THE ROLE OF PHYSICAL AND BIOLOGICAL SOIL CRUSTS ON THE WATER BALANCE IN SEMIARID ECOSYSTEMS

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PhD Thesis

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TESIS DOCTORAL

THE ROLE OF PHYSICAL AND BIOLOGICAL SOIL CRUSTS ON THE WATER BALANCE IN SEMIARID ECOSYSTEMS

INFLUENCIA DE LAS COSTRAS FÍSICAS Y BIOLÓGICAS DEL SUELO EN EL BALANCE DE AGUA EN ECOSISTEMAS SEMIÁRIDOS

Memoria presentada por Sonia Chamizo de la Piedra para optar al Grado de Doctor en Ciencias Ambientales por la Universidad de Almería

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A mi familia

"La verdadera ciencia enseña, por encima de todo, a dudar y a ser ignorante"
Miguel de Unamuno

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CONTENTS

INTRODUCTION

Background

A brief introduction to physical and biological soil crusts

Arid and semiarid areas throughout the world are characterised by a patchy distribution of vegetation and open spaces surrounding the higher plants, commonly occupied by physical and biological soil crusts. Physical crusts are formed by densely packed mineral particles resulting from either the disruption of soil aggregates due to the impact of raindrops and later “in situ” reorganisation of the disaggregated particles into “structural crusts”, or the deposition and reorganisation of particles transported by runoff or wind in accumulation zones forming “depositional crusts” (Valentin and Bresson, 1992; Cerdan et al., 2001; Fox et al., 2004). Most soils exposed to rainfall in drylands are prone to the formation of this type of crust (Catt, 2001). In the Mediterranean region, the formation of physical crusts on the soil surface is very frequent (Singer and Le Bissonnais, 1998) due to climate conditions and soils characterised by low organic matter content and poor structure and aggregate stability (Singer, 1991). When conditions are stable enough, bare soils and physical crusts are often colonised by a complex community of specialized organisms comprised of cyanobacteria, algae, microfungi, lichen, mosses and other microorganisms, which together are known as biological soil crusts (BSCs).

BSCs, which are found worldwide in hyper-arid, arid, semiarid, sub-humid, alpine and polar regions, together comprise more than 40% of the world’s land surface (Reynolds et al., 2007) and can cover up to or more than 70% of the soil surface in these areas (Belnap et al., 2005). BSC organisms have a limited capacity for growing upward from the soil surface, and thus are unable to compete with vascular plants for light. Therefore, BSCs are not present where climate conditions permit growth of a closed vascular plant canopy or thick litter layers (Belnap et al., 2003a), and their distribution is restricted to ecosystems with adverse climatic conditions where organisms able to develop self-protection strategies, like BSCs, are successful. Thus BSC organisms are only active when wet. When dry, their biological activity ceases (Rosentreter, 1986). As BSCs have low moisture requirements and are able to make use of light rainfall, snow, fog and even dew, they survive where low water content limits the growth and productivity of vascular plants (Belnap et al., 2003a).

BSCs are composed of various organisms and morphological groups. Because it is so difficult to identify the specific species that compose the BSC (e.g., cyanobacteria and other microscopic organisms), BSCs are usually classified by the predominant morphological group into cyanobacterial, green algal, moss or lichen crusts (Fig. 1). Depending on their morphology, lichen crusts can also be classified as: i) *crustose,* lichens which appear flat and are attached to the substrate; *squamulose,* clusters of individual lichen flakes; *foliose,* lichens with a leaf-like appearance loosely affixed to the substrate; *gelatinose,* flat or three-dimensional lichens; or *fruticose,* three-dimensional lichens forming branches (Belnap and Lange, 2001). Another classification of BSCs proposed by Belnap (2003a) is based on crust morphology and factors that influence runoff, infiltration, and sediment production. Thus, depending on climate characteristics (rainfall intensity and timing, and potential evapotranspiration), BSCs ranging from hyper-arid to arid-cool and cold drylands were classified by Belnap et al. (2003a) as smooth, rugose, pinnacled or rolling crusts. Smooth crusts are found in hot hyper-arid drylands, where potential evapotranspiration is very high. Rugose crusts appear in drylands with lower potential evapotranspiration than hyper-arid deserts. Pinnacled crusts are located in more mesic desert regions where potential evapotranspiration is lower than in hot deserts. Rolling crusts grow in colder regions with lower potential evapotranspiration than pinnacled crusts. Cyanobacteria and fungi predominate in smooth and rugose crusts, whereas lichens and mosses abound in pinnacled and rolling crusts.

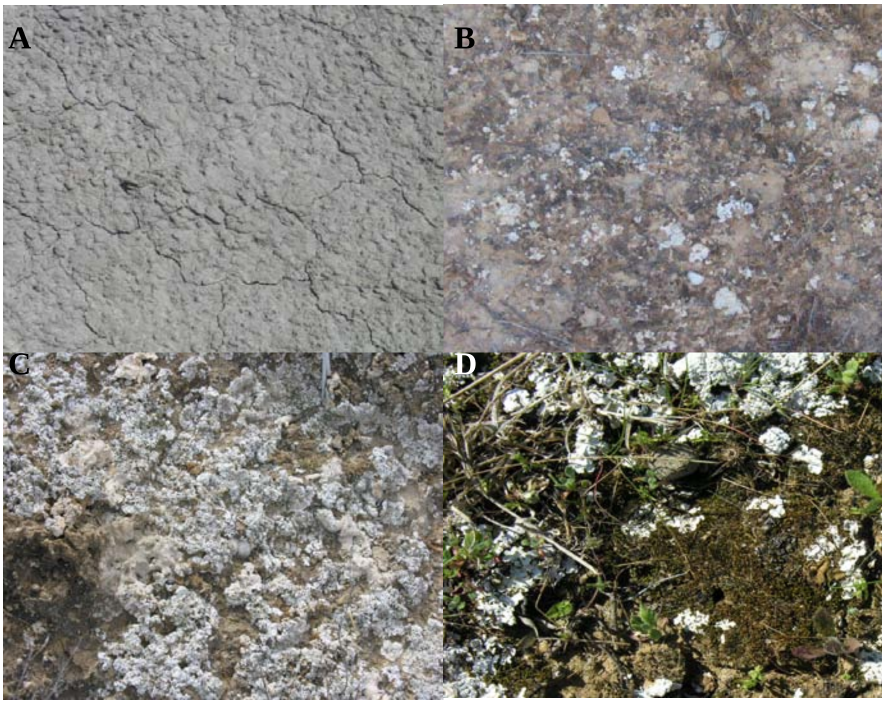

Fig. 1. Types of soil crusts. A) Physical crust; B) Cyanobacterial BSC; C) Lichen BSC; D) Lichen-moss BSC.

The crucial role of BSCs in ecosystem functioning

Although physical crusts and BSCs are an almost negligible portion of the soil profile (from less than one to a few millimetres thick), they have a number of crucial roles, especially where water is scarce (Maestre et al., 2011). Soil crusts form the boundary between soil and atmosphere and therefore control gas, water and nutrient exchange into and through soils (Belnap et al., 2005). As the role of BSCs in numerous processes in arid and semiarid areas is increasingly recognized, their study has drawn the attention of a growing number of researchers, especially in the last decade. BSCs greatly differ from physical crusts in physical and chemical properties. Unlike physical crusts, BSCs are involved in the stabilization and fertility of arid and semiarid soils (Zhang, 2005). They prevent erosion by water and wind (Eldridge and Greene, 1994b), and contribute carbon and nitrogen to soils (Housman et al., 2006). In semiarid areas, where distribution of nutrients is mainly concentrated beneath plants and interplant spaces receive little plant material, BSCs are the main agent of nutrient input in the interplant spaces (Evans and Lange, 2003). Through their influence on roughness, albedo, porosity and cracking, BSCs also play a key role on water processes, such as infiltration and runoff, evaporation and soil moisture (Alexander and Calvo, 1990; Malam Issa et al., 2009; Miralles-Mellado et al., 2011). BSCs exert a strong influence on the emergence, establishment and survival of vascular plants, either through competition for cover and biomass, or through changes in soil properties (Eldridge and Greene, 1994a; Belnap et al., 2003c; Escudero et al., 2007). However, interactions between BSCs and vascular plant species are complex and studies have reported that BSCs can either promote or retard plant colonization (Maestre et al., 2011).

Because of all these important ecosystem functions, BSCs have been described as “ecosystem engineers” in drylands (Bowker et al., 2005, 2006), and have been proposed as indicators of ecological health (Zhang, 2005), and for rehabilitation and restoration of degraded and damaged ecosystems (Bowker, 2007). However, it should be pointed out that the rate and magnitude of ecosystem services provided by BSCs greatly depend on BSC composition and developmental stage. As BSCs develop, one species replaces others. Thus, later successional species are likely to have a different role in ecosystem processes than early-successional ones.

Successional dynamics of BSCs

BSCs are dynamic over time. Succession usually starts with the colonization of bare soils by large mobile filamentous cyanobacteria, usually of the genus *Microcoleus*, which live 1-4 mm below the soil surface. *Microcoleus* filaments are surrounded by sticky polysaccharide sheaths that bind soil particles and contribute to the formation of soil aggregates. When wet, filaments migrate to the surface, and moisture enables photosynthesis by these organisms, thus providing energy and organic matter for the ecosystem (Zhang, 2005). Upon drying, the filaments retreat to the surface. This movement spreads sheath material throughout the uppermost soil layer (Belnap et al., 2003a), improving soil aggregation in the top soil profile. As the succession advances, smaller, less mobile cyanobacteria, which live on or just below the soil surface, colonise (García-Pichel and Belnap, 1996; Belnap, 2003a). Both cyanobacteria filaments and extracellular secretions act as gluing agents, binding soil particles and increasing the formation of soil aggregates (Fig. 2), thus increasing soil stability (Mazor et al., 1996). Exopolysaccharides secreted by cyanobacteria also protect microorganisms from desiccation and nutrient limitation and help them survive (Mazor et al., 1996; Zhang, 2005).

Once soil has been stabilized by cyanobacteria, fungi and small pioneer lichens appear. In the later successional stages, larger lichens and mosses colonise (Belnap and Eldridge, 2003; Lázaro et al., 2008). Lichens and mosses grow above the soil surface, and thus provide soils with better protection from raindrop impact and detachment of particles during overland flow events than cyanobacteria (Belnap, 2006). Lichen and moss anchoring structures also form a cohesive mulch on the soil surface that strongly contributes to soil stability (Belnap and Gardner, 1993; Belnap, 2003a).

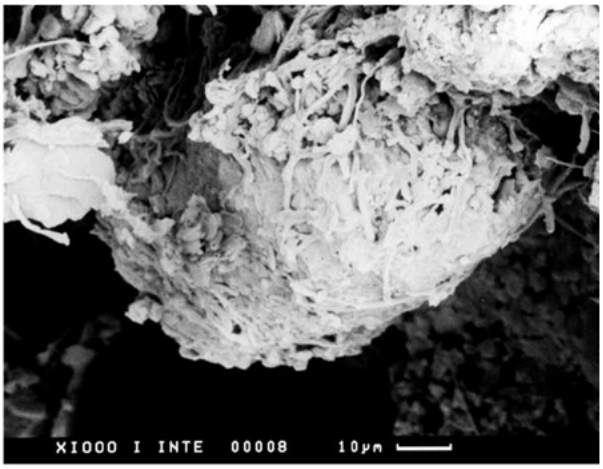

Fig. 2. Electron microscope photograph showing soil aggregate with fungus hiphae binding soil particles
(Picture by Yolanda Cantón).

One of the main impacts on BSC successional dynamics is their disturbance by human activities. Moreover, the role of BSCs in ecosystem processes is also severely affected by disturbances. The implications of disturbance on BSC functioning in drylands are discussed below.

Impacts of disturbance on BSCs

Disturbances can intensely affect the cover, species composition, species richness, and functioning of BSCs. Increasing activities in dry areas, such as livestock grazing, vehicle traffic, and trampling by livestock and humans cause deterioration or loss of BSCs, and often revert late-successional BSCs (lichens and mosses) to early ones (cyanobacterial BSCs). The impact of disturbance depends on the type of substrate, the crust type and climate characteristics, but also on the intensity, frequency, timing and type of disturbance (Belnap and Eldridge, 2003). More developed BSCs (lichens and mosses) are more vulnerable to disturbance than less developed ones (cyanobacterial BSCs) (Harper and Marble, 1988). Herbicides and pesticides kill crust organisms entirely and increase the time necessary for BSCs to recover compared to trampling in which the crust fragments remain in place (Belnap and Eldridge, 2003). Thus, BSC recovery times are quite variable and can range from only a few years to decades or even a century depending on the type, severity and extent of disturbance, and biotic (BSC composition, vascular plant community) and abiotic factors (soil texture, topography, rainfall patterns) (Belnap and Eldridge, 2003; Bowker, 2007).

