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The role of biological soil crusts in soil moisture dynamics in two semiarid ecosystems with contrasting soil textures

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SUMMARY

The interplant soil surfaces in most arid and semiarid ecosystems are covered by biological soil crusts (BSCs). These crusts regulate water inputs and losses through soils and play major roles in local hydrological regimes. In recent years, the role of BSCs in infiltration and runoff has gained increasing importance and better knowledge of their effects on these processes has been acquired. However, the role of BSCs in other important components of the water balance, such as evaporation or soil moisture has hardly been studied, so their effects on these processes remain unknown. The aim of this study was to explore the influence of BSCs on soil moisture regimes in the top layer of the soil in two semiarid ecosystems in SE Spain with different particle-size distributions. At both study sites, soil moisture was monitored at 0.03 and 0.10 m under two types of BSCs, a cyanobacteria-dominated BSC and a lichen-dominated BSC, and in adjacent soils where they had been removed. Our results showed that during wet soil periods, removal of BSCs led to decreased soil moisture, especially in the upper layer (0.03 m), compared to soils covered by BSCs. Decrease in soil moisture was more noticeable after removal of lichens than cyanobacterial BSCs, and more so in fine than in coarse-textured soils. Soil water loss was also generally faster in soils with no BSCs than in soils covered by them. However, no difference was found in soil moisture under either crusted or scalped soils during soil drying periods. The type of BSC influenced soil moisture differently depending on soil water content. During wet soil periods, soil water loss was faster and soil moisture lower under cyanobacterial than under lichen BSCs. On the contrary, during soil drying periods, soils covered by lichens lost water faster and showed lower moisture than those covered by cyanobacteria. Our results show the major role of the presence of BSCs, as well as the types, in soil water content in semiarid ecosystems.

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1. Introduction

Water and nutrient availability are the most limiting factors for ecosystem functioning in drylands (Gebauer and Ehleringer, 2000). However, when water is limited, it becomes the primary driver of productivity (Rodríguez-Iturbe et al., 1999). An essential variable of the water balance is soil moisture, which strongly affects the distribution pattern and survival of vegetation. In these systems, where water is a limiting resource, productivity is maximised when water and other resources are unevenly distributed in patches (Noy-Meir, 1973; Tongway and Ludwig, 1990). Thus, spatial distribution of resource-poor and resource-rich patches is not random but structured in a zonal pattern of decline and accumulation (Tongway, 1995). Interplant patches usually represent areas of water depletion, whereas vegetation patches act as areas of water accumulation (Ludwig et al., 2005). Thus, the type of cover in the interplant spaces has a decisive role in water redistribution in drylands.

Interplant soil surfaces in most undisturbed arid and semiarid areas are covered by a community of organisms that comprise cyanobacteria, lichens, algae and bryophytes, known as biological soil crusts (BSCs), which play a major role in local hydrological processes. BSCs regulate water fluxes into and through soils (Belnap et al., 2003a), thereby affecting soil water availability (Cantón et al., 2004), and consequently, essential ecological processes such as C and N assimilation, mineralisation of N and organic compounds (Rodríguez-Iturbe et al., 1999), activity of soil biota, and productivity and distribution patterns of vegetation in semiarid ecosystems (Belnap et al., 2005). Several papers have highlighted the source-sink association between runoff generated in BSC patches and the use of this water surplus by adjacent vegetation (Eldridge et al., 2002; Ludwig et al., 2005; Li et al., 2008; Cantón et al., 2011). However, in the open spaces surrounding shrub patches the presence of BSCs increases infiltration and strongly

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reduces erosion compared to physical crusts (Chamizo et al., 2012a). Despite their recognised importance in water processes, the effect of BSCs on subsurface soil moisture has received little attention. Only a few studies have dealt with this subject, with conflicting results. BSCs are able to increase soil moisture compared to bare or uncrusted soils and even compared to plant covered surfaces during periods with very negative soil water potential (Cantón et al., 2004) because of their ability to seal the soil surface and reduce evaporation (Verrecchia et al., 1995). In addition, higher roughness (Rodríguez-Caballero et al., 2012) and water holding capacity (Chamizo et al., 2012b) in well-developed BSCs can enhance water absorption by the crust and increase moisture at the soil surface (Gao et al., 2010). Alternatively, some BSCs darken the soil surface raising surface temperature, and could thus increase evaporation and decrease soil moisture. It has also been pointed out that BSC influence on soil moisture depends on soil type and BSC composition (Belnap and Lange, 2001).

In general, most studies on the effect of BSCs on soil moisture have found moisture to be higher in soils with prominent BSCs than in bare or uncrusted soils (Brotherson and Rushforth, 1983; Pérez, 1997; Malam Issa et al., 1999; Warren, 2003; Cantón et al., 2004). One exception to this generally reported positive effect was found by Harper and Marble (1988), who in a study of soil moisture in lichen-crusted surfaces in Utah (USA), found less moisture in the upper 0.075 m of soil underneath lichen crusts than under bare soils. They attributed this decrease in soil moisture to soil surface darkening by BSCs and consequent rise in soil temperature. However, this effect could be the opposite if BSC colour is light (Cantón et al., 2004). In all these studies, soil moisture was analysed in specific periods of the year. However, factors such as initial soil water content and ambient conditions throughout the year are likely to affect the influence of BSCs on soil moisture. Soil texture also appears to condition evaporation, and therefore, soil moisture in biologically crusted soils (Xiao et al., 2010).

A previous study on soil moisture regimes under various cover types, including vegetation, lichen BSCs and physical crusts in the Tabernas badlands (SE Spain) demonstrated the positive effect of lichen BSCs on soil moisture conservation (Cantón et al., 2004). However, in this study, cover types were associated with different landforms and soil surface properties, so that differences in soil moisture could not be exclusively attributed to the presence of the lichens. Other studies have compared soil moisture in undisturbed areas covered by BSCs with areas disturbed by grazing (reviewed in Warren, 2003) or uncrusted soils (Gao et al., 2010), which also makes it difficult to compare them, as differences in soil moisture could be linked to differences in soil properties, not to the presence of BSCs. Furthermore, as far as we know, the influence of the type of BSC on soil moisture and its temporal dynamics have not yet been studied.

We hypothesised that soil moisture would be higher in soils covered by BSCs than in the same soils without BSCs, and higher under lichen than under cyanobacterial BSCs, due to the light colour of the lichens and the better physicochemical soil properties underneath them than under cyanobacterial BSCs (Chamizo et al., 2012b). We also hypothesised that, due to the lower water retention capacity of coarse soils than fine soils, the presence of BSCs would increase water retention and thereby soil moisture more in coarse than in fine-textured soils. In this study, moisture content was monitored over time at 0.03 and 0.10 m in undisturbed soils covered by two representative types of BSCs, dark cyanobacteria-dominated BSCs and light-coloured lichen-dominated BSCs, and in adjacent soils where these BSCs had been scraped off, in two semiarid ecosystems of SE Spain with different soil textures (silty loam and sandy loam) where BSCs are well-represented. Thus the purposes of this study were to find out: (i) whether soil moisture varies under BSCs compared to soils where the BSCs have been removed; (ii) whether the type of BSC influences soil moisture; (iii) whether BSC is able to influence soil moisture below the uppermost layer of the soil; and (iv) whether the influence of BSCs on soil moisture varies with soil texture.

