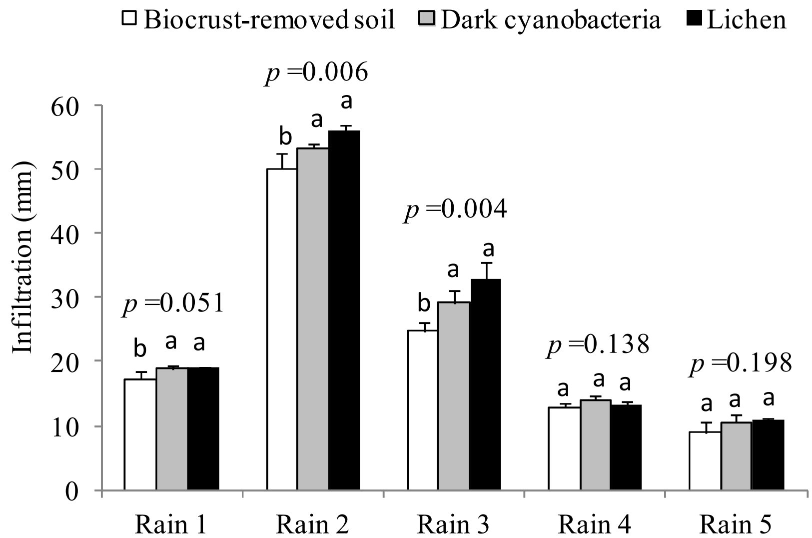


Figure 3. Total infiltration (mean±sd, n=3) in small plots (~1m^2) covered by biocrust-removed soil and the two types of biocrust, after five rainfall events of different amount (PP, mm) and intensity (maximum rainfall intensity in 5 minutes: I_5max, mm h^{-1}): Rain 1 (PP=19.4 and I_5max=8.9); Rain 2 (PP=37.2 and I_5max=15.5); Rain 3 (PP=57.8 and I_5max=12.4); Rain 4 (PP=19.8 and I_5max=27.9); Rain 5 (PP=11.9 and I_5max 29.7).

The *p*-value is shown for each rain. Different letters indicate significant differences among crust types for each rain.