Disturbance of BSCs can lead to changes in primary ecosystem processes, such as erosion and hydrological processes, and nutrient cycling. Disturbance generally flattens the soil surface and causes soil compaction, thus increasing runoff, and sediment and nutrient losses (Barger et al., 2006). Lichens and mosses fix more carbon (C) and nitrogen (N) than cyanobacteria (Housman et al., 2006) and, due to their greater roughness, are also more effective in trapping nutrient-enriched dust and reducing erosion than cyanobacterial BSCs (Belnap, 2006). Therefore, the replacement of late successional species by earlier ones as a consequence of disturbance is expected to lead to significant changes in local hydrological regimes, reduce C and N inputs in the ecosystem, and increase erosion.

Despite the high vulnerability of BSCs to disturbances and their increasing exposure to them because of growing human activity in drylands, few studies have specifically tackled the consequences of BSC alteration on soil hydrology (e.g., Eldridge et al., 2000; Herrick et al., 2010). Even though their roles in soil stability and as crucial agents for prevention of soil erosion are widely known, there has been little research exploring the implications of disturbance of BSCs on water (e.g., Eldridge and Kinnell, 1997; Herrick et al., 2011) and wind erosion (McKenna Neuman et al., 1996). Moreover, no previous studies have explored the consequences of BSC disturbance on soil hydrology or erosion in a variety of crust types ranging from less-developed (incipient-cyanobacterial BSCs) to well-developed BSCs (lichens and mosses). Knowledge of the consequences of such alterations on hydrological and ecological processes is of the highest interest for proper decision-making and management of drylands.

Influence of BSCs on hydrological processes

Factors conditioning the BSC response to hydrological processes

Stage of crust development, climate regime, surface roughness, time since disturbance, soil structure and soil texture all have a major influence on BSC hydrologic response at any given place (Belnap and Lange, 2001). Under similar climate characteristics and type of substrate, the type of soil crust has a strong influence on water processes. Physical crusts (structural and depositional), due to absence of large pores and poor soil structure, are known to reduce hydraulic conductivity and increase runoff and soil erosion (Römkens et al., 1990; Neave and Rayburg, 2007). It is more difficult to know how BSCs affect water flow into soils (Eldridge and Greene, 1994a). Some studies indicate that BSCs increase infiltration, and consequently, decrease runoff (e.g., Greene and Tongway, 1989; Eldridge, 1993; Pérez, 1997), whereas others have reported that they have no effect on either of them (e.g., Eldridge et al., 1997) or that they decrease infiltration and increase runoff (e.g., Solé-Benet et al., 1997; Eldridge et al., 2000; Cantón et al., 2002).

This controversy arises for several reasons:

a) The influence of BSCs on infiltration is usually studied by comparing undisturbed crusted soils and soils where the crust has been disturbed in different ways (scalping, trampling, burning), or by comparing surfaces with different crust cover and composition (Eldridge, 2003). The first methodology has the disadvantage that the structure of surface and sub-surface soil is modified with respect to the original surface and thus, differences in infiltration can only be assigned to a combination of crust removal and soil surface disturbance. The second methodology assumes that soils with different crust covers and compositions have similar inherent characteristics. Moreover, what is often identified as bare soil is colonised by cyanobacteria and other microscopic organisms.

b) Most studies hardly ever report crust characteristics and surface and sub-surface soil properties, such as crust cover, biomass and composition, soil surface roughness, soil texture, aggregate stability, percentage of shrink-swell clays, existence of other types of crusting (physical, chemical or vesicular) and macroporosity, which makes it difficult to separate the relative contribution of different crust types to infiltration and runoff relative to other soil factors.

c) The use of different instruments and methodologies or the measurement of different variables makes it difficult to compare results of different studies (Belnap, 2006).

A review by Warren (2003a) helped enlighten part of the contradictory results regarding the influence of BSCs on infiltration. According to this author, the relationship between BSCs and infiltration appears to be conditioned by soil texture, so that BSCs decrease infiltration on soils where the sand content exceeds 80%, but increase infiltration on soils where the sand content is less than 80%. In sandy soils, characterised by rapid infiltration, the presence of BSCs seals the surface, limiting downward movement of water through the sand and increasing runoff. Moreover, the sticky sheaths of cyanobacteria trap windblown silt and clay particles on the surface which, along with fungal hyphae, cyanobacteria filaments, and lichen and moss anchoring structures, can occupy soil pores when wet, causing pore clogging and reducing infiltration. The opposite effect occurs in soils with significant fine particle content in the presence of BSCs, increasing the formation of soil aggregates and consequent porosity, thus enhancing infiltration compared to uncrusted soils. According to Warren (2003a), this enhancement in infiltration in fine-textured soils can be negated in soils with a high percentage of silt due to the development of vesicular horizons which are known to restrict infiltration. However, Miralles-Mellado et al. (2011) found that in fine-textured soils with high silt content, the presence of well-developed BSCs greatly enhanced the formation of elongated soil pores. Indirect factors, such as the modification of soil roughness and porosity by BSCs, are often not considered. In general, where BSCs roughen the soil surface, infiltration is increased. On the contrary, where cyanobacterial and algal filaments or lichens block soil pores, infiltration is reduced. However, even when taken into consideration, it is difficult to determine the relative contributions of these factors to the BSC infiltration response, as all of them act simultaneously and usually in opposite directions.

Although numerous studies have dealt with the topic, the controversy on the influence of BSCs on infiltration and runoff has not yet been resolved. Very little is known about the influence of BSCs on other critical components of the water balance, such as soil moisture or evaporation either. Most studies on this topic have speculated on how crusts might affect them, but few have actually measured them. In addition, the few existing studies show conflicting results. It has been suggested that BSCs may reduce evaporation and increase soil moisture by clogging soil pores due to swelling of exopolysaccharides and the presence of organisms at the surface (Kidron et al., 1999; Belnap et al., 2005; Fischer et al., 2010) and reducing soil surface cracks (Verrecchia et al., 1995). In contrast, BSCs may enhance evaporation by increasing water retention at the soil surface, thus prolonging the time available for evaporation, by creating greater surface roughness and increasing the surface area for potential evaporation (Belnap et al., 2005), or by darkening the soil surface and increasing soil temperatures compared to adjacent uncrusted soils (Harper and Marble, 1988). Thus some studies have reported higher soil moisture in soils covered by well-developed BSCs than in bare or uncrusted soils (Brotherson and Rushforth, 1983; Cantón et al., 2004b), whereas others have found higher soil moisture in uncrusted than in BSC-covered soils (Harper and Marble, 1988).

Therefore, the influence of BSCs on infiltration, evaporation and soil moisture is an unresolved question that deserves special interest given the widespread extension of this type of ground cover in arid and semiarid lands and the importance of their effects on hydrological processes, especially in drylands where water is an important limiting factor. Moreover, as different types of soil crusts and their developmental stages might have a different effect on hydrological processes, such a study should consider a variety of crust types, that is, from physical crusts to BSCs in different stages of their development. This would also make it possible to include variability in the hydrological behaviour of crusted soils in semiarid areas.

Importance of spatial and temporal scales in the study of BSC hydrological behaviour

Both erosion and hydrological processes are characterised by high temporal and spatial variability in arid and semiarid areas (Puigdefábregas et al., 1999; Calvo-Cases et al., 2003). While temporal variability mostly depends on rainfall characteristics and antecedent soil moisture (Gómez-Plaza et al., 2001), spatial variability of hydrological processes is largely associated with the high spatial heterogeneity of soil surface characteristics such as vegetation cover, rock fragment cover and position, and soil crust types (Calvo-Cases et al., 2003; Arnau-Rosalén et al., 2008; Cantón et al., 2011). Most efforts made to acquire infiltration-runoff data for BSCs have been at plot scale (less than 1 m^2) and under simulated rainfall. However, the influence of BSCs on erosion and hydrological processes varies depending on their spatial and temporal scales. Most publications agree that, compared to vegetation, BSCs increase runoff, and although they are known to reduce sediment yield at plot scale, the effect of runoff generated by BSCs on erosion should be evaluated on larger spatial scales, as it can either increase erosion risk downslope or increase water harvesting in adjacent vegetated areas (Cantón et al., 2011). Thus the hydrological and erosion response to BSCs must be analysed on different temporal and spatial scales, and incorporated in current hydrological and erosion models. Moreover, this is crucial to understanding how BSCs modulate water, sediment and nutrient redistribution from interplant spaces to vegetation patches, and in this way, condition the structure and distribution pattern of vegetation and, ultimately, affect functioning of dryland ecosystems.

A tool for identifying the distribution of soil crusts and monitoring their spatial and temporal changes is required to incorporate the effect of crusted surfaces in current hydrological and erosion models. So far, the crusted surfaces included in runoff and erosion models have mainly been physical (see e.g., Cerdan, 2001; King et al., 2005). In recent years, visible and near infrared (350–2500 nm) diffuse reflectance spectroscopy has become a powerful tool for large-scale mapping of the distribution of BSCs, but few spectral indices have been developed for mapping BSCs as distinguished from bare soil and vegetation, and there is no spectral classification able to distinguish between different types of BSCs. The development of a spectral classification to distinguish various types of BSCs, vegetation and bare soil, potentially applicable to multispectral and hyperspectral images, would enable these common ground covers to be mapped in semiarid areas. This is essential for monitoring BSC temporal and spatial dynamics, improving hydrological and erosion modelling capabilities by incorporating BSC-crusted surfaces, and for quantification of C and N stocks in arid and semiarid areas.

JUSTIFICATION

Water is one of the most limiting resources for ecosystem functioning and plant productivity in arid and semiarid ecosystems. Given that BSCs can cover up to or more than 70% of the soil surface in most arid and semiarid ecosystems, the knowledge of how they affect hydrological processes is a relevant question of importance. However, the few studies which have addressed the effect of BSCs on infiltration and runoff have had conflicting results. Furthermore, the influence of BSCs on hydrological processes, such as evaporation and soil moisture, has hardly been studied. As BSC composition can strongly influence the hydrological response of BSCs, the inclusion of a variety of BSC types, including from early-successional BSCs, such as cyanobacterial crusts, to late-successional BSCs, such as lichens and mosses, is recommended to better understand the role of BSCs on soil hydrology in drylands. This could also help understand the existing controversy regarding the influence of BSCs on water processes, possibly because of the different crust types in the studies.

In this thesis, the effects of physical crusts and various developmental stages of BSCs on infiltration-runoff, evaporation and soil moisture, along with their temporal variability, is examined at plot scale. A spectral classification system is also proposed for differentiation of vegetation, physical crusts and various types of BSCs in order to be able to map these common ground covers in semiarid areas in the future. This document sets an essential basis for further examination of how BSCs can affect hydrological processes on larger spatial scales (hillslope and catchment scales).

HYPOTHESIS

Binding of soil particles and improvement of aggregation and soil stability by cyanobacteria filaments, anchoring structures of lichens and mosses, and polysaccharides synthesized by crust organisms have been documented. Cyanobacteria and cyanolichens present in the BSC fix C and N, and the synthesis of exopolysaccharides by BSCs also increases soil organic carbon in the form of carbohydrates. In addition, it has been suggested that BSC organisms increase soil surface roughness, and are able to absorb large amounts of water and increase water retention at the soil surface.

In view of this, we hypothesised that physical and chemical properties would be better in biologically crusted soils than in physically crusted soils and that these properties would improve with BSC development. Microtopography would also increase with BSC development. As consequence of increased soil roughness and quality of physicochemical soil properties, we expected BSCs to increase infiltration and soil moisture, and reduce soil water loss by evaporation compared to physical crusts. Within BSCs, we expected more infiltration and soil moisture and less evaporation in well-developed than in less-developed BSCs. Thus, the presence of BSCs and especially the presence of well-developed ones would increase water “inputs” and have an overall positive effect on the water balance compared to physical crusts or little-developed BSCs in arid and semiarid regions.

GOALS

The general purpose of this thesis is to determine how physical crusts and different developmental stages of BSCs, through properties inherent to the crust or the properties that the crust types confer to underlying soils, affect infiltration-runoff, evaporation and soil moisture at plot scale in semiarid environments, and to establish a classification system based on distinctive spectral features of the crust types that allows their future mapping and upscaling of their hydrological effects in semiarid regions.