2. Material and methods

2.1. Study sites

Two types of BSCs representing different successional stages common in semiarid areas throughout the world were selected in two areas of SE Spain. The two study sites had different soil textures and were representative of the spatial distribution of vegetation in semiarid ecosystems, which is characterised by dispersed patches of plants with BSCs occupying the bare interplant spaces.

El Cautivo site in the Tabernas Desert was chosen as an area with fine-textured soils, where BSCs cover a large portion of the open spaces surrounding vegetation patches. A detailed description of this area and the most typical types of BSCs present can be found in Cantón et al. (2001, 2003), Lázaro et al. (2008) and Chamizo et al. (2012a,b). The Tabernas Desert is a badlands area developed over gypsiferous mudstones and calcareous sandstones. Mean annual rainfall is 235 mm, mostly in autumn and winter, with very dry summers. Soils are thin, poorly developed and with a silty loam texture. They are classified as Epileptic and Endoleptic Leptosols, Calcaric Regosols and Eutric Gypsisols (FAO, 1998). The mean percentages of sand, silt and clay in soil (0.05 m depth) under BSCs are 29.2 ± 5.4, 58.6 ± 5.8% and 12.2 ± 4.2, respectively, and organic carbon content (g kg^{-1}) is 6.3 ± 2. Topography is rough in a landscape made up of a wide diversity of fine-grained landforms. The most common species of plants are *Macrochloa tenacissima* (=*Stipa tenacissima*), *Helianthemum almeriense*, *Artemisia barrelieri*, *Salsola genistoides* and *Euzomodendron bourgaeanum*. In the oldest stable landforms, the BSCs occupy the open spaces among shrubs, but they completely cover the younger stable landforms and even the soil under plant canopies on these hillslopes. On the whole, BSCs may represent up to 50% of the soil surface cover in the area.

Las Amoladeras, in the Cabo de Gata-Níjar Natural Park, was selected as an area with coarse-textured soils where BSCs are also well represented. For a more detailed description of this area see Chamizo et al. (2012a,b). The area forms part of an alluvial fan system at the base of the Alhamilla Mountains. Mean annual rainfall is 200 mm, also mostly in winter. Soils are thin with a sandy loam texture. They are classified as Calcaric Leptosols and Haplic Calcisols (FAO, 1998). Soil (0.05 m depth) under BSCs has mean percentages of sand, silt and clay of 61.5 ± 5.1, 28.4 ± 4.8 and 10.1 ± 2.1, respectively, and organic carbon content (g kg^{-1}) of 10.9 ± 1.9. Livestock grazing is frequent in the area. Vegetation consists of scattered shrubs dominated by *Macrochloa tenacissima*, and frequent dwarf shrubs such as *Helianthemum almeriense*, *Thymus hyemalis*, *Hammada articulata*, *Sideritis pusilla*, *Lygeum spartum*, *Salsola genistoides*, and *Launaea lanifera*. BSCs cover the open areas surrounding the shrubs and may represent up to 30% of the whole soil surface.

2.2. Soil moisture monitoring

In both study sites, soil moisture was monitored in soils covered by two types of BSCs representative of the most common BSCs in semiarid areas of SE Spain: dark cyanobacteria-dominated BSCs (Fig. 1a), which also contained some pioneer lichens (*Collema* spp, *Fulgensia* spp, *Placinthium nigrum*, *Psora decipiens*, *Endocarpon pusillum*, *Toninia sedifolia*), and lichen BSCs (Fig. 1b), which consisted of cyanobacterial BSCs with a significant cover of light-coloured lichen species, predominantly *Squamarina lentigera* and

Fig. 1. Picture of the different types of surfaces and the moisture probes inserted in the soil: (a) cyanobacterial BSC; (b) lichen BSC; (c) BSC-scalped soil (6 months after BSC removal); and (d) installation of the moisture probes in the soil, at 0.03 and 0.10 m soil depths.

Diploschistes diacapsis. BSC cover on each crust type was similar at both study sites (Table 1). BSCs from El Cautivo were characterised by higher surface roughness (tortuosity index of 1.39 ± 0.19) and thickness (0.5–1 cm thick) than those from Las Amoladeras (tortuosity index of 1.17 ± 0.07, and less than 0.5 cm thick). Three pairs of plots were set up for each BSC type. In each pair, the plots were located about 1 m away from each other. To find out whether the presence of the BSC caused any differences in soil moisture, it was scraped off a 1.5 × 1.5 m area in one plot of each pair (Fig. 1c). In each plot, soil moisture was monitored at a depth of 0.03 m with 0.05-m-long probes with a small volume of influence (0.3 l) (EC-5 soil moisture sensors, Decagon Devices, Inc., Pullman, Washington), and at 0.10 m with 0.10-m-long probes with a larger volume of influence (1 l) (10HS soil moisture sensors, Decagon Devices, Inc., Pullman, Washington). These sensors have a resolution of 0.001 $m^3\,m^{-3}$ (EC-5) and 0.0008 $m^3\,m^{-3}$ (10HS), from 0 to 0.50 $m^3\,m^{-3}$ (Decagon's soil moisture sensors manual). A total of 48 moisture sensors were installed (3 probes × 2 depths × 2 treatments × 2 crust types × 2 study sites). All plots were located on flat ground to minimise the contribution from runoff, and close to each other to ensure the same type of soil and rainfall distribution. There was no vascular vegetation in the area surrounding the plots. The probes were carefully installed in previously wetted soil, to prevent damage to the prongs. Probes were installed

Table 1
Plot cover (mean ± sd, *n* = 3) on each undisturbed crust type at both study sites.

Cover (%)	El Cautivo site (fine-textured soils)		Las Amoladeras site (coarse-textured soils)	
	Cyanobacterial BSC	Lichen BSC	Cyanobacterial BSC	Lichen BSC
Cyanobacteria	66.7 ± 5.6	42.6 ± 2.5	73.1 ± 4.3	44.3 ± 12.8
Lichen	5.4 ± 0.5	30.9 ± 3.4	4.8 ± 2.2	36.8 ± 6.3
Bare soil	27.9 ± 5.8	26.5 ± 5.8	22.1 ± 5.6	18.9 ± 6.5

Table 2
Factors affecting soil moisture at each study site according to GLMM. The second column shows the model estimates for the fixed factors, and the standard deviation for the random factors (the *time* in days and the *block*, which corresponds to each pair of BSC-undisturbed and scalped plot) and the residuals. The third column shows the mean estimates across Markov chain Monte Carlo (MCMC) sampling. HPD95 lower and HPD95 upper are the 95% lower and upper, respectively, highest posterior density (HPD) confidence intervals. The final two columns show *P*-values based on the posterior distribution (pMCMC) and on the *t*-distribution, respectively.