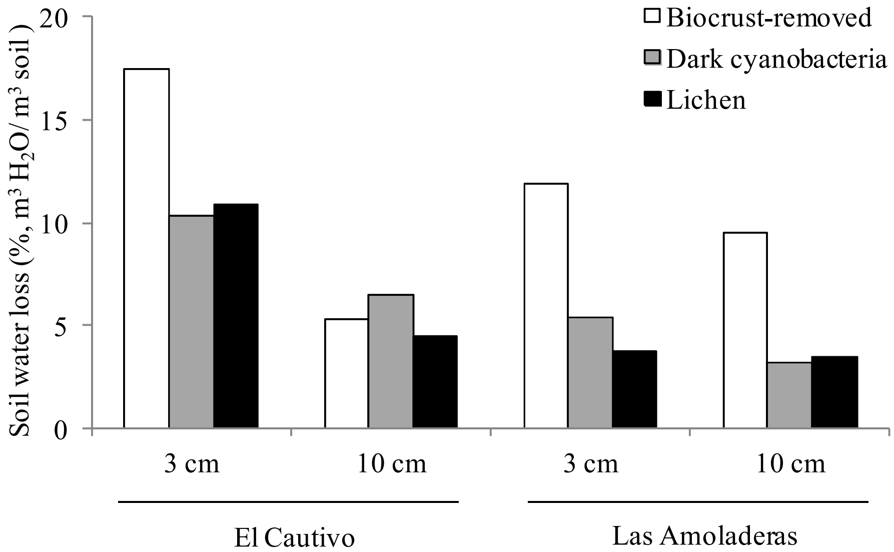
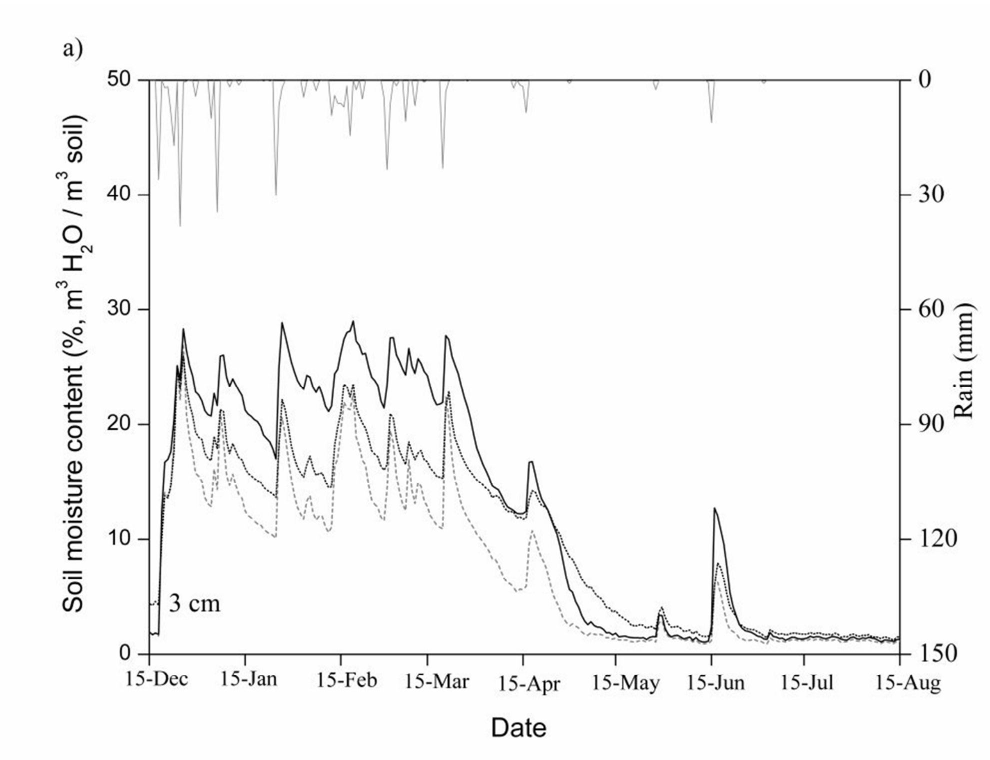


Figure 4. Soil water loss (m^3H_2O/m^3soil) under the types of biocrusts and biocrust-removed soil at 3 and 10 cm depths, after 19 days of soil drying following a rainfall in January (PP=39 mm at El Cautivo and PP=35 mm at Las Amoladeras).



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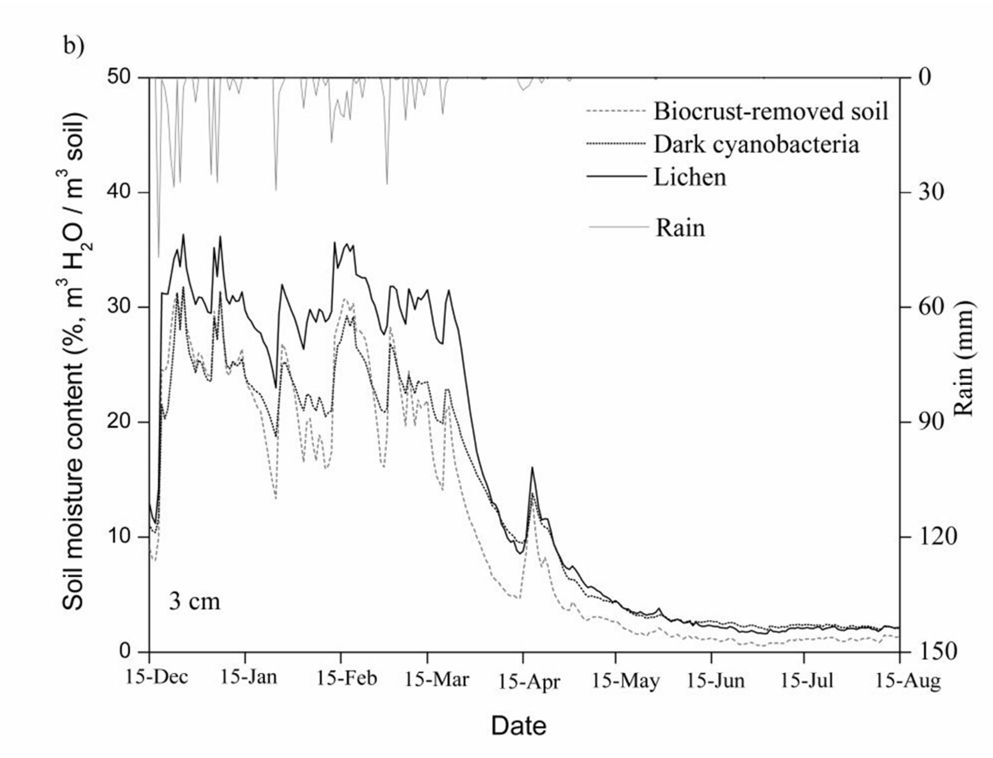