Our specific objectives are to:

1) Analyse the modification of surface properties associated with hydrological processes that physical crusts and the developmental stages of BSCs confer to soil for a better understanding of the influence of crusts on water processes.

2) Explore how physical crusts and BSCs in different stages of development and their disturbance affect infiltration-runoff processes at plot scale under extreme simulated rainfall and natural rainfall conditions.

3) Examine the effect of BSCs on the temporal dynamics of soil moisture by its monitoring for a long period of time at fine temporal resolution.

4) Analyse the influence of physical crusts and various developmental stages of BSCs on soil water evaporation.

5) Develop a spectral classification able to distinguish between vegetation, physical crusts and BSCs in different developmental stages, in order to provide a tool for future mapping of BSCs and upscaling of their hydrological effects in semiarid areas.

STUDY AREAS AND CHARACTERISATION OF SOIL CRUSTS

Two sites representing key spatial distributions of BSCs in semiarid ecosystems were chosen: a) El Cautivo, in the Tabernas desert, with crusts (physical and biological) on most of the soils and often covering complete landforms as the unique ground cover and located on fine-textured soils; b) Las Amoladeras, with crusts (mainly BSCs) representing almost a third of the soil cover, occupying intershrub spaces and on coarser-textured soils. Both sites are located in the province of Almeria in SE Spain.

a) El Cautivo (N37º00´37”, W2º26´30”) (Fig. 3) is located in the Neogene–Quaternary Tabernas depression, 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. Several studies on its geomorphology, hydrology and erosion provide a good general description of the area (see e.g., Solé-Benet et al., 1997; Cantón et al., 2002, 2003; Lázaro et al., 2008). The climate is semiarid thermo-Mediterranean, which is characterised by long, dry summers and most rainfall falling in winter (31% to 55%), with the rest being distributed between spring and autumn. The average annual precipitation is 235 mm and the mean annual temperature is 17.8 ºC, 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 (Cantón et al., 2003). Soil under BSCs has average percentages of sand, silt and clay of 29.2 ± 5.4, 58.6 ± 5.8 and 12.2 ± 4.2, respectively. There is no grazing at this site, and the most important land use is low-intensity hunting. The landscape is characterised by narrow valleys mostly dissected 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 (Epileptic Regosol) and are practically devoid of vegetation (Cantón et al., 2004a). On these SW-facing hillslopes, runoff and erosion are high (Cantón et al., 2001) and stability is too low for the establishment of BSCs or vascular vegetation. Thus, the soil surface is mainly covered by physical crusts, except in some areas where it is covered by incipient BSCs and isolated shrubs (mainly *Salsola* sp.). The annual *Moricandia foetida* cover entire landforms of these hillslopes in rainy years. In contrast, the upper parts of NE-facing slopes have incipient soils (Endoleptic Regosol) densely covered by lichen crusts and scattered annual and perennial plants. Pediment soils are thicker (Haplic Calcisol) and covered by annual and perennial plants. The most common species of plants are *Macrochloa tenacissima* (L.) Kunth (=*Stipa tenacissima* L.) (Blanca et al., 2009), *Helianthemum almeriense* Pau, *Artemisia barrelieri* Besser, *Salsola genistoides* Juss. ex Poir., *Euzomodendron bourgaeanum* Cosson*)*. On these slopes, BSCs range from those with a low biomass of cyanobacteria to those with high cover of lichens. In summary, physical crusts (30%) and BSCs (50%) cover around 80% of the soil surface in the area, appearing to be the only soil cover on many landforms, and also covering the open areas among shrubs and under plant canopies (Cantón et al., 2004a).

Fig. 3. El Cautivo site (Tabernas Desert).

The identification of the most representative crust types at this site was done according to Lázaro et al. (2008), who classified the main types based on the crust development stage, using crust composition and colour as indicators. The most representative crust types were (Fig. 4): 1) physical soil crust, formed by raindrop impact (structural crust) and which usually develops over the SE-facing hillslopes, 2) a light-coloured BSC with incipient colonization by cyanobacteria or incipient-cyanobacterial crust (IC), 3) a dark BSC mainly dominated by cyanobacteria or cyanobacteria-dominated crust (C), which also contained numerous pioneer lichens. This crust represents an intermediate-successional stage between the incipient-cyanobacterial and lichen crust, and 4) a light-coloured lichen BSC (L) mainly composed of *Diploschistes diacapasis* (Ach.) Lumbsch (crustose) and *Squamarina lentigera* (Weber) Poelt (squamulose) species of lichens.

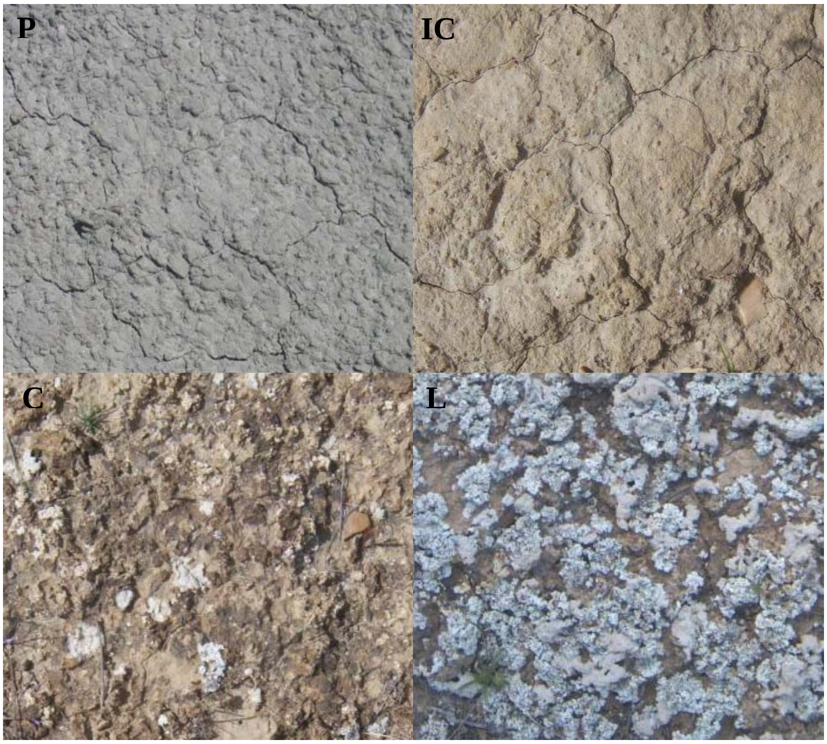

Fig. 4. Main crust types identified at El Cautivo site (Tabernas Desert): P, physical crust; IC, incipient-cyanobacterial BSC; C, cyanobacteria-dominated BSC; L, lichen-dominated BSC.

b) Las Amoladeras (N36º48´34”, W2º16´6”) (Fig. 5) is located in Cabo de Gata-Níjar Natural Park and approximately 22 km east of the city of Almería. 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 a mean annual rainfall of 200 mm and a mean annual temperature of 18° C. Soils are thin (average 0.1 m and maximum 0.3 m), 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. Soil under BSCs has average percentages of sand, silt and clay of 61.5 ± 5.1, 28.4 ± 4.8 and 10.1 ± 2.1, respectively. Trampling by grazing sheep and goats is frequent. Vegetation consists of grasses and scattered shrubs (*Macrochloa tenacissima* (L.) Kunth, with other relatively frequent dwarf shrubs such as *Helianthemum almeriense* Pau, *Thymus hyemalis* Lange, *Hammada articulata* (Moq.) O. Bolòs & Vigo, *Sideritis pusilla* (Lange) Pau, *Lygeum spartum* L., *Salsola genistoides* Juss. ex Poir.*, and Launaea lanifera* Pau*)* covering around 30% of the area. Annual plants develop among the grasses and shrubs and cover from 10 to 25% of the soil surface depending on rainfall. BSCs occupy the open areas in between the shrubs and can represent up to 30% of the whole soil surface. The rest of the area is occupied by caliche outcrops and rock fragments. As soil texture is sandy, physical crusts are not frequent in this area and most soil crusts are BSCs.

The most representative crust types in this area were (Fig. 6): 1) cyanobacterial crust (C), 2) lichen crust (L), and 3) cyanobacterial crust with abundant moss (M). The species composition of the first two crust types was similar to the same BSC types in El Cautivo. The cyanobacterial crust represents an early-successional stage of BSCs, whereas the lichen and moss crusts represent late-successional stages.

Fig. 5. Las Amoladeras site (Cabo de Gata-Níjar Natural Park).

Fig. 6. Main crust types identified at Las Amoladeras site (Cabo de Gata Natural Park): C, cyanobacteria-dominated BSC; L, lichen-dominated BSC; M, moss-dominated BSC.

It should be pointed out that at both sites, except for the physical crust and the incipient cyanobacterial BSC at El Cautivo, the other crust types are complex communities, which even at microplot scale, do not imply a ‘pure’, constant kind of soil surface, but represent the predominant community in the crust. The cyanobacterial crust, apart from high cyanobacterial cover, includes a remarkable diversity of pioneer lichens, such as *Placynthium nigrum* (Huds.) Gray, *Collema sp.*, *Endocarpon pusillum* Hedw., *Catapyrenium rufescens* (Ach.) Breuss and *Fulgensia sps.*, particularly, *F. fulgida* (Nyl.) Szatala. The lichen or white crust also includes considerable cyanobacterial cover and other lichen species as *Buellia zoharyi* Galun and *B. epigea* (Pers.) Tuck., *Lepraria crassissima* (Hue) Lettau and *Acarospora nodulosa* (Dufour) Hue. *Toninia sedifolia* (Scop.) Timdal, *Psora decipiens* (Hedwig) Hoffm., and *Teloschistes lacunosus* (P. Rupr.) Savicz are also more or less frequent. In Las Amoladeras, mosses are very frequent in the most developed crusts.

STRUCTURE OF THE THESIS

This thesis is organized in six chapters, a general discussion integrating the results arrived at each chapter and the final general conclusions of the thesis. A brief description of each chapter is given below.

CHAPTER I

This chapter examines the influence of crust type on soil properties which potentially affect the movement and availability of water in the soil for a more comprehensive understanding of the role of soil crusts in water processes. Different physicochemical properties of the crust and underlying soils driving hydrological processes were analysed in physical crusts and various developmental stages of BSCs at both study sites.

We collected samples of the following layers of each crust type in the field: the crust itself (around 0.005 m thick), 2) the top soil layer (0.01-m layer of soil immediately underneath the crust), and 3) deep soil layer (0.01-0.05-m layer of soil underneath the crust). Properties associated with hydrological processes, such as aggregate stability, water content, organic carbon and nitrogen content or cation exchange capacity, among others, were determined in the different layers of each crust type.

After analysis of these properties, the following four chapters are devoted to the influence of BSCs on the main water balance variables. Thus, Chapters II and III focus on the influence of BSCs on infiltration-runoff, Chapter IV explores the effect of BSCs on soil evaporation and Chapter V examines the influence of BSCs on soil moisture. Finally, Chapter VI makes an analysis of the spectral characteristics of BSCs and develops a classification system that could potentially be used for mapping BSCs in semiarid areas.

CHAPTER II

High intensity rainfalls are known to be the most important in causing changes in the geomorphology of drylands. Because of this, this chapter examines the influence of the crust type, physical or biological, and the developmental stage of the BSC, on infiltration under an extreme rainfall event. We carried out high-intensity rainfall simulations in microplots (area~0.25 m^2) containing the different crust types at both study sites. As disturbance can lead to profound changes in infiltration by BSCs, the consequences of disturbance on crust infiltration were analysed by applying two treatments to each crust type: trampling and crust removal. Moreover, in order to examine the influence of antecedent soil moisture on crust infiltration, we conducted two rainfall simulations in each microplot, the first one on dry soil and the second one on wet soil. Soil characteristics that were expected to influence infiltration, such as slope, cover and roughness were also measured in the undisturbed crust types.

CHAPTER III

Although intense rainfalls are the most important type from the perspective of geomorphologic processes, low-intensity rainfalls are the most frequent in our study areas. Moreover, rainfall parameters, such as size and kinetic energy of rain drops and intensity during the event in simulated rainfalls differ from those under natural conditions. Therefore, the influence of BSCs and the consequences of their disturbance for runoff, were also examined under natural rain conditions. In addition, as the influence of BSCs on runoff processes is likely to change depending on the spatial scale considered, runoff in biologically crusted soils was analysed at two contrasting spatial scales.