Fixed factors	Estimate	MCMCmean	HPD95lower	HPD95upper	pMCMC	Pr(>|t|)
El Cautivo (fine-textured soils)						
(Intercept)	0.1509	0.1509	0.1365	0.1658	0.0001	0.0000
Crust type	−0.0134	−0.0134	−0.0331	0.0073	0.1364	0.0426
Disturbance	−0.0134	−0.0134	−0.0159	−0.0109	0.0001	0.0000
Depth	−0.0658	−0.0658	−0.0683	−0.0633	0.0001	0.0000
Crust type*disturbance	0.0055	0.0055	0.0018	0.0089	0.0028	0.0002
Crust type*depth	0.0129	0.0129	0.0094	0.0164	0.0001	0.0000
Disturbance*depth	0.0211	0.0211	0.0176	0.0247	0.0001	0.0000
Crust type*disturbance*depth	−0.0045	−0.0045	−0.0095	0.0007	0.0798	0.0283
Random factor	Std.Dev	MCMCmean	HPD95lower	HPD95upper		
Day (Intercept)	0.0836	0.0278	0.0270	0.0284		
Block (Intercept)	0.0080	0.0110	0.0042	0.0215		
Residual	0.0240	0.0294	0.0289	0.0300		
Las Amoladeras (coarse-textured soils)						
(Intercept)	0.1762	0.1763	0.1623	0.1921	0.0001	0.0000
Crust type	−0.0157	−0.0158	−0.0360	0.0051	0.0932	0.0268
Disturbance	0.0074	0.0074	0.0045	0.0100	0.0001	0.0000
Depth	−0.0716	−0.0716	−0.0745	−0.0691	0.0001	0.0000
Crust type*disturbance	−0.0013	−0.0013	−0.0050	0.0028	0.5366	0.4222
Crust type*depth	0.0152	0.0152	0.0114	0.0192	0.0001	0.0000
Disturbance*depth	−0.0025	−0.0025	−0.0064	0.0013	0.2148	0.1224
Crust type*disturbance*depth	0.0049	0.0049	−0.0006	0.0105	0.0802	0.0275
Random factor	Std.Dev	MCMCmean	HPD95lower	HPD95upper		
Day (Intercept)	0.1029	0.0326	0.0318	0.0332		
Block (Intercept)	0.0086	0.0112	0.0046	0.0213		
Residual	0.0272	0.0344	0.0338	0.0350		

horizontally with the flat side of the prongs perpendicular to the surface to minimise any effect on vertical water fluxes (Fig. 1d). Installation was made 2 months before the beginning of measurements to allow the probes to become stabilized in the soil. Soil moisture was simultaneously monitored in the crusted and scalped surfaces every 10 min from October 2009 to September 2010. The standard calibration equations developed by Decagon for the EC-5 and 10HS sensors were used to obtain volumetric water content (in%) from the raw data stored in Decagon's Em50 loggers. These standard calibration equations are applicable to most mineral soils, providing results with an accuracy of better than ±3% (0.03 $m^3\ m^{-3}$), and therefore, calibration of the sensors for a particular soil type is unnecessary (Kizito et al., 2008). Daily soil moisture was the average of the 10-min soil moisture records. The results presented correspond to the average of the three repetitions per surface type (undisturbed cyanobacteria, cyanobacteria-scalped, undisturbed lichen, and lichen-scalped) at each site. To examine the influence of BSCs on soil temperature, and thereby its possible relationship with soil moisture content, surface temperature was also registered in one plot of each surface type (cyanobacterial BSC, lichen BSC and BSC-scalped soil) using ECT temperature probes (Decagon Devices, Inc., Pullman, Washington).

2.3. Data analyses

The influence of BSC type, disturbance (unaltered BSC/scalped BSC) and soil depth on daily soil moisture during the whole study year (October 2009–September 2010) was analysed using generalised linear mixed models (GLMM). This tool is being increasingly used in ecological studies, as it allows the effects of predictor variables with random variation in space and time to be quantified. The potential of GLMMs lies in their ability to combine linear mixed models (which include random effects) and generalised linear models (which handle non-normal data) (Bolker et al., 2008). We used GLMMs to analyse the effect of our fixed predictor factors (BSC type, disturbance treatment and depth) on soil moisture, including the time (in days) and the block (each pair of undisturbed BSC and its adjacent scalped plot) as random factors in order to remove the spatial and temporal autocorrelation of the moisture data and to isolate the effect of our fixed factors with respect to the effects of time and space. GLMMs were performed separately for each study site. The variance component estimates and confidence intervals were calculated using the Markov chain Monte Carlo (MCMC) method for Bayesian models. MCMC draws random samples from the distribution of parameters for fixed and random effects that converge on the posterior probability distribution of the parameters, which is defined by the prior data distributions and likelihood function (Bolker et al., 2008). Unlike other approaches that estimate the standard deviations of the random effects by assuming that the fixed-effect estimates are accurate, the MCMC approach takes uncertainty in both fixed and random-effect parameters into account (Baayen et al., 2008; Bolker et al., 2008). MCMC sampling is also an efficient procedure for evaluating a model's parameters and to estimate parameters with narrow highest posterior density (HPD) intervals (Baayen et al., 2008).

Statistical analyses were done using R software version 2.14 (R Development Core Team, 2010). GLMM models were performed using the "lmer" function, included in the "lme4" package (Bates et al., 2011). The "pvals.fnc" function implemented in the R library (Baayen, 2011) was used to compute the *P*-values and the 95% MCMC confidence intervals for the GLMM model parameters. Significant fixed-factor partial effects for soil moisture in the GLMM models were plotted using the "all effects" function included in the "effects" package (Fox, 2003).

Soil water loss (%) after rainfall throughout the year was calculated as the difference between actual volumetric water content (VWC) during drying and the starting volumetric water content (VWC_0) after rain.