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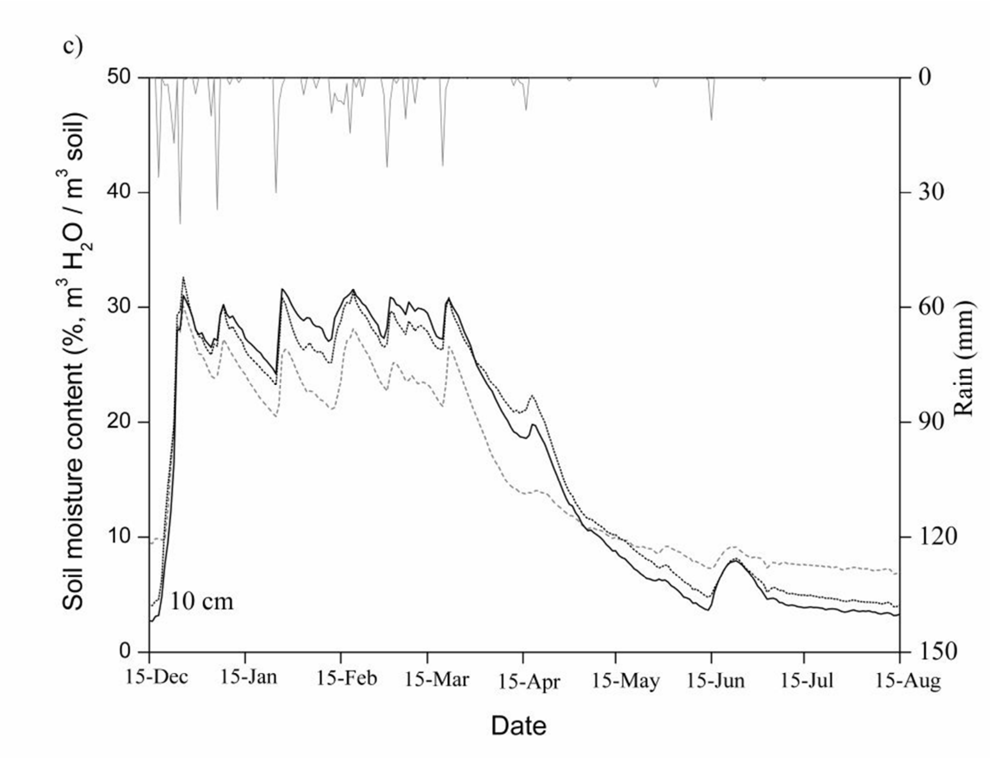