Open plots with two representative types of BSCs, each in its three stages of development after disturbance, were set up in El Cautivo. Plots were set up at two spatial scales: microplot (around 1 m^2) and small hillslope (6.7 ± 1.9 m^2). Direct and indirect relationships among soil surface characteristics (BSC cover and type), topography, rainfall characteristics (duration, amount and intensity) and runoff at each spatial scale were tested using structural equation modelling (SEM).

CHAPTER IV

The purpose of this chapter is to examine the influence of physical crusts and various developmental stages of BSCs on soil evaporation, as measured by microlysimeters. The experiment was conducted at the El Cautivo site. PVC microlysimeters (0.05 m radius and 0.05 m high) were inserted in the soil under the different crust types. To check if differences in soil evaporation could be attributed to the presence of the crust, we also selected a set of microlysimeters where the crust had been removed. Daily evaporation and drying curves from saturation to dry soil were examined under the crust types and scalped surfaces. We also tested the hypothesis that BSCs can increase evaporation by increasing soil surface temperature by measuring soil temperature under BSC-crusted and scalped surfaces. In addition, variables known to affect evaporation in physical crusts and BSCs, such as roughness and exopolysaccharide content, and characteristics of the underlying soil (0-0.05 m), such as particle size distribution, organic carbon, and available water for plants, were determined.

CHAPTER V

The aim of this chapter is to explore the influence of BSCs on soil moisture content in the top soil profile, the temporal dynamics of such response, and variability with the type of soil texture. Soil moisture was monitored at high temporal resolution for one year in soils covered by different types of BSCs at both study sites. To prevent factors other than the crust from affecting moisture measurements, moisture was always measured in plots with similar soil conditions and topography. The relative contribution of BSCs to soil moisture was also examined by comparison with adjacent soils where the BSC had been removed. Temperature in BSC-crusted and scalped soils was measured to explore its possible effect on evaporative losses and thus moisture content in biologically crusted soils.

CHAPTER VI

With the aim of future upscaling of the effects of BSCs on hydrological processes, in this chapter we analyse the possibility of using the spectral features of vegetation, physical crusts and developmental stages of BSCs for developing a classification system for these ground covers that could potentially be applicable to remote sensing data and provide reliable mapping of BSCs in semiarid areas. We also test the possibility of identifying spectral features for differentiation of BSC disturbance.

Field spectral measurements were taken of vegetation, physical crusts, and various types of BSCs prior to and following trampling or removal, in the two study areas, using a portable spectroradiometer. Linear discriminant analysis (LDA) was applied to spectral data to find out its ability to distinguish between the different types of ground cover (vegetation, physical crusts and BSCs at different developmental stages) and different BSC disturbances. In addition, the appropriateness of variables defined from the spectral data for classification of vegetation, physical crusts and types of undisturbed BSCs was tested. From the analysis of these variables and the outcome of the LDA analysis, a classification scheme based on distinctive spectral features was developed for distinguishing the various types of ground cover.

CHAPTER I

Biological soil crust development affects physicochemical characteristics of soil surface in semiarid ecosystems

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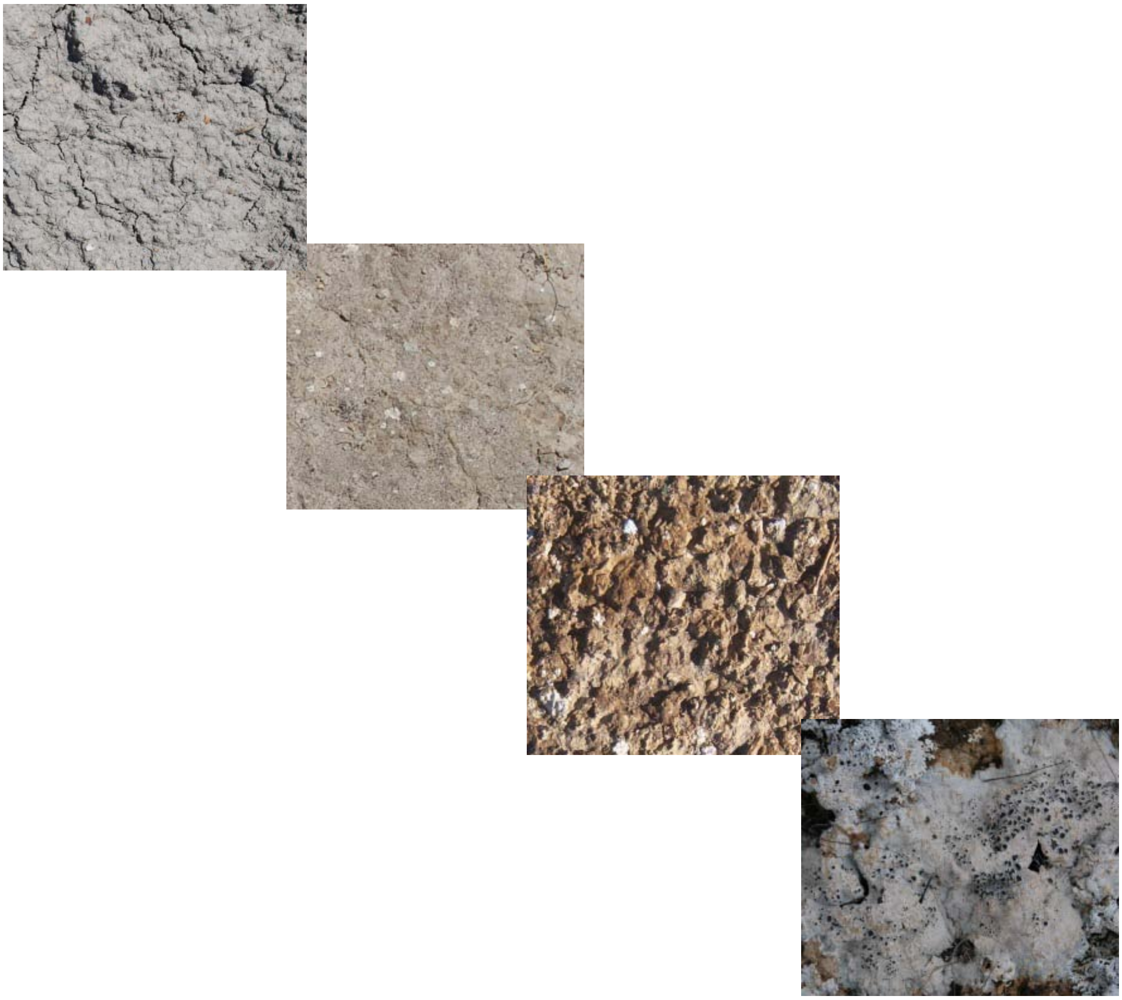

ABSTRACT

Water and nutrients are scarce resources in arid and semiarid ecosystems. In these regions, biological soil crusts (BSCs) occupy a large part of the soil surface in the open spaces surrounding patches of vegetation. BSCs affect physicochemical soil properties, such as aggregate stability, water retention, organic carbon (OC) and nitrogen (N) content, associated with primary ecosystem processes like water availability and soil fertility. However, the way BSCs modify soil surface and subsurface properties greatly depends on the type of BSC. We hypothesised that physicochemical properties of soil crusts and of their underlying soils would improve with crust development stage. Physicochemical properties of various types of soil crusts (physical crusts and several BSC development stages) and of the underlying soil (soil layers 0-0.01 m and 0.01-0.05 m underneath the crusts) in two semiarid areas in SE Spain were analysed. The properties that differed significantly depending on crust development stage were aggregate stability, water content (WC) (at -33 kPa and -1500 kPa), OC and N content. Aggregate stability was higher under well-developed BSCs (cyanobacterial, lichen and moss crusts) than under physical crusts or incipient BSCs. WC, OC and N content significantly increased in the crust and its underlying soil with crust development, especially in the first centimetre of soil underneath the crust. Our results highlight the significant role of BSCs in water availability, soil stability and soil fertility in semiarid areas.

Keywords: physical crust, cyanobacteria, lichen, moss, aggregate stability, water content, organic carbon, nitrogen.

INTRODUCTION

Biological soil crusts (associations of soil particles with cyanobacteria, algae, fungi, lichens or bryophytes) are common ground cover in open spaces surrounding vascular plants in arid and semiarid areas. Biological soil crusts (BSCs) significantly influence primary ecosystem processes (Maestre et al., 2011), and have been described as ecosystem engineers in drylands, as they cause changes in soil surface conditions that affect the habitat for other organisms (Bowker et al., 2005, 2006). Some of the functions that BSCs perform are: 1) The microtopography associated to the BSCs and the polysaccharides secreted by BSC organisms make soil particles adhere to each other, increasing soil aggregation and stability, thereby reducing erosion by water and wind (Belnap and Gardner, 1993; Mazor et al., 1996) and increasing the retention of nutrients in the top soil, thus making soil more fertile (Reynolds et al., 2001). 2) BSCs modify soil surface features such as roughness (Rodríguez-Caballero et al., 2012), porosity (Miralles-Mellado et al., 2011), water retention (Chamizo et al., 2012a) and aggregation (Shulten, 1985), all of which affect the way water moves into and through soils. This BSC layer in the boundary between atmosphere and soil therefore plays a major role in infiltration and runoff, evaporation and soil moisture (Belnap, 2006). It regulates vertical and horizontal fluxes of water and critically influences water availability and redistribution, as well as sediment and nutrient resources, in arid and semiarid ecosystems (Belnap et al., 2003a; Chamizo et al., 2012b). 3) BSCs are capable of C and N fixation (Beymer and Klopatek, 1991; Evans and Ehleringer, 1993), and also of decomposing and mineralizing organic compounds (Mager, 2010). While distribution of soil nutrients in semiarid areas is concentrated under the plant canopy (Pugnaire et al., 1996), BSCs occupy the nutrient-poor zones surrounding patches of vegetation, so that most nutrient inputs and losses in interplant spaces are regulated by them (Belnap et al., 2003a). Thus, BSCs strongly affect nutrient cycling (Maestre et al., 2011) and represent major sources of C and N in arid ecosystems (Housman et al., 2006). 4) BSCs affect the germination, emergence and survival of vascular plants, either through competition with cover and biomass, or changes in soil properties (Eldridge and Greene, 1994a; Belnap et al., 2003c).

When BSC organisms colonise the soil, they spread until they occupy extensive areas of soil surface, and later, as development continues one species replaces others (Lázaro et al., 2008). In arid and semiarid ecosystems, which represent around 40% of the Earth´s land surface, BSCs can cover up to or more than 70% of the soil surface (Belnap et al., 2003a). Cyanobacterial BSCs represent the earliest successional stages of BSCs, whereas lichens and mosses appear during the later stages (Lange et al., 1997). Some of the factors that have been reported to condition BSC cover and composition are radiation intensity and topographic attributes, such as slope aspect, which affect soil moisture (Eldridge and Tozer, 1997; Lange et al., 1997) and soil surface stability (Lázaro et al., 2008), vascular plant structure (Maestre and Cortina, 2002), environmental variables, such as soil pH, texture, soil organic matter (SOM), and soil nutrients (Anderson et al., 1982; Eldridge and Tozer, 1997; Bowker et al., 2005, 2006), and disturbances and their intensity (Dougill and Thomas, 2004). For instance, Martinez et al. (2006) related the abundance of lichen and moss in two semiarid gypsiferous areas of Spain to soil-aggregate stability, soil respiration and potassium content. Bowker et al. (2005) demonstrated a positive correlation between lichen and moss abundance and higher moisture and manganese and zinc availability. These authors also suggested the existence of feedback between crust and nutrient availability in the soil, so that lichen (*Collema spp*) was more abundant where manganese and zinc were available, but as a consequence of the modification of the soil environment by lichens, more micronutrients were available in the soil.

Soil stability and fertility losses are two of the most pressing problems involved in the degradation of ecosystem functioning and desertification in drylands (Bowker et al., 2006, 2008). Given the key role of BSCs in increasing soil stability, reducing erosion, and retaining soil nutrients, their loss is considered a major cause of land degradation (Belnap, 1995). In addition, BSCs are considered essential components of healthy, functional ecosystems and both local and regional biodiversity (Eldridge, 2000). Some studies have suggested total BSC cover as an indicator of ecological health (Tongway and Hindley, 1995; Pellant et al., 2000). Less in the literature is BSC composition as such an indicator. However, this could only be taken into consideration, as the rate and type of vital ecosystem services that BSCs perform greatly vary depending on species abundance and crust composition (Housman et al., 2006).