3. Results

3.1. Factors influencing soil moisture

The GLMM results for each study site are shown in Table 2. The *P*-values based on the posterior distribution (pMCMC) showed significant interactions between all pairs of factors for soil moisture in fine-textured soils (El Cautivo). In coarse-textured soils (Las Amoladeras), disturbance and interaction between crust type and soil depth had a significant effect on soil moisture. In both types of soils, there was a marginally significant interaction among the three predictor factors for soil moisture. Partial effects of the

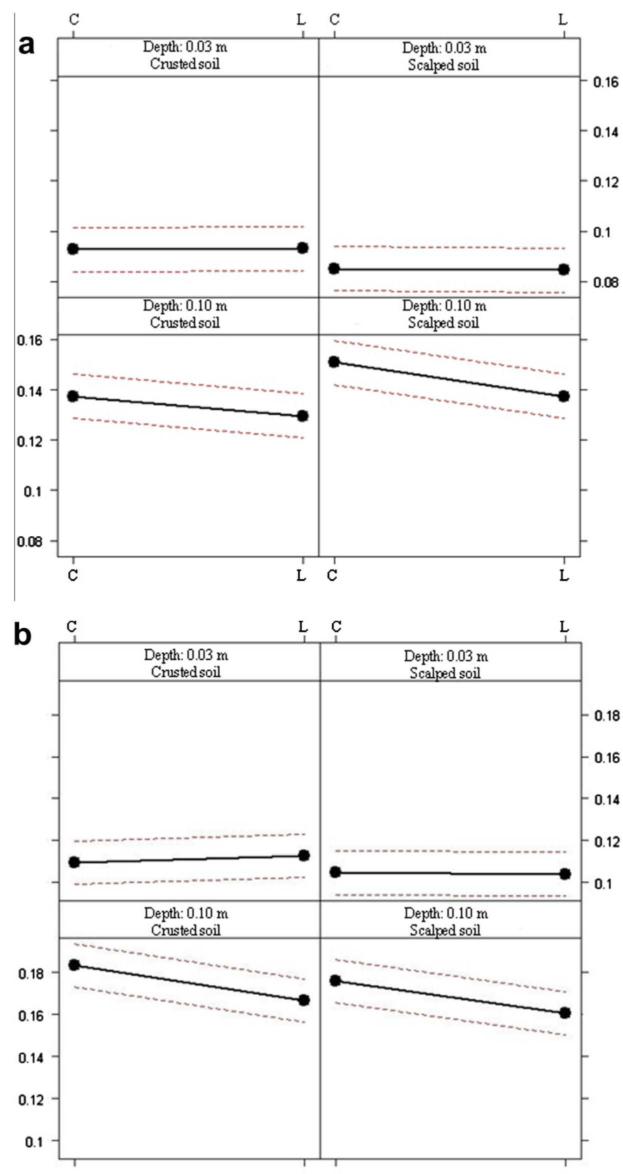

Fig. 2. Partial effects of the significant factors in the GLMM affecting soil moisture in fine (a) and coarse-textured soils (b). The factors were: BSC type (cyanobacterial-BSC or C and lichen- BSC or L), indicated by the black points; disturbance treatment (BSC-crusted and scalped soil, on the left and right squares, respectively); and soil depth (0.03 m and 0.10 m, on the upper and bottom squares, respectively). The vertical axis is labeled on soil moisture content ($m^3\ m^{-3}$), and a 95% pointwise confidence interval is drawn around the estimated effect.

predictor factors affecting soil moisture are shown in Fig. 2. Soil moisture values at 0.03 m were similar both in fine and coarse-textured soils. Similar values at 0.03 m were also obtained for cyanobacterial and lichens BSCs within a site. Values obtained for the two types of BSC were higher compared to those obtained on the same soils where BSCs had been removed. At 0.10 m, moisture was higher in soils covered by cyanobacterial BSCs than in those covered by lichen BSCs, and more so in coarse (Fig. 2b) than in fine-textured soils (Fig. 2a). The analysis showed that the removal of the BSCs had a different effect on soil moisture at 0.10 m depending on soil texture. In fine-textured soils, moisture at 0.10 m was higher in the soils where the BSCs had been removed than in the soils covered by them. In contrast, in coarse-textured soils, moisture at 0.10 m was similar under both undisturbed BSCs and scalped soils.

3.2. Influence of BSC removal

BSC removal had different effects on soil moisture depending on depth and soil water content. During wet soil periods (soil volumetric water content over 15%), at 0.03 m scalped soils showed lower values of soil moisture than undisturbed BSCs. Removal of BSCs led to a soil moisture decrease by up to 5% compared to values obtained on undisturbed BSCs (Fig. 3a and b). In contrast, at 0.10 m undisturbed BSCs and BSC-scalped soils showed similar values of moisture in both fine and coarse-textured soils (Fig. 3c and d), with the exception of undisturbed cyanobacterial BSCs on coarse-textured soils which showed higher moisture than scalped soils.

Fig. 4 shows soil water loss in the undisturbed and scalped soils following several rains in winter (total rainfall 58 mm). As expected, soils dried more slowly at 0.10 m than at 0.03 m. Soil water loss was faster in the BSC-scalped than in the undisturbed BSC soils, in both fine (Fig. 4a) and coarse-textured soils (Fig. 4b), but these differences were mainly at 0.03 m. At 0.10 m, both undisturbed and scalped soils showed similar evaporative losses (Fig. 4c and d). These soil moisture loss patterns in undisturbed and scalped soils were usually observed after rain throughout the year.

During soil drying periods (soil volumetric water content under 15%), removal of BSCs did not lead to any significant change in soil moisture at 0.03 m compared to soils covered by them (Fig. 5a and b). A similar behaviour was found at 0.10 m, with undisturbed and scalped soils showing similar soil moisture (Fig. 5c and d), except for some of the scalped plots on fine-textured soils, which showed higher moisture than adjacent soils with undisturbed BSCs (Fig. 5c).

3.3. Influence of BSC type

The type of BSC influenced soil moisture differently depending on soil water content. During wet soil periods, soil moisture at both 0.03 m and 0.10 m was higher under lichen than under cyanobacterial BSCs (Fig. 3), with the exception of the coarse-textured soils, which showed higher moisture under cyanobacterial than lichen BSCs at 0.10 m (Fig. 3d). Under these wet soil conditions, soil water loss was faster in soils under cyanobacterial than under lichen BSCs at 0.03 m (Fig. 4a and b), but similar in both at 0.10 m (Fig. 4c and d), in fine and coarse-textured soils.

During soil drying periods, no difference was found in soil moisture underneath cyanobacterial or lichen BSCs at 0.03 m, in either fine (Fig. 5a) or coarse-textured soils (Fig. 5b). However, some differences were found between BSCs at 0.10 m, where soils under