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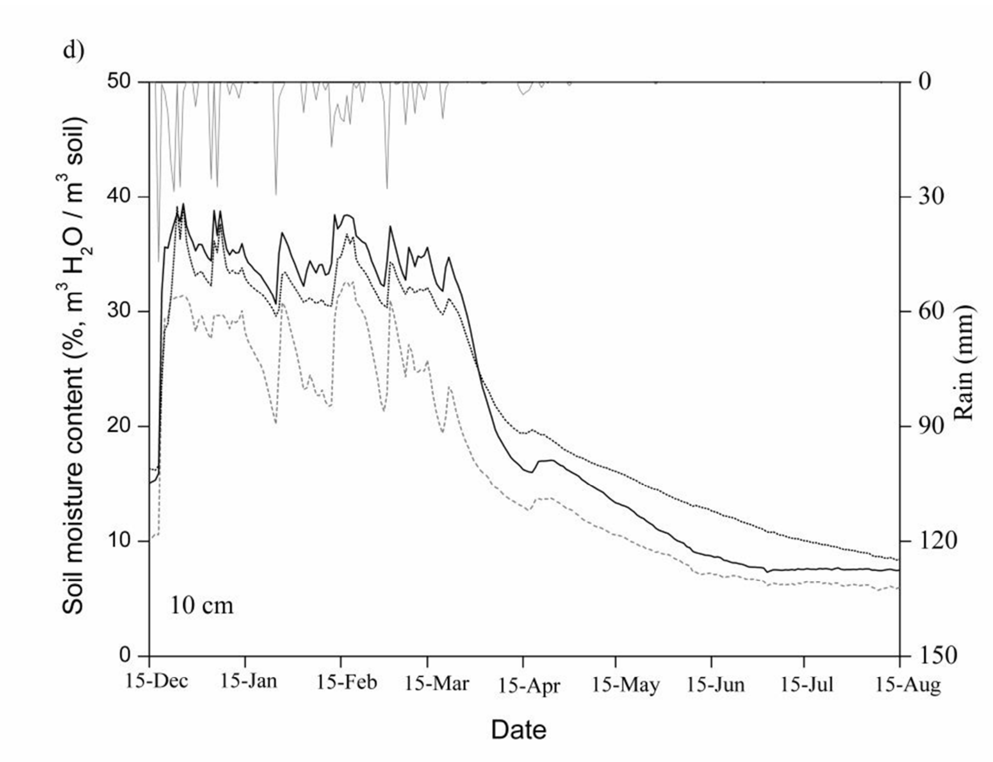
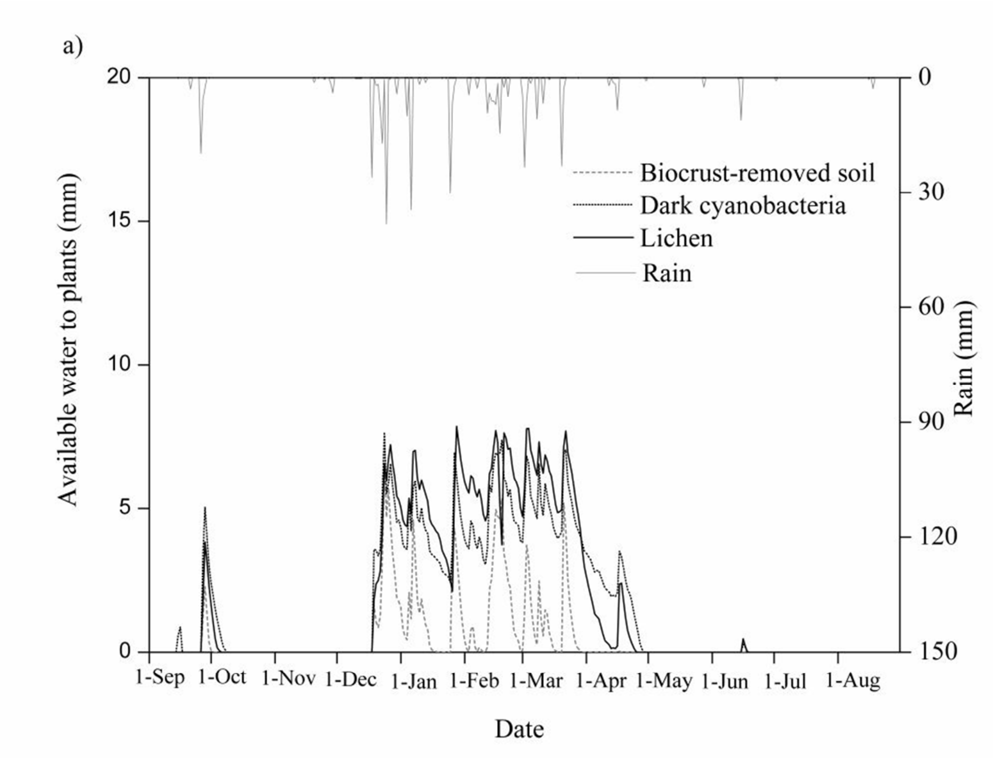