Thus, the presence of one BSC or another can affect soil properties, such as water retention, aggregate stability, and nutrient availability, among other variables, differently, and in turn, soil surface properties can affect the presence of one type of BSC or another by making habitat conditions more favourable for the establishment of one species than another. Moreover, how or how much the crust type, or development stage, might modify soil properties or these might favour the growth of specific BSC species can vary from one ecosystem to another. However, no study has yet simultaneously analysed the physicochemical characteristics of different types of soil crusts, including both physical and biological crusts, and BSC stages of development, as well as their underlying soils, in two different ecosystems with similar BSC composition. Even if an association between the crust type and soil properties were to be found, the crust type could potentially be used as an indicator of soil quality.

The aim of this study was to find out whether the physicochemical characteristics of soil crusts and the soil beneath them varied with physical or biological crust type and BSC development stage, in two semiarid ecosystems with contrasting lithology where BSC development stages are well-represented. More specifically, our objectives were to: 1) determine whether physicochemical properties of the crust improve with development stage, 2) analyse how crust development affects the physicochemical characteristics of the underlying soils, and 3) analyse the vertical variation in soil physicochemical characteristics (from the crust to a soil depth of 0.05 m) by crust development. We hypothesised that the quality of the physicochemical properties of the crust and their underlying soils would increase with crust development, from the physical crusts to the most highly developed BSCs, and that these properties would decrease with depth, from the uppermost to the deepest layer. In addition, the ratio between the crust and the underlying soil was determined in order to find out the relative importance of the crust with respect to the underlying soil, and to examine the ratio’s trend with crust development.

MATERIAL AND METHODS

Types of soil crust

A progressive classification of soil crust types from physical through various BSC development stages were selected in the two study areas.

The types of soil crusts in El Cautivo site were: 1) physical soil crust, 2) light-coloured BSC with incipient colonization by cyanobacteria (incipient-cyanobacterial BSC; 3) dark BSC mainly dominated by cyanobacteria (cyanobacteria-dominated crust or well-developed cyanobacterial BSC), and 4) a light-coloured BSC mainly composed of the *Diploschistes diacapasis* and *Squamarina lentigera* species of lichens (lichen BSC). This selection was based on a sequence of increasing crust development, from abiotic (physical crusts) to wide BSC cover by late-successional species. BSC developmental stages were identified based on Lázaro et al. (2008).

The main types of BSCs identified in Las Amoladeras were: 1) cyanobacteria-dominated BSC, 2) lichen-dominated BSC, and 3) moss-dominated BSC, which also contained around 15% of cyanobacterial cover. The species composition of the first two crust types was similar to the same BSC types in El Cautivo. The cyanobacterial BSCs represent an early-successional stage, whereas the lichen and moss BSCs represent late-successional stages (Lange et al., 1997).

Sampling and determination of physicochemical characteristics of the crusts and their underlying soils

Four samples per crust type were collected in the field from the following soil layers: 1) the “crust layer” (around 0.005 m thick), 2) the “top layer” (0-0.01-m layer of soil immediately underneath the crust), and 3) the “deep layer” (0.01-0.05-m-deep layer of soil underneath the crust). As BSCs are expected to strongly influence aggregate stability in the top millimetres of soil, aliquots were carefully separated from the top-layer samples for later determination of aggregate stability. Sampling sites in each study area were near each other, ensuring similar topography and the same soil type.

In the laboratory, the crust and soil samples were air-dried and sieved to 2 mm to acquire the fine earth fraction. Aliquots of these samples were taken and mashed in a mechanical agate mortar to obtain 0.5-mm particle size necessary for determination of organic carbon, exchangeable cations and cation exchange capacity.

The following physical properties were determined in the samples: a) particle size distribution underneath crusts in the top and deep layers by the Robinson's pipette method (Gee and Bauder, 1986); b) water content (WC) at -33 kPa and at -1500 kPa in intact and repacked crusts, and sieved fine earth samples from the top and deep layers, with a Richard´s pressure-membrane extractor, and c) aggregate stability of 4-5 mm aggregates by the drop test (Imeson and Vis, 1984). Due to the high variability in aggregate stability in semiarid regions (Cantón et al., 2009), this test was replicated in 40 aggregates per crust type.

The following chemical properties were analysed in all three layers per crust type: a) organic carbon (OC) by the Walkley and Black method modified by Mingorance et al. (2007), b) total nitrogen (N) by the Kjeldhal method (Bremner, 1996), and c) exchangeable cations (Ca, Mg, Na, K) and cation exchange capacity (CEC) by formation of Cu (II) complexes with triethylenetetramine followed by photometric analyses (Meier and Kahr, 1999). Exchangeable cations and CEC in the crust samples were determined by analysing soil particles scraped off the crust, referred to as “crust-layer soil particles”. Electrical conductivity, pH, and calcium carbonate in the soil samples were also determined from the top and deep layers underneath the different crust types. The electrical conductivity and pH were measured in a 1:1 soil-water suspension (Thomas, 1996), and calcium carbonate was determined by Bernard's calcimeter (Loeppert and Suarez, 1996). Finally, as the parent material in El Cautivo is gypsiferous mudstone, total sulphates were analysed as a measure of soil gypsum using the gravimetric method based on sulphate ion precipitation, in acid medium, as barium sulphate (Porta et al., 1986). As this method is not reliable when gypsum content is less than 1%, and its content in the top-layer samples was negligible, gypsum was only determined in the deep layer below the different crust types. Due to the high gypsum content found underneath the physical and lichen crusts, average Ca content under these crusts was overestimated and therefore not taken into account in the results or the statistical analyses.

Statistical analysis

To find out whether the site characteristics and crust development stage, or type, affected soil physicochemical properties, and whether these properties varied significantly among soil layers (crust layer, top layer, deep layer), general linear models (GLMs) were performed for the properties determined, using site, crust type and soil layer as predictors (the last factor was not included in the analysis when the variable was determined in only one layer). First, to examine the influence of the site on the dependent variables, GLM analyses were performed only for the crusts that were common to both study sites, and using site, crust type and soil layer as predictors. Then, to test for the significance of the predictor factors (crust type and layer) at a site, GLM analyses were done separately for each study site. When the factors or their interaction were significant for the dependent variables, planned orthogonal contrasts (see Quinn and keough, 2002) were performed to test the significance of our *a priori* hypothesis about the horizontal (crust type or development) and vertical (layers) trends of the variables determined. We tested the hypothesis that there would be a horizontal increase in the variable with crust development, i.e., physical < incipient-cyanobacterial < cyanobacterial < lichen crusts in El Cautivo, represented by the contrast vector [-2, -1, 1, 2], and cyanobacterial < lichen and moss crusts in Las Amoladeras, represented by the contrast vector [-2, 1, 1]. We also tested the hypothesis of a vertical decrease of the variable with depth, i.e., crust layer > top layer > deep layer, represented by the contrast vector [-1, 0, 1]. The exception was soil texture, which, as a very stable property, was not expected to vary significantly under the crust types.The level of significance was established at P<0.05. STATISTICA 8.0 was used to perform the analyses (StatSoft, Inc., Tulsa, Oklahoma, USA).

Soil property means underneath the crust were weighted by the thickness of the top (0.01 m) and deep (0.04 m) soil layers, and then the crust-to-underlying soil (top and deep layers) ratio was determined. Ratios over 1 would indicate that the crust was more influential on the property, whereas ratios lower than 1 would indicate that the underlying soil was more important.

RESULTS

Physical properties

The study site was a significant factor for all the physical properties determined. Soil texture, aggregate stability and WC at -33 and -1500 kPa significantly differed between sites (Table 1).

Table 2 shows the percentage of sand, silt and clay in the top and deep layers underneath the crust types at both study sites. Silt was predominant at El Cautivo, whereas the particle size at Las Amoladeras was mainly sand. Contrary to expectations, sand, silt and clay content varied significantly under the crust types in El Cautivo (Table 1). Sand content was lower and clay content was higher under physical crusts and lichen BSCs than under incipient and well-developed cyanobacterial BSCs (Table 2). No significant difference in soil texture was found between the top and deep layers. At Las Amoladeras, no difference was found in soil particle distribution underneath the crust types. The soil layer influenced silt content (Table 1), which was higher in the top than in the deep layer underneath the BSCs (Table 2). Aggregate stability was lower at El Cautivo than at Las Amoladeras (Table 2). Crust development influenced aggregate stability at the first site, but not at the second (Table 1). At El Cautivo, the planned contrast revealed an increase in the number of drops needed to break down the aggregates with crust development (Table 2). At Las Amoladeras, although the planned contrast was not significant, more drops were needed under the lichen and moss than under the cyanobacterial BSCs.

Table 1. Result of the GLM showing the effect of the predictor factors on physicochemical soil properties. It is only shown the variables for which the crust type or the layer had a significant effect in one of the two sites. *P*-value for the interaction is only shown when interaction between the two predictor factors at each site (crust type and layer) resulted significant for one property. Significance was established at 95% confidence interval.

	Site factor			El Cautivo		Las Amoladeras	
	F	*P*		F	*P*	F	*P*
Sand	320.72	**0.000**	Crust type	9.65	**0.000**	1.15	0.338
			Layer	0.54	0.472	1.76	0.200
Silt	347.43	**0.000**	Crust type	5.21	**0.007**	3.45	0.054
			Layer	0.00	0.945	6.42	**0.021**
Clay	19.29	**0.000**	Crust type	6.84	**0.002**	1.38	0.278
			Layer	1.25	0.277	2.95	0.103
Aggregate stability	10.15	**0.005**	Crust type	6.99	**0.002**	1.02	0.399
WC at -33 kPa	1262.21	**0.000**	Crust type	14.52	**0.000**		
			Layer	3.44	**0.043**		
			Crust type*Layer			4.84	**0.005**
WC at -1500 kPa	16.88	**0.000**	Crust type	2.01	0.130		
			Layer	13.63	**0.000**		
			Crust type*Layer			21.37	**0.000**
OC	11.71	**0.001**	Crust type*Layer	21.64	**0.000**	5.73	**0.001**
N	12.78	**0.001**	Crust type*Layer	4.41	**0.002**	8.30	**0.000**
*Ca	---	---	Crust type			6.09	**0.007**
			Layer			16.38	**0.000**
			Crust type*Layer	6.98	**0.000**		
Mg	1.81	0.187	Crust type	0.45	0.716	0.22	0.803
			Layer	6.62	**0.004**	4.11	**0.028**
K	4.11	**0.050**	Crust type	0.78	0.511	1.39	0.265
			Layer	7.88	**0.001**	9.07	**0.001**
CEC	22.72	**0.000**	Crust type	3.62	**0.022**		
			Layer	6.58	**0.004**		
			Crust type* Layer			5.15	**0.003**
pH	1.56	0.226	Crust type	3.28	**0.038**	0.61	0.563
			Layer	0.74	0.398	0.00	0.972
Electrical conductivity	25.29	**0.000**	Crust type	47.28	**0.000**	0.99	0.404
			Layer	9.77	**0.005**	1.97	0.191
Gypsum content	---	---	Crust type	6.20	**0.018**	---	---

* The GLM for this variable was performed only for each site separately. Due to the high gypsum content under physical crusts and lichen BSCs at El Cautivo, Ca content in these soils was overestimated and therefore, not taken into account in the statistical analysis.

Table 2. Mean (± SD, *n*=40) number of drops needed to break down the aggregates (4-5 mm size) under the different crust types, and mean (±SD, *n*=4) percentage of sand, silt and clay in the top and deep soil layers under the crust types, at both study sites. The crust types are: P, physical crust; IC, incipient-cyanobacterial BSC; C, cyanobacteria-dominated BSC; L, lichen-dominated BSC; M, moss-dominated BSC. Differences among crust types in aggregate stability were analysed using planned contrasts. As soil texture significantly varied under the crust types (see table 1) and no planned contrast was hypothesised for this variable, differences in soil texture under the crust types were analysed with the LSD post hoc test. Different letters indicate significant differences within a column.