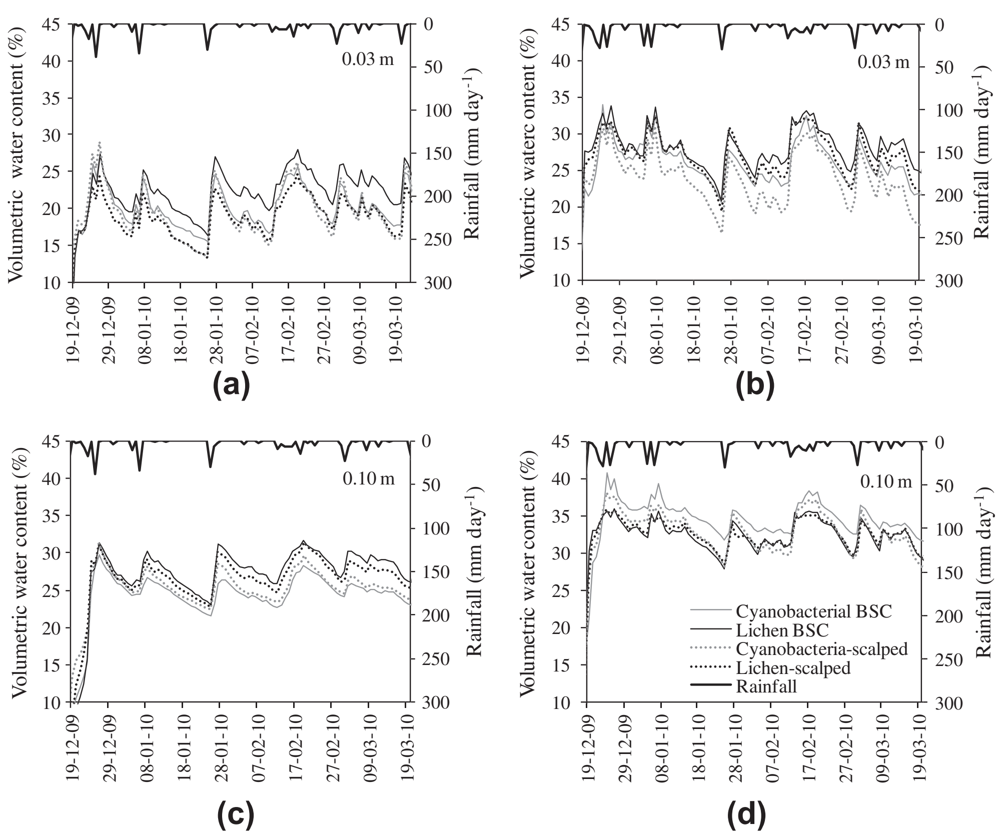

Fig. 3. Soil moisture under the types of BSC and in the adjacent scalped soils (average of the three plots per type of surface) during wet soil periods (soil volumetric water content over 15%). (a) Soil moisture at 0.03 m in fine-textured soils; (b) soil moisture at 0.03 m in coarse-textured soils; (c) soil moisture at 0.10 m in fine-textured soils; and (d) soil moisture at 0.10 m in coarse-textured soils.

cyanobacterial BSCs showed higher moisture than under lichen BSCs (Fig. 5c and d). In addition, contrary to the pattern observed during wet soil periods, soil water loss during soil drying periods was faster under lichen than under cyanobacterial BSCs at both 0.03 m and 0.10 m, in fine (Fig. 6a) and coarse-textured soils (Fig. 6b).

3.4. Influence of soil texture

Removal of BSCs, and especially the removal of lichen BSCs, caused a greater decrease in soil moisture in fine (Fig. 3a) than in coarse-textured soils (Fig. 3b). The increase in soil moisture with the presence of lichens compared to cyanobacterial BSCs during wet soil periods was also more remarkable in fine than in coarse-textured soils. In general, coarse-textured soils showed higher moisture peaks during rain and higher moisture content throughout the year than fine-textured soils (Fig. 3). During wet soil periods, soil water loss was slightly faster in fine than in coarse soils, especially at 0.03 m (Fig. 4). However, during soil drying periods, soil water loss tended to be somewhat faster in coarse than in fine-textured soils (Fig. 6).

4. Discussion

4.1. Influence of BSC removal and BSC type on soil moisture

The presence of BSCs showed different effects on soil moisture depending on soil water content. During wet soil periods (soil volumetric water content over 15%), BSCs increased soil moisture compared to soils where the BSC had been removed. This effect was particularly significant at 0.03 m (Fig. 3a and b), as BSCs improve soil properties, such as water retention and organic matter content, immediately beneath the crust more than deeper in the soil (Chamizo et al., 2012b).

Previous studies have also reported higher moisture in soils covered by BSCs than in uncrusted or bare soils. Brotherson and Rushforth (1983) found that the presence of well-developed BSCs increased the depth of water penetration, and thereby soil moisture, compared to uncrusted soils. Gao et al. (2010) reported that with high soil water content, moisture in the upper 0.10 m of soil was higher in soils with BSCs than in those without BSCs. This effect of BSCs can be explained by the role of cyanobacteria filaments and lichen anchoring structures in binding soil particles and forming mats on the soil surface which store water and strongly increase water retention at the soil surface (Belnap, 2006). In addition, swelling of polysaccharide cyanobacterial sheaths and algal and cyanobacteria filaments block soil pores when wet (Kidron et al., 1999), leading to a reduction in evaporation and contributing to soil moisture conservation (Verrecchia et al., 1995). Contrary to this positive effect on soil moisture, some authors have found lower moisture under BSCs, attributed to soil darkening by some types of BSCs and the consequent increase in soil temperature and thus evaporation (Harper and Marble, 1988; Kidron and Tal, 2012).

Our field data showed that soil temperature under BSCs appeared to have no influence on soil moisture. Fig. 7 shows soil temperature under cyanobacterial BSC, lichen BSC and BSC-scalped soil during drying after rainfall in winter and during several days in summer, in fine-textured soils. Soil temperature under the types