Figure 5. Soil water content (m3H2O/m3soil) under the biocrust types and biocrust-removed soil at 3 cm at El Cautivo (a) and (b) Las Amoladeras, and at 10 cm at El Cautivo (c) and Las Amoladeras (d).
265x203mm (96 x 96 DPI)



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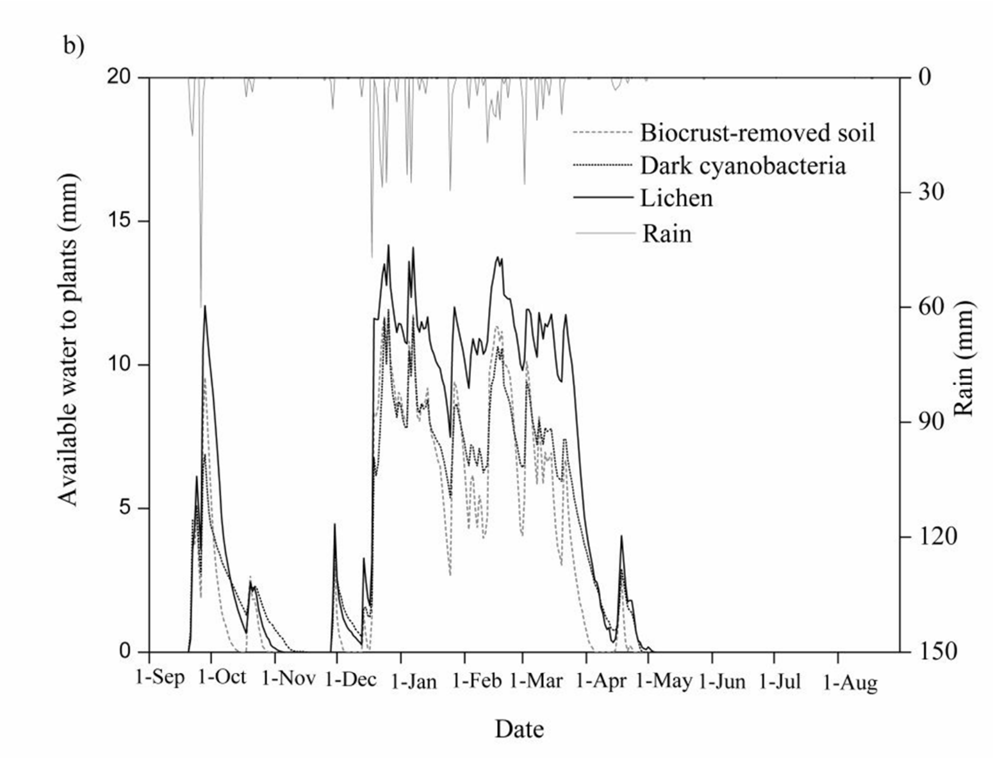

Figure 6. Amount of available water to plants (mm) in the upper 5 cm of soil under the biocrust types and biocrust-removed soil, at El Cautivo (a) and Las Amoladeras (b).
265x203mm (96 x 96 DPI)