		Top layer (soil layer 0-0.01 m underneath the crust)				**Deep layer** (soil layer 0.01-0.05 m underneath the crust)		
Site	Crust type	Aggregate stability*	Sand (%)	Silt (%)	Clay (%)	Sand (%)	Silt (%)	Clay (%)
El Cautivo	P	14.6 ± 7.4	15.4 ± 1.3^{b}	62.8 ± 1.5^{b}	21.8 ± 2.8^{a}	13.9 ± 4.0^{b}	63.8 ± 1.1^{ab}	22.3 ± 3.3^{a}
	IC	16.9 ± 8.2	27.9 ± 8.9^{a}	58.9 ± 5.9^{ab}	13.2 ± 4.2^{b}	32.6 ± 2.9^{a}	54.0 ± 3.8^{c}	13.4 ± 3.6^{b}
	C	42.1 ± 9.1	31.3 ± 9.2^{a}	54.5± 6.0^{a}	14.2 ±3.3 ^{b}	28.1 ± 7.1^{a}	57.2 ± 5.5^{bc}	14.7 ± 1.8^{b}
	L	32.1 ± 9.6	26.4 ± 4.1^{a}	59.7 ± 3.1 ^{ab}	13.9 ± 1.4^{b}	20.3 ± 4.2^{b}	61.9 ±2.8^{b}	17.8 ± 6.5^{ab}
		Aggregate stability	Sand (%)	Silt (%)	Clay (%)	Sand (%)	Silt (%)	Clay (%)
Las Amoladeras	C	49.3 ± 20.2	58.4 ± 3.7^{a}	30.4 ± 4.2^{a}	11.2 ± 2.8^{a}	61.6 ± 2.0^{a}	27.1 ± 3.7^{a}	11.2 ± 3.2^{a}
	L	65.3 ± 15.8	56.5 ± 3.7^{a}	36.6 ± 4.2^{a}	6.9 ± 1.0^{a}	58.8 ± 2.8^{a}	29.4 ± 2.7^{a}	11.8 ± 0.2^{a}
	M	56.6 ± 9.8	60.1 ± 7.3^{a}	29.1 ± 4.3^{a}	10.8 ± 3.3^{a}	62.8 ± 7.9^{a}	26.3 ± 5.9^{a}	10.9 ± 2.0^{a}

* Significant planned contrast (i.e. significant increase in the variable with crust development).

WC at -33 and -1500 kPa was higher at El Cautivo than at Las Amoladeras (Table 3). At El Cautivo, the planned contrast indicated a significant increase in WC at -33 kPa from the least to the most developed crusts in all the layers. At -1500 kPa, the crust types showed similar WC (Table 3). The soil layer affected WC at -33 kPa and -1500 kPa (Table 1). However, WC did not follow a decreasing trend with soil depth, as was hypothesised. At -33 kPa, the top layer showed higher WC than the other layers, and at -1500 kPa, WC was generally higher in the deep soil than in the other layers. At Las Amoladeras, the interaction between crust type and soil layer was significant for WC at -33 and -1500 kPa (Table 1). The planned contrast showed that WC at both pressures was higher in the lichen and moss BSCs than in the cyanobacterial BSCs. WC was also higher in the top layer under the lichen and moss BSCs than under the cyanobacterial BSCs at -33 kPa, but similar at -1500 kPa in the top layer under the BSCs. No difference in WC was found at either pressure in the deep layer under the BSCs (Table 3). Differences among layers were observed in the most developed BSCs (lichen and moss BSCs), where the crust layer showed higher WC at -33 and -1500 kPa than the underlying soil layers. WC at both pressures was similar in the crust and the underlying soil layers in the cyanobacterial BSCs (Table 3). The crust-to-underlying soil ratio for WC at -33 and -1500 kPa (Table 3) was around 1 at El Cautivo, with the exception of the lichen BSCs at -1500 kPa, where the ratio was over 1. These ratios indicated that on fine-textured soils, WC in the crusts and their underlying soils was similar. At Las Amoladeras, the WC ratio at both pressures was over 1 in all BSCs and increased in order from cyanobacterial to lichen and moss BSCs, thus indicating higher WC in the crust with respect to its underlying soil with increasing BSC development.

Table 3. Mean (±SD, *n*=4) water content (WC) at -33 kPa and-1500 kPa, in the three soil layers per crust type: the crust layer (0.005 m thickness), the top layer (soil layer 0-0.01 m underneath the crust) and the deep layer (soil layer 0.01-0.05 m underneath the crust). The crust-underlying soil (top and deep layers) ratio for WC at -33 kPa and-1500 kPa for each crust type is also shown. The crust types are: P, physical crust; IC, incipient-cyanobacterial BSC; C, cyanobacteria-dominated BSC; L, lichen-dominated BSC; M, moss-dominated BSC.

	Water content at -33 kPa (%)					Water content at -1500 kPa (%)				
	Crust type	Crust*	Top layer*	Deep layer*	Crust-underlying soil ratio	Crust type	Crust	Top layer	Deep layer	Crust-underlying soil ratio
El Cautivo	P	23.2 ± 2.0	23.9 ± 0.8	23.5 ± 0.7	0.99 ± 0.07	P	9.3 ± 0.1	9.3 ± 1.3	12.2 ± 1.1	0.81 ± 0.08
	IC	23.6 ± 4.8	27.3 ± 3.7	24.9 ± 4.3	0.95 ± 0.06	IC	9.4 ± 1.6	8.9 ± 3.4	11.6 ± 1.6	1.05 ± 0.40
	C	28.7 ± 2.2	30.8 ± 3.0	27.8 ± 3.7	1.02 ± 0.08	C	11.2 ± 0.5	9.0 ± 0.7	11.9 ± 2.2	1.01 ± 0.20
	L	27.9 ± 1.7	30.8 ± 0.6	28.9 ± 1.4	0.95 ± 0.08	L	14.0 ± 3.3	7.9 ± 1.0	13.2 ± 1.1	1.14 ± 0.34
		Crust*	Top layer*	Deep layer	Crust-underlying soil ratio		Crust*	Top layer	Deep layer	Crust-underlying soil ratio
Las Amoladeras	C	16.8 ± 2.3	14.6 ± 2.3	14.1 ± 2.1	1.22 ± 0.14	C	8.9 ± 1.9	7.2 ± 1.7	7.0 ± 1.4	1.28 ± 0.05
	L*	25.5 ± 1.9	21.0 ± 1.8	16.5 ± 0.9	1.43 ± 0.07	L*	16.3 ± 2.2	9.5 ± 1.0	8.8 ± 0.8	1.86 ± 0.30
	M*	26.8 ± 4.0	16.8 ± 3.5	14.6 ± 1.1	1.80 ± 0.29	M*	21.9 ± 4.1	8.3 ± 1.5	7.0 ± 1.1	2.80 ± 0.27

*Significant planned contrast. An asterisk (*) next to the name of the soil layer indicates a significant increase in the variable with crust development in that layer. The same symbol next to the name of the crust type indicates a significant decrease in the variable with depth (from the crust towards the 0.05-m-deep soil layer) in the specified crust type.

Chemical properties

The study site was a significant factor for OC and N content (Table 1). As seen in Fig. 1, the content of both were higher in the crusts and soils at Las Amoladeras than at El Cautivo. The interaction between crust type and soil layer was significant for OC and N at both sites (Table 1). At El Cautivo (Figs. 1a and 1b), the planned contrast indicated an increase in OC and N from the least to the most developed crusts in all the soil layers. Nevertheless, differences among crusts were especially strong in the crust layer and decreased in the underlying soil layers. For instance, lichen BSCs had twice as much OC as cyanobacterial BSCs, six times as much as physical crusts and over twice as much N as physical crusts. OC and N content did not differ among soil layers in the physical crusts and incipient-cyanobacterial BSCs, but did in the cyanobacterial and lichen BSCs, where the contents in both decreased with soil depth (Figs. 1a and 1b). At Las Amoladeras (Figs. 1c and 1d), the planned contrast indicated that lichen and moss BSCs had higher OC and N content than cyanobacterial BSCs in the crust and top layers, but that their content did not differ in the deep layer under the BSCs. Lichen and moss BSCs had nearly twice as much OC and around 1.5 times more N than cyanobacterial BSCs. OC content was higher in the crust than in the underlying soil layers in all the BSC types. N content was higher in the crust than in the underlying soil layers in the lichen and moss BSCs, but similar in the crust and underlying soil layers in the cyanobacterial BSCs.

The crust-to-underlying soil ratio for OC and N (Fig. 1) was around 1 in the physical crusts. In the BSCs, this ratio was over 1, and increased with BSC development at each site, meaning higher OC and N in the crust with respect to its underlying soil as the BSC was more developed.

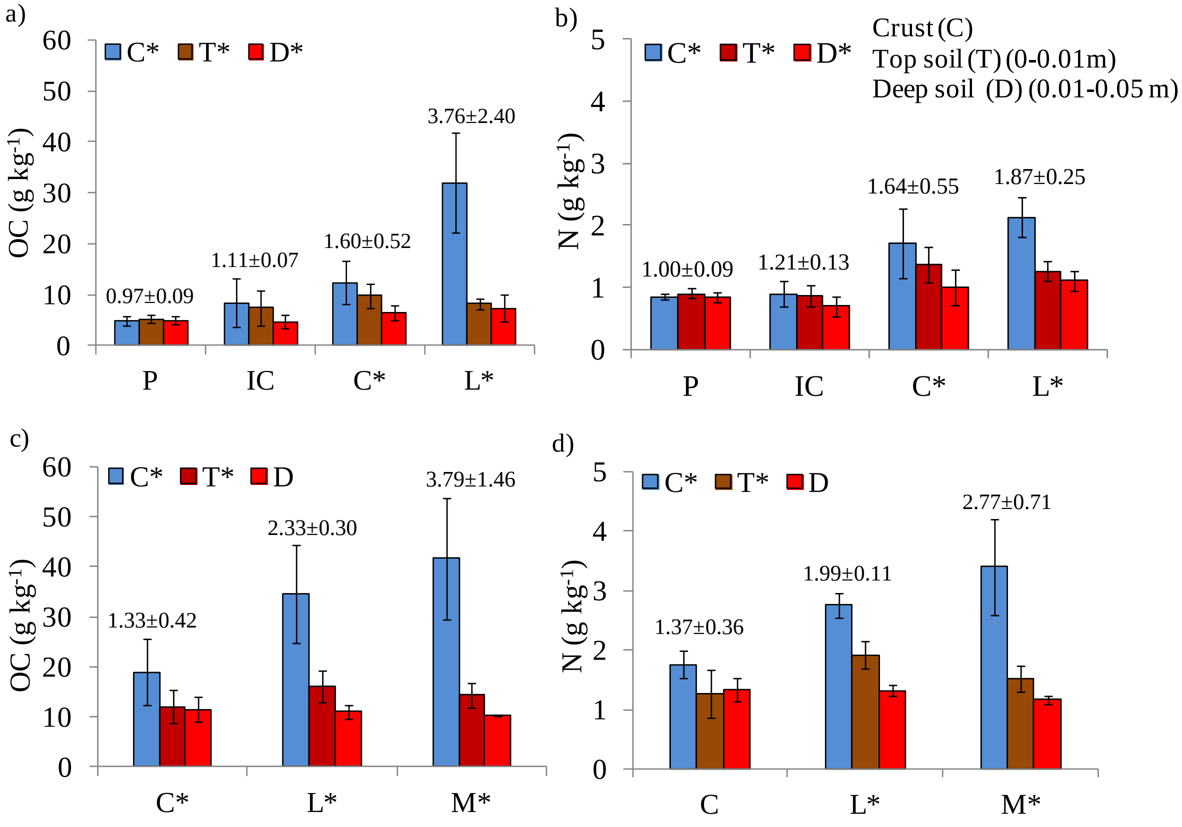

Fig. 1. Mean (± SD, *n*=4) organic carbon content (OC) (a) and total nitrogen (N) (b) at El Cautivo, and OC (c) and N (d) at Las Amoladeras, in the three soil layers per crust type. Numbers correspond to the crust-underlying soil (including the top and deep soil layers) ratio for each crust type. The crust types are: P, physical crust; IC, incipient-cyanobacterial BSC; C, cyanobacteria-dominated BSC; L, lichen-dominated BSC; M, moss-dominated BSC.

*Significant planned contrast. An asterisk (*) next to the name of the soil layer indicates a significant increase in the variable with crust development in that layer. The same symbol next to the name of the crust type indicates a significant decrease in the variable with depth (from the crust towards the 0.05-m-deep soil layer) in the specified crust type.