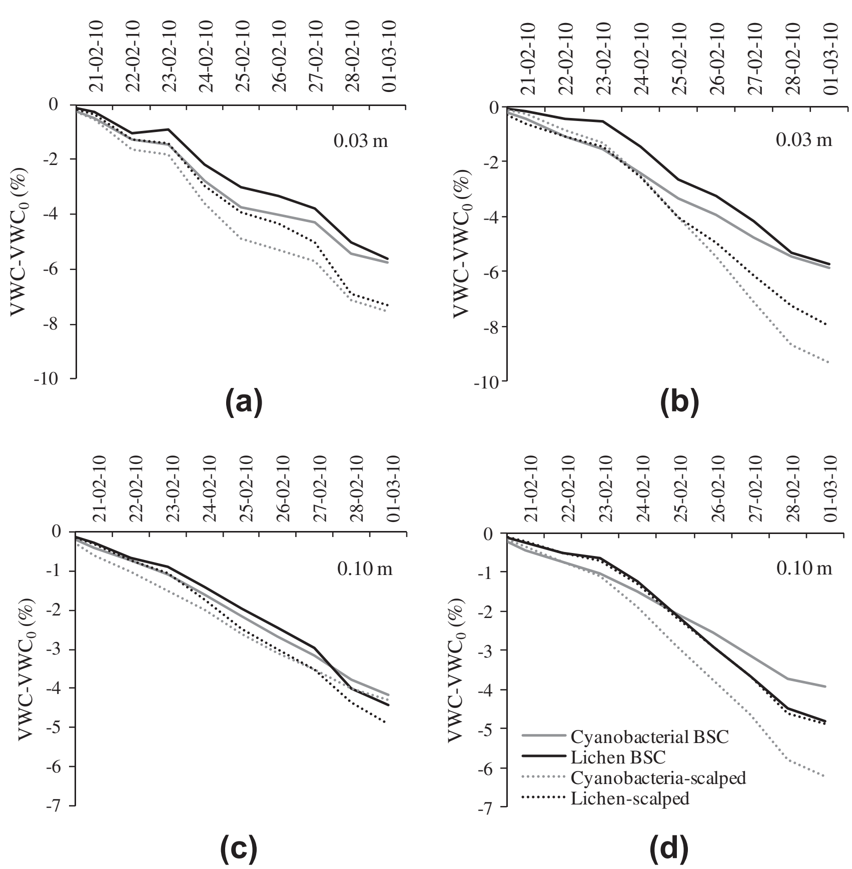

Fig. 4. Soil water loss after several rainfalls in winter (determined as the difference between actual volumetric water content (VWC) during drying and the starting volumetric water content (VWC_0) after rain) under the types of BSC and in the adjacent scalped soils (average of the three plots per type of surface). (a) Soil water loss at 0.03 m in fine-textured soils; (b) soil water loss at 0.03 m in coarse-textured soils; (c) soil water loss at 0.10 m in fine-textured soils; and (d) soil water loss at 0.10 m in coarse-textured soils.

of surfaces was similar throughout the day, and small differences were only found during the hours of maximum radiation. During the drying period in winter, maximum daily temperature was slightly higher under lichens and scalped soils than under cyanobacteria (Fig. 7a). During summer, maximum daily temperature was higher under cyanobacteria, followed by scalped soils and lichens (Fig. 7b). Therefore, lower surface moisture in BSC-scalped soils with respect to undisturbed BSCs was not related to soil temperature.

The type of BSC influenced soil moisture. As in our starting hypothesis, during wet soil periods, soil moisture was higher under more developed lichen BSCs than in soils covered by less developed cyanobacterial BSCs (Fig. 3). The decrease in soil moisture was also more noticeable after removal of lichens than in soil covered by cyanobacterial BSCs (Fig. 3a). This pattern was not observed in the site with coarse-textured soils, where growth of moss was significant (up to 35% of the plot) during the rainy season, especially in the cyanobacterial BSCs. The large surface area available for water absorption in mosses provides them with a high infiltration and water holding capacity (Bowker et al., 2010; Chamizo et al., 2012b). They are also highly permeable (Maestre et al., 2002; Eldridge et al., 2010; Chamizo et al., 2012a). This abundant moss contributed to higher moisture at 0.10 m under cyanobacterial BSCs than under lichens (Fig. 3d).

Higher moisture under well developed BSCs (lichens) can be attributed to an increase in soil water holding capacity and organic matter content with higher BSC development (Belnap, 2006; Housman et al., 2006; Chamizo et al., 2012b). More organic matter contributes to soil aggregation, which enhances the proportion of pores, and thereby infiltration (Warren, 2003; Ludwig et al., 2005). Several studies have documented the increase in the volume of larger pores with the presence of well-developed BSCs (Malam Issa et al., 2009; Miralles-Mellado et al., 2011). Moreover, during low-intensity rainfall, which is predominant in our study areas, the rougher lichen BSCs and the better soil properties underneath them contribute to higher infiltration than under the cyanobacterial BSCs (Rodríguez-Caballero et al., 2012). Well-developed BSCs also retain surface moisture longer after rain than bare soil or thin cyanobacterial crusts (Belnap et al., 2003b).

In addition to lower moisture, water loss was faster under cyanobacteria than under lichen-covered soils during wet soil periods (Fig. 4). This result can be attributed to: (i) greater exopolysaccharide content in lichen than cyanobacterial BSCs (Chamizo et al., 2013) and swelling of these compounds upon wetting, blocking soil pores, and thereby limiting evaporation; (ii) synthesis of hydrophobic compounds by lichen species during periods of biological activity, since hydrophobic soil layers decrease evaporation by interrupting capillarity flow through soil (Shokri et al., 2008).

During soil drying periods (soil volumetric water content under 15%), contrary to the pattern observed during wet soil periods, both undisturbed and scalped soils showed similar moisture content (Fig. 5). Whereas in wet soil, by blocking soil pores, BSCs contribute to maintaining higher soil moisture, during soil drying, the pore-clogging effect of BSCs ceases, causing soil moisture to be similar in undisturbed BSCs and scalped soils. In agreement with our findings, Booth (1941) found higher soil moisture in the upper 0.025 m soil layer under BSCs than under physical crusts after rain, but similar moisture under both when soil was dry. Previous results on evaporative losses in undisturbed BSCs and scalped soils in our study sites have also shown lower evaporation in lichen BSCs than in lichen-scalped soils under saturation conditions, but no difference between them with moderate or low soil water con-

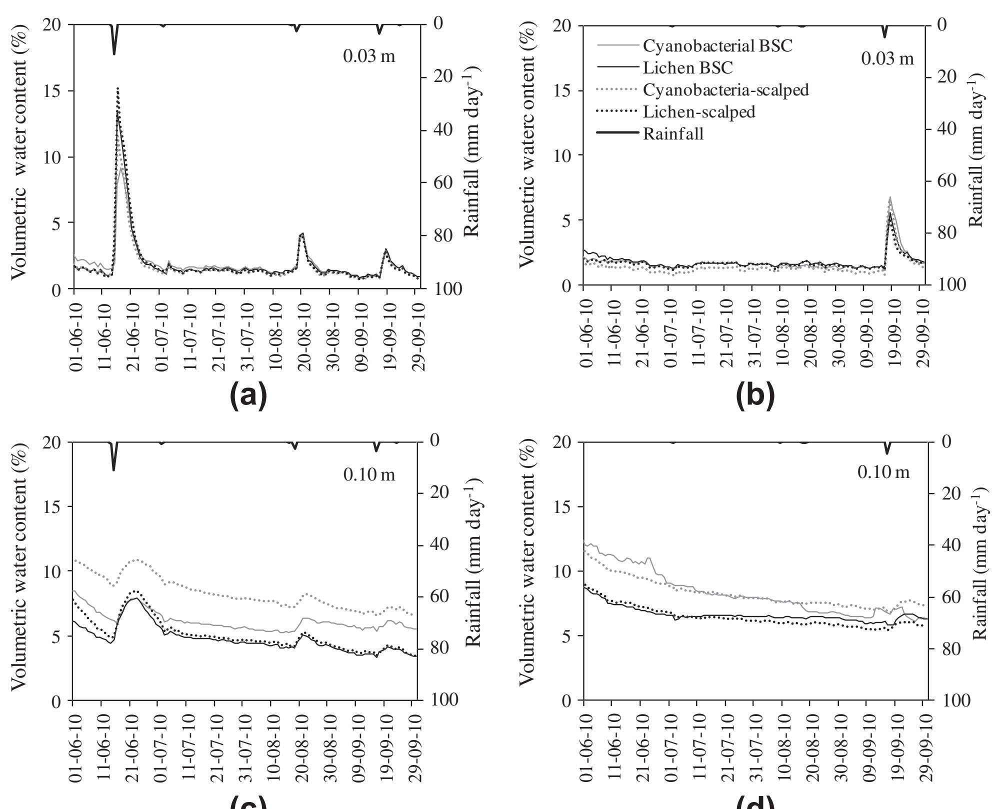

Fig. 5. Soil moisture under the types of BSC and in the adjacent scalped soils (average of the three plots per type of surface) during soil drying periods (soil volumetric water content under 15%). (a) Soil moisture at 0.03 m in fine-textured soils; (b) soil moisture at 0.03 m in coarse-textured soils; (c) soil moisture at 0.10 m in fine-textured soils; and (d) soil moisture at 0.10 m in coarse-textured soils.