Fig. 2 shows the average exchangeable cations and CEC in the crust-layer soil particles, and top and deep layers at both study sites. The site was significant for Na (*P*=0.02), K (*P*=0.05) and CEC (*P*=0.00). These properties were higher in crusts and soils at Las Amoladeras than at El Cautivo (Fig. 2). Contrary to what was expected, crust type did not have a significant effect on exchangeable cations at either of the two sites, with the exception of Ca content at Las Amoladeras, where moss BSCs showed higher content of this element than the other BSCs (data not shown). The soil layer significantly affected Ca, Mg and K content at both sites (Table 1). These properties were higher in the crust-layer soil particles than in the underlying soil (top and deep layers) (Fig. 2), except for Ca content in El Cautivo, which was higher in the top and deep layers than in the crust-layer soil particles (Fig. 2a). Crust type and layer significantly influenced CEC at El Cautivo (Table 1). This property increased with crust development stage in all layers (e.g., average CEC in the crust-layer soil particles was 3.32 ± 0.22 in the physical crust and 4.18 ± 0.61 in the lichen BSCs), and was higher in the crust-layer soil particles than in the soil underneath the crusts (Fig. 2a). At Las Amoladeras, crust type only significantly influenced CEC in the crust-layer soil particles, where CEC increased with BSC development, from cyanobacterial (mean 4.27 ± 0.49 cmol kg^{-1}) to lichen (mean 4.38 ± 0.28 cmol kg^{-1}) and moss BSCs (mean 5.12 ± 0.92 cmol kg^{-1}). No difference in CEC was found in the top or deep layers under the BSCs. Differences in CEC between layers were only significant in the moss BSCs, where the crust-layer soil particles showed higher CEC (P=0.00) than the soil underneath the crust.

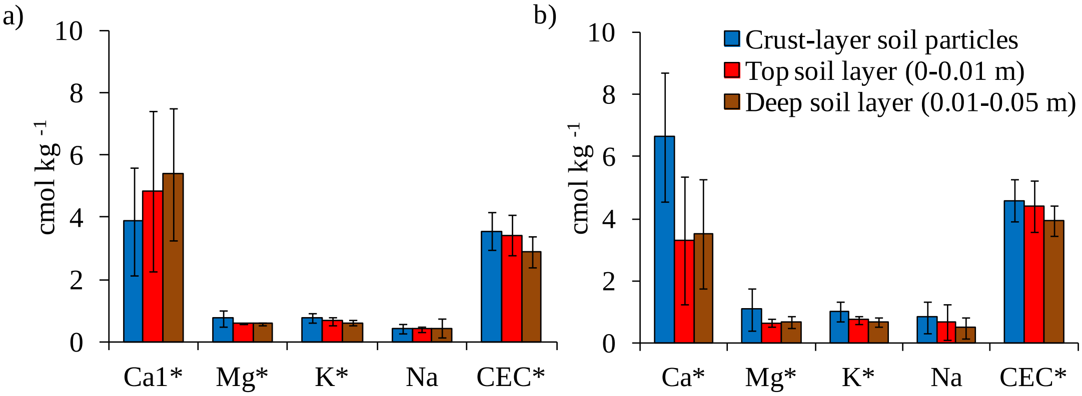

Fig. 2. Mean (± SD, *n*=4) Ca, Mg, K, Na and CEC (including all crust types) in each soil layer, at El Cautivo (a) and Las Amoladeras (b). An asterisk (*) next to the variable indicates a significant decrease in the variable with depth (from the crust towards the 0.05-m-deep soil layer).

[1] Ca in the crust-layer soil particles under physical crusts and in the top and deep layers under the physical crusts and lichen BSCs at El Cautivo were excluded for the determination of average Ca content, due to the high gypsum content in those layers.

Soil pH did not vary between sites (Table 1). Crust development influenced pH at El Cautivo, but not at Las Amoladeras. However, contrary to expected, pH did not increase with crust development at El Cautivo, although it was higher in the soil under BSCs than under physical crusts. No difference in pH was found between the top and deep soil layers at either of the two sites (Table 1).

Calcium carbonate content, which differed between sites (P=0.00), was higher at El Cautivo than at Las Amoladeras (Table 4). Neither crust development nor soil layer influenced calcium carbonates at either of the two sites.

Electrical conductivity also differed between sites (Table 1). This property was much higher in the soils at El Cautivo than at Las Amoladeras (Table 4). Crust development and soil layer influenced electrical conductivity at El Cautivo, but not at Las Amoladeras (Table 1). At the first site, electrical conductivity was higher in the soils under the physical crusts and lichen BSCs than under the incipient and well-developed cyanobacterial BSCs, and higher in the deep layer than in the top one underneath those crusts (physical crusts and lichen BSCs). Gypsum was also higher in the soil underneath the physical crusts and lichen BSCs than under the incipient and well-developed cyanobacterial BSCs (Table 4).

Site	Crust type	Calcium carbonate (g kg^{-1})	pH	Electrical conductivity (S m$^{-1)}$	Gypsum (g kg^{-1})
El Cautivo	P	226.0 ± 4.1	7.3 ± 0.1	1.94 ± 0.04	53.5 ± 3.8
	IC	245.9 ± 28.7	7.8 ± 0.4	0.49 ± 0.29	1.6 ± 1.1
	C	265.5 ± 17.7	7.6 ± 0.4	0.25 ± 0.07	0.7 ± 0.1
	L	242.2 ± 35.0	7.7 ± 0.3	1.68 ± 0.19	47.8 ± 39.4
Las Amoladeras	C	128.0 ± 9.5	7.9 ± 0.1	0.25 ± 0.04	---
	L	129.7 ± 15.1	7.7 ± 0.2	0.21 ± 0.06	---
	M	140.8 ± 9.7	7.8 ± 0.1	0.16 ± 0.02	---

Table 4. Weighted mean (±SD, n=4) of calcium carbonate, pH and electrical conductivity, for the top (soil 0-0.01 m underneath the crust) and deep (soil 0.01-0.05 m underneath the crust) layers under the different crust types. As the parent material at El Cautivo is gypsiferous mudstone, gypsum was only determined in the soils from this site. The value of gypsum shown corresponds just to the deep layer (soil 0.01-0.05 m underneath the crust), as its content in the top layer was negligible (<1%). The crust types are: P, physical crust; IC, incipient-cyanobacterial BSC; C, cyanobacteria-dominated BSC; L, lichen-dominated BSC; M, moss-dominated BSC.

DISCUSSION

BSCs affect many soil properties involved in primary ecosystem processes in drylands, such as nutrient cycling and hydrological processes. Although numerous studies have reported an increase in water retention (Malam Issa et al., 2009), aggregate stability (Shulten, 1985) and OC and N content (Rogers and Burns, 1994; Gao et al., 2010) due to the presence of BSCs separately, to our knowledge, no previous publication has simultaneously reported on the changes in all these properties in the crust and their underlying soils considering a sequence from less to more developed crust types. We examined all these changes in soil properties with crust development in two ecosystems with contrasting lithologies and representative of the most common BSC habitats and spatial distributions in semiarid areas. Our results fill in these gaps and demonstrate that the type of soil crust, in terms of crust development stage, strongly influences soil physicochemical properties.

Influence of crust development on physical soil properties

Soil particle-size distributions in the two study sites contrasted considerably (Table 2). Due to the complex topography of El Cautivo, soil texture underneath the crust types differed significantly in this area. Incipient and well-developed cyanobacterial BSCs often colonise depositional landforms with coarser soils due to the transport of fine sand from the top of the hillslopes where the rest of the overlying calcaric sandstone remain, while physical crusts and lichen BSCs develop on hillslope positions over mudstone regolith that is composed of 80% silt (Cantón et al., 2003) and with hardly any calcaric sandstone deposition (Cantón et al., 2004a). Thus, silt content was higher and sand content lower in the soils underneath the physical crusts and lichen BSCs than under the incipient and well-developed cyanobacterial BSCs (Table 2). On the flat sandy loam soils at Las Amoladeras, soil texture did not vary with crust type.

Aggregate stability was higher under well-developed BSCs (cyanobacterial, lichen and moss BSCs) than under physical crusts or poorly-developed BSCs (incipient-cyanobacterial BSCs) (Table 2). The importance of BSCs in enhancing the stability of soil aggregates has been widely described (Shulten, 1985; Belnap and Gardner, 1993; Eldridge and Greene, 1994b; Mazor et al., 1996). Mechanically, fungal hyphae, cyanobacteria filaments, and lichen and moss attachment structures form a network in the upper soil layers that greatly enhances aggregate stability. Chemically, the sticky polysaccharides secreted by BSC organisms bind soil particles, favouring soil aggregation (Schulten, 1985; Belnap and Gardner, 1993). This is especially significant within the first millimetres of the soil surface and strongly contributes to reducing erosion by water and wind (Eldridge and Greene, 1994b). McKenna Neuman et al. (1996), studying the influence of BSCs on wind transport of sand particles, pointed out that the mechanical entanglement of particles by cyanobacteria filaments was more effective in increasing surface shear stresses and decreasing wind speed than the chemical entrapment of particles by polysaccharides. Soil cohesion by algae has been reported to be indispensable at early stages, while later growth of lichens, mosses and fungi improve cohesion by changes in soil physicochemical properties (Hu et al., 2002). Chamizo et al. (2012b) also found, under simulated extreme rainfall, that physical crusts generated much higher sediment yield than BSCs and that sediment yield significantly decreased with BSC development. Furthermore, the removal of BSCs dramatically increased erosion by water (Chamizo et al., 2012b). The higher aggregate stability found under the most developed BSCs and in the soils at Las Amoladeras than at El Cautivo can also be attributed to the higher soil OC content (Fig. 1). Rogers and Burns (1994) also reported a positive correlation between increased soil carbohydrate C induced by inoculation of soil with BSCs and increased soil aggregate stability.

Because of the textural differences between sites, WC at -33 and -1500 kPa were higher in the finer-textured soils at El Cautivo than at Las Amoladeras (Table 3). WC at each site increased with BSC development stage (Table 3). Cyanobacterial sheaths, moss stems and lichen thalli trap airborne silt and clay particles that increase water retention at the surface (Verrecchia et al., 1995; Malam Issa et al., 1999). We found that silt content on coarse-textured soils (Las Amoladeras) was higher in the top layer underneath the BSCs than in the deep layer (Table 2). Moreover, BSCs are able to absorb large amounts of water in a short period of time. Cyanobacteria polysaccharide sheaths can absorb up to 10 times their volume of water (Verrecchia et al., 1995). Moss can absorb water directly through hair-points on their leaves and expand their cover and biomass up to 13 times (Galun et al., 1982). On fine-textured soils (El Cautivo), the presence of BSCs compared to physical crusts and increased BSC development resulted in increased WC in the crust and its underlying soil at -33 kPa, but not at -1500 kPa (Table 3). As fine soils have a high water retention capacity, the soil underneath the crust generally had a higher WC than the crust itself and the crust-to-underlying soil ratio was close to or lower than 1 (crust-to-underlying soil ratio, Table 3). At Las Amoladeras, where soil texture was coarser, WC at -33 and -1500 kPa was higher in the crust than in the underlying soil, and significantly increased in order from cyanobacterial to lichen to moss BSCs (Table 3). Furthermore, the increase in WC in the crust with respect to its underlying soil increased with BSC development stage (ratio over 1; Table 3). Malam Issa et al. (2009) reported that WC at -33 kPa in sand dunes was twice as high in samples with dense microbial cover and four times as high as in samples thinly covered or devoid of microbial cover. However, no differences were found between samples with and without microbial cover at -1500 kPa. We also found that the presence of well-developed BSCs (lichens and mosses) on coarse soils increased WC in the underlying top layer at -33 kPa, but did not induce significant differences in WC in the top and deep layers at -1500 kPa. Our results suggest that greater BSC development increases WC at the soil surface, especially on coarse-textured soils, and that the improvement in WC of the underlying soil is mainly restricted to the upper layer. In deeper soils (0.05 m deep), the difference in WC is mainly between well-developed (cyanobacterial and lichen BSCs) and poorly-developed (physical and incipient-cyanobacterial BSCs) crusts. Thus the presence of well-developed BSCs, in addition to increasing WC in the top layer, is also able to increase WC in deeper soil layers.

Influence of crust development on chemical soil properties

OC and N stocks were substantially larger at Las Amoladeras than at El Cautivo. The Las Amoladeras site has better conditions, characterised by higher infiltration rates and less erosion due to its coarser soil texture, and less hydric stress because of its proximity to the Mediterranean Sea than El Cautivo, which is located in a badlands on a highly erodible lithology with fine-textured soils and higher runoff and erosion rates (Cantón et al., 2011; Chamizo et al., 2012b;). Both sites showed the same pattern of higher OC and N content in the crust and its underlying soil as development progressed (Fig. 1). Previous studies have shown that BSCs mainly affect nutrient cycling in the top soil (Mager and Thomas, 2011). We also found that the effect of the crust on soil OC and N was especially significant in the top layer. In the deep layer, differences were mainly between soils under poorly (physical crusts and incipient-cyanobacterial BSCs) and well-developed (cyanobacterial and lichen BSCs) crusts (Figs. 1a and 1b), which is why no differences in OC and N were found in the deep layer underneath the BSCs at Las Amoladeras (Figs. 1c and 1d).