tent (Chamizo et al., 2013). It may be observed that scalped soils showed higher moisture than undisturbed BSCs at 0.10 m in fine-textured soils during soil drying periods (Fig. 5c). This can be explained by the frequent rainfalls during the study year that favoured proliferation of annual plants, which had higher cover in the scalped soils than in the undisturbed BSCs, probably due to an inhibiting effect of BSCs on seedling emergence (Escudero et al., 2007). In winter and early spring, annual roots can increase soil moisture by increasing soil organic matter content and creating channels for water infiltration (Evans et al., 1981), whereas they decrease soil moisture by consuming water during growth. However, in late spring, when their activity ceases, minimal consumption of water by annual roots and increased soil organic matter contribute to maintaining soil moisture, thus explaining the higher soil moisture in scalped than in adjacent undisturbed BSCs (Fig. 8a). Undisturbed BSCs and adjacent scalped soils with similar or no annual cover showed similar soil moisture at 0.10 m during these soil drying periods (Fig. 8b).

BSC type affected soil moisture differently during the soil drying periods, when soil moisture at 0.10 m was higher under cyanobacterial than under lichen BSCs, in both fine (Fig. 5c) and coarse-textured soils (Fig. 5d). In addition, soil water loss at both 0.03 m and 0.10 m was faster under lichen than under cyanobacterial BSCs in fine (Fig. 6a) and coarse-textured soils (Fig. 6b). Coinciding with this, Cantón et al. (2004) found that at this site, despite higher initial soil moisture under lichens, it dried out at a rate similar to soils covered by vegetation or physical crusts, probably because of their high macroporosity (up to 37%). Thus after the exopolysaccharide and hydrophobic compounds decompose, and soil water content is moderate or low, larger meso and macroporosity in soils covered by lichens (Cantón et al., 2003; Malam Issa et al., 2009; Miralles-Mellado et al., 2011) results in more rapid evaporative losses (Fig. 6) and lower moisture than in soils covered by cyanobacteria (Fig. 5c and d). Similarly, George et al. (2003) reported that soil profiles covered by lichens dried out faster than cyanobacteria-covered soils. These authors attributed differences in soil water loss between the two BSCs to their different chemical composition (mucilaginous polysaccharide sheaths in cyanobacteria and chitin in lichen) and variations in water absorption from dew deposition that could result in different drying patterns.

4.2. Influence of soil texture

Removal of BSCs caused a greater decrease in soil moisture in fine (Fig. 3a) than in coarse-textured soils (Fig. 3b). This is probably because the importance of BSCs in enhancing pore formation and infiltration, and thereby soil moisture, is greater in fine soils, which are characterised by lower porosity and lower infiltration rates than coarse soils, in which porosity is larger and infiltration is faster (Warren, 2003).

On the other hand, our fine-textured soil had a significantly higher water retention capacity (mean water holding capacity at −33 kPa is 26.7% ±3.3) than coarse-textured soils (mean water holding capacity at −33 kPa is 15.7% ±1.8), and we therefore expected higher moisture in the former than in the latter. Contrary to expected, coarse-textured soils showed higher moisture peaks during rain and higher moisture content throughout the year than fine-textured soils (Fig. 3). During wet soil periods, water loss was slightly faster in fine than in coarse-textured soils, especially at 0.03 m (Fig. 4). This higher moisture content in coarse-textured soils is attributed to their better soil properties and more favourable ambient conditions. Whereas the site with fine-textured soils is a badlands characterised by steep slopes, poorly-developed soils, with low organic matter and poor soil aggregation (Chamizo et al., 2012b) and soil structure, all of which favour high runoff coefficients (Chamizo et al., 2012a), the site with coarse-textured soils has a flat topography, and soil has a higher organic matter content and infiltration capacity, as well as a petrocalcic horizon that inhibits water loss from deep infiltration. This site is also close (±2 km) to the Mediterranean Seacoast and undergoes less hydric stress due to its lower vapour pressure deficit (mean annual vapour pressure deficit at 12 p.m. was 1.3 ± 0.8 kPa at the site with coarse soils and 1.9 ± 1.2 kPa at the site with fine soils) and consequent evaporation. Thus negligible water loss from drainage combined with the source of highest soil water loss being evaporation causes an "inverse texture effect" in arid areas by which higher infiltration, as well as other factors such as denser vegetation cover in coarse than in fine soils, is responsible for higher soil moisture in coarse than in fine-textured soils (Noy-Meir, 1973). Nevertheless, we found that during soil drying periods (Fig. 6), soil water loss tended to be somewhat slower in fine-textured soils, which might indicate that, as soils dry out, these soils are more efficient in retaining water than coarse-textured soils.

4.3. Ecological aspects

Available soil moisture influences many aspects of plant ecology, from individual to plant community (Ehrenfeld et al., 2005). In arid and semiarid areas, soil moisture is the major factor controlling plant photosynthesis, and thus the flow of energy into the ecosystem (Noy-Meir, 1973). On the other hand, evapotranspiration represents the most important process conditioning loss of soil moisture. BSCs play a crucial role in soil water availability in drylands by promoting both reduction of soil moisture loss from evaporation and retention of soil moisture, especially when soil

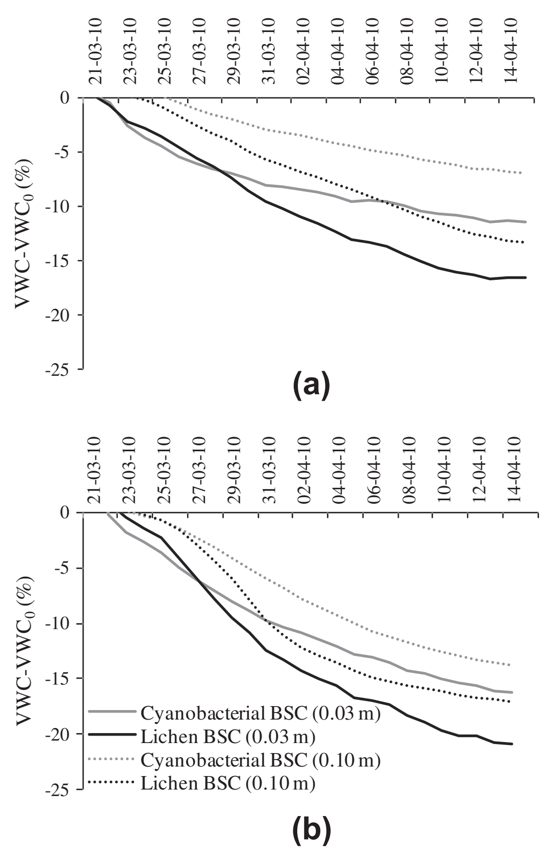

Fig. 6. Soil water loss (determined as the difference between actual volumetric water content (VWC) during drying and the starting volumetric water content (VWC_0) after rain) at 0.03 and 0.10 m under the types of BSC (average of the three plots per crust type) during soil drying in spring. (a) Soil water loss in fine-textured soils and (b) soil water loss in coarse-textured soils.