Several publications have reported up to a 300% increase in soil C content (Rao and Burns, 1990; Rogers and Burns, 1994) and an increase in soil N of up to 200% (Rogers and Burns, 1994; Harper and Belnap, 2001) due to the presence of BSCs. Malam Issa et al. (1999) found that the presence of BSCs improved surface OC over bare and litter-covered soils. Thomas and Dougill (2007) reported that cyanobacterial BSCs significantly increased soil N and SOM compared to unconsolidated surfaces. Gao et al. (2010) also found that BSCs significantly increased OC and N in the surface soil layer (0–0.05 m) under wet conditions, although no difference was found in the soil profile at a depth of 0.6 m.

BSCs are able to fix atmospheric C (Beymer and Klopatek, 1991) and increase the soil C pool by producing extracellular polysaccharides (Mager and Thomas, 2011). Polysaccharide content may be 1.5 to 3 times higher in samples of dense BSC cover than sparse cover (Malam Issa et al., 2001). Belnap et al. (2008) found a significant relationship ($R^2 = 0.71$) between cyanobacteria-dominated BSC development and exopolysaccharide content. Moreover, Mager

(2010) reported that in the south-west Kalahari, surface carbohydrate content produced by cyanobacterial BSCs may represent up to 75% of total soil OC. Exopolysaccharide content in the crusts at our study sites has also been shown to significantly increase from the least (physical crusts) to the most developed (lichens and mosses) crusts (Chamizo et al., 2012a). The higher OC found in the more developed BSCs and their underlying soil can be attributed to this increased polysaccharide content.

After water, soil N availability is another critical limiting factor for semiarid ecosystem functioning (Gebauer and Ehleringer, 2000). N inputs occur through atmospheric deposition and N fixation (Hawkes, 2003), whereas N outputs occur through N mineralization and subsequent gaseous losses by volatilization, nitrification, and denitrification (Evans and Lange, 2003). BSCs largely regulate N input and losses in arid regions. In xeric and N-limited ecosystems, N fixation by BSCs has been reported to be the dominant source of N input (Evans and Ehleringer, 1993; Evans and Lange, 2003). Cyanobacteria and cyanolichens fix atmospheric N (Evans and Ehleringer, 1993) and make it available for vascular plants and other microorganisms (Hawkes, 2003; Veluci et al., 2006). Ammonium is the preferred form of combined-N for cyanobacteria. In the absence of ammonium, cyanobacteria can use other N forms (i.e. nitrate) that are then reduced to ammonium (Luque and Forchhammer, 2008). Only during depletion of combined-N forms through mineralization, volatilization or leaching, cyanobacteria use atmospheric N-fixation (Luque and Forchhammer, 2008; Mager and Thomas, 2011). N fixation by BSCs varies considerably depending on temperature, moisture, light and BSC composition (Belnap, 2003). In general, later successional BSCs have higher N fixation rates and therefore contribute higher N content to surrounding soils than early successional cyanobacterial BSCs (Housman et al., 2006; Belnap et al., 2008). However, high N fixation rates do not necessarily imply enhanced productivity. Recent studies have reported higher nitrate content in areas with low BSC cover than in areas dominated by well-developed lichen BSCs (Castillo-Monroy et al., 2010; Delgado-Baquerizo et al., 2010). In contrast, Veluci et al. (2006) found more ammonium leaching in lichen BSCs than moss and bare soils, while nitrate leaching was lower in lichen than in moss BSCs and bare soils. Cyanobacterial BSCs are also thought to limit loss of N by leaching (Mager, 2009). Thus, BSCs are able to increase nutrient availability in the soil surface by reducing nutrient losses to the subsoil (Mager and Thomas, 2011). BSCs also increase nutrient inputs by trapping aeolian dust enriched in micro and macronutrients. Physical crusts exhibit low N content due to the absence of microorganisms capable of fixing and retaining N. Because well-developed BSCs are more effective in fixing N, trapping nutrient-enriched dust and reducing erosion than less developed BSCs, we found higher N content in more developed lichens and moss BSCs than in less developed incipient-cyanobacterial BSCs (Fig. 1). This is also supported by the crust-to-underlying soil ratio found, which showed that OC and N were higher in the crust than in the underlying soil, and that the increase in the crust with respect to the underlying soil rose with BSC development (Fig. 1).

In the rest of the variables analysed, differences were found only among some of the crust types. Crusted surfaces often trap silt and clay particles which bind positively charged particles such as Ca, Mg, Na and K cations. Polysaccharides also cause these cations to be bound more strongly (Belnap et al., 2003c). Although exchangeable cations did not differ significantly among crusts (Table 1), CEC did increase with BSC development in all layers at El Cautivo and in the crust-layer soil particles at Las Amoladeras, which seems to indicate that well-developed BSCs especially improve CEC in lesser-quality soils. This increase in CEC can be attributed to a parallel increase in OC with BSC development. A positive relationship between increased soil CEC and SOM was reported by Miralles et al. (2007, 2009) in other semiarid environments.

BSCs have been reported to increase pH in the top soil from 8 to 10.5 (García Pichel and Belnap, 1996). Rivera-Aguilar et al. (2009) found a positive correlation between lichens and soil pH, attributed to calcium carbonates and the preference of some lichen species for an alkaline pH (Bowker et al., 2006). Increased soil pH could also be related to increased SOM (Miralles et al., 2009). Although calcium carbonates in the soils under the crust types from our study sites did not differ significantly, their content was higher underneath BSCs than physical crusts, which together with the also higher OC under BSCs, could explain the higher pH in soils underneath BSCs than physical crusts (Table 4).

Gypsum was higher in the soils underneath physical crusts and lichen BSCs than under incipient and well-developed cyanobacterial BSCs at El Cautivo (Table 4). At this site, runoff and erosion rates on physical soil crusts are very high (Cantón et al., 2001). This limits soil development, making that many soil properties underneath them, like the gypsum content, are inherited from the parent material, a gypsiferous mudstone (Cantón et al., 2003). On the other hand, the lichens *Diploschistes diacapsis* and *Squamarina lentigera* are gypsum specialists (Martínez et al., 2006). Some studies have also suggested that lichen cover grows with increased soil gypsum (Büdel and Lange, 2003). The higher electrical conductivity in soils under physical crusts and lichen BSCs is associated to the higher gypsum content underneath these crusts (Table 4).

Our results demonstrate that BSCs have a major role in soil water content, soil stability and fertility in drylands, and that these functions become more significant as the BSC is more developed. For instance, in the badlands, mean OC and N in the lichen-covered soil profile including the crust and underlying 0.05 m of soil was 9.04 ± 1.77 g kg^{-1} and 1.23 ± 0.12 g kg^{-1} , respectively, whereas it was 4.99 ± 0.76 g kg^{-1} and 0.85 ± 0.07 g kg^{-1}, respectively, in soils underneath physical crusts. Well-developed BSCs are therefore able to increase soil OC and N up to twice as much as soils covered by physical crusts. The better quality of soil physicochemical properties with BSC development also supports our progressive classification of BSCs based on their development stage. Nevertheless, it should be noted that these results could be interpreted as either the improvement of soil properties due to the presence of well-developed BSCs or as the establishment of well-developed BSCs in soils with better physicochemical properties. We suggest a feedback process by which more developed BSCs colonise soils with better soil properties and in turn, the presence of well-developed BSCs improves soil surface physicochemical properties in the long-term. As also reported by other studies, the relationship between BSC development and soil physicochemical properties could potentially be used to develop a qualitative (or even quantitative) soil quality indicator in semiarid areas based on total BSC cover (Chaudhary et al., 2009), the presence of well-developed BSCs, such as lichens and mosses, or on attributes associated with BSCs, such as exopolysaccharides (Belnap et al., 2008), chlorophyll *a* (Bowker et al., 2008), or OC and N content (this study). Moreover, remote sensing applied to mapping of BSCs (see Weber et al., 2008; Chamizo et al., 2012d), could provide a powerful tool for estimating soil surface conditions and critical information about soil stability, C and N stocks, and associated hydrological and erosive dynamics in arid and semiarid regions.

CONCLUSIONS

After determining the physicochemical properties of different types of soil crusts, we found that the main properties which showed significant differences with crust development were aggregate stability, WC, OC and N. Aggregate stability was higher under well-developed BSCs than under physical crusts and poorly-developed BSCs. BSCs increased WC, especially in coarse-textured soils, and OC and N compared to physical crusts. The more developed the BSC stage was, the better the quality of these properties in the crust and its underlying soil. However, the improvement in physicochemical properties of the soil underneath the crusts was especially important in the top soil layer (0.01 m of soil under the crust) and diminished in deeper soil (0.01-0.05 m), where differences among crusts were mainly between physical crusts or incipient-cyanobacterial BSCs and well-developed cyanobacterial and lichen BSCs. The improvement in the physicochemical characteristics of BSCs with their development supports our BSC development stage classification. From these findings, we can infer that the presence or type of BSCs could be used as a qualitative indicator of soil surface properties in arid ecosystems. Thus, well-developed BSCs (lichens and mosses) would be indicators of better-quality soils (more aggregate stability, WC, OC and N) than soils dominated by physical crusts or incipient-cyanobacterial BSCs. Therefore, BSCs play a crucial role in water availability, soil stability and reduction of erosion, and represent significant stocks of C and N in arid and semiarid areas, where these sources are important limiting factors.

CHAPTER II

Crust composition and disturbance drive infiltration through biological soil crusts in semiarid ecosystems

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ABSTRACT

Soil crusts influence many soil parameters that affect how water moves into and through the soil, and therefore, critically influence water availability, erosion processes, nutrient fluxes, and vegetation distribution patterns in semiarid ecosystems. Soil crusts are quite sensitive to disturbance, and their alteration can lead to modification of the local hydrological regime, thus affecting general functioning of the ecosystem. The aim of this work was to analyse the influence of different types of soil crusts, physical, and biological in different developmental stages, as well as the impact of their disturbance, on infiltration. This was assessed by means of rainfall simulations conducted in two semiarid ecosystems in SE Spain characterised by different lithologies, topographies, and soil crust distributions. Two consecutive rainfall simulation experiments (50 mm h^{-1} rainfall intensity), the first on dry soil and the second on wet soil, were carried out in microplots (0.25 m^2) containing the most representative soil crust types at each site, each crust type subjected to three disturbance treatments: a) undisturbed, b) trampling, and c) removal. Infiltration in the crusts was higher on coarse than on fine-textured soils and almost two times greater on dry than on wet soil. Biological soil crusts (BSCs) showed higher infiltration rates than physical soil crusts. Within BSCs, infiltration increased as cyanobacterial biomass increased and was the highest in moss BSCs. However, late-successional crustose and squamulose lichen BSCs showed very low infiltration rates. Trampling reduced infiltration rates, especially when soil was wet, whereas crust removal enhanced infiltration. But this increase in infiltration after removing the crust decreased over time as the soil sealed again due to raindrop impact, making runoff rates in the scraped microplots approach those registered in the respective undisturbed crust types. Our results demonstrate that water redistribution in semiarid ecosystems strongly depends on the type of crusts that occupy the interplant spaces and the characteristics of the soils which they overly, as well as the antecedent moisture conditions of the soil. Disturbance of these crust patches results in increased runoff and erosion, which has important consequences on general ecosystem functioning.

Keywords: physical soil crust, biological soil crust, developmental stage, infiltration, trampling, scraping.

INTRODUCTION

Semiarid areas are heterogeneous landscapes characterised by patches of vegetation and open spaces between the scattered vascular plants usually occupied by physical soil crusts and biological soil crusts (BSCs). These crust patches are usually considered as sources of runoff, sediments and nutrients, which are transferred downslope and trapped within the vegetation patches, usually considered as sinks of these materials (Schlesinger et al., 1990; Ludwig et al., 2005; Li et al., 2008; Cantón et al., 2011). In semiarid ecosystems, the transfer of resources from bare to vegetated areas has been proposed to be crucial for the maintenance of vegetation patches (Ludwig and Tongway, 1995). Disturbance of the relationship between these source and sink areas may alter water and nutrient fluxes downslope and impact plant communities (Barger et al., 2006). Therefore, the knowledge of how crusts and their disturbance affect runoff generation and by this way influence nutrient cycling, erosion and vegetation patterns in drylands is of vital importance.

Physical crusts and BSCs are widespread in arid and semiarid areas, which comprise over 40% of the world´s land surface (Reynolds et al., 2007). Although physical crusts and BSCs are an almost negligible portion of the soil profile (from less than one to a few millimetres in thickness), they play multiple roles, especially where