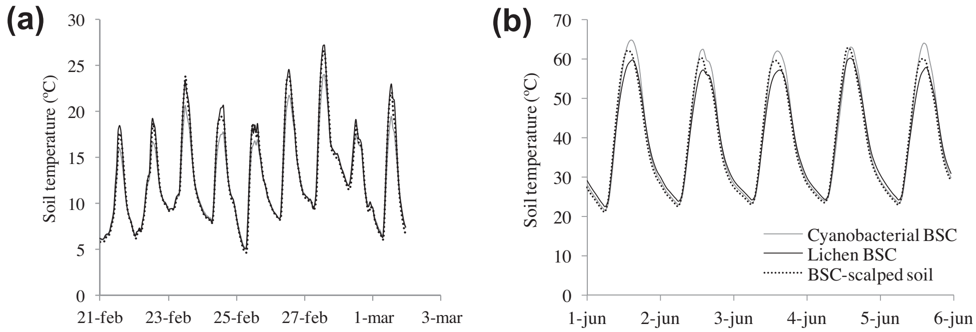

Fig. 7. Soil temperature at 0.02 m depth under the cyanobacterial BSC, lichen BSC and BSC-scalped soil (one plot of each cover type), in fine-textured soils (El Cautivo), during drying after a rainfall in winter (a), and during several days in summer (b).

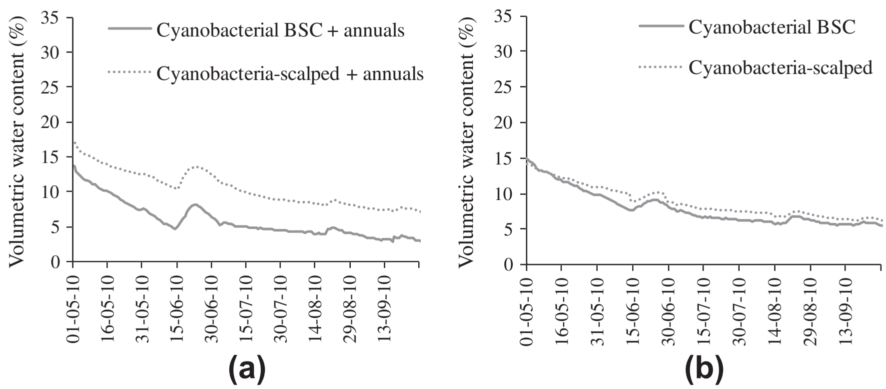

Fig. 8. Soil moisture at 0.10 m in undisturbed cyanobacterial soils and adjacent scalped soils, in fine-textured soils, during soil drying periods. (a) Plots with considerable cover of annuals (mainly the scalped soils) and (b) plots with scarce cover of annuals.

moisture content is high. BSC removal would therefore be expected to have dramatic consequences on soil moisture loss. However, though a significant decrease in soil moisture was found, this effect was less than expected, possibly because previous long-term colonisation by BSCs may have modified the physicochemical properties of the underlying soil, thereby ameliorating the impact of their removal on soil moisture. Greater differences might be expected in comparisons with typically bare or uncrusted soils. Previous work at the El Cautivo site has shown that moisture under lichen BSCs is higher than under physical crusts and that, even during summer, lichen-crusted surfaces keep moisture higher than surfaces covered by vegetation or physical crusts (Cantón et al., 2004). This higher moisture may be crucial for a number of biological soil processes and for vascular vegetation in water-limited environments, especially during the periods when the water deficit is greater.

After a soil moisture pulse event, BSCs trigger a series of ecological processes which differ depending on the pulse size (Schwinning and Sala, 2004). Light rainfall generates brief, shallow pulses that are likely to affect only organisms with fast response times, such as surface-dwelling soil micro-fauna or BSC organisms, while deeper and longer soil moisture pulse events are usually required to trigger reproduction, germination or growth of higher plants (Schwinning and Sala, 2004). Like most arid and semiarid areas in the world, most of the rainfall in the semiarid areas of SE Spain is low-magnitude (small amount) (Lázaro et al., 2001; Cantón et al., 2002; Mayor et al., 2011), and therefore, biological activity by BSCs may have a major role in numerous small-scale ecological processes (which in turn can have a strong influence on larger-scale processes) under conditions in which the soil moisture pulse size is not enough to trigger larger ones, for example, physiological activity of higher plants. During moist soil periods, increased soil moisture promoted by BSCs is likely to stimulate primary production and nutrient uptake, as well as biological activity of soil biota, which in turn, affect nutrient cycling, and thereby, plant productivity. Loss of BSCs due to disturbances provoked by trampling or grazing in semiarid areas would therefore be expected to decrease soil moisture in the upper layers. Disturbance of BSCs also favours soil compaction (Chamizo et al., 2012a), thus increasing evaporative loss and resulting in less overall water available to plants (Schlesinger et al., 1990). Under this scenario, important changes in structure and composition of plant communities, and more broadly, general ecosystem functioning might be predicted if BSCs are disturbed.

5. Conclusions

Biological soil crusts have a key role in the maintenance of soil moisture during periods of high soil water content (soil volumetric water content over 15%). Disturbance of BSCs during these periods decreased soil moisture content of the uppermost layer of the soil (5 cm) up to a 5%. During soil drying periods (soil volumetric water content under 15%), however, both undisturbed BSCs and BSC-scalped soils showed similar moisture content. The influence of BSC removal on soil moisture was soil texture-dependent. Because BSCs have a stronger influence on increasing soil porosity and infiltration in fine than in coarse soils, removal of BSCs had a more negative effect on soil moisture in soils with finer than coarse soil texture. Our results emphasise the important role of BSCs in the conservation of soil moisture in interplant spaces, where water inputs are generally lower compared to patches of vegetation.

The type of BSC also affected soil moisture dynamics. Our study suggests that well-developed BSCs (lichen BSCs) are more efficient in maintaining soil moisture during periods of high soil water content, whereas less-developed BSCs (cyanobacterial BSCs) are more efficient in maintaining soil moisture during soil drying periods. Therefore, not only the presence of BSCs, but also the types of BSC covering the interplant spaces plays a significant role in water fluxes and soil water content in drylands.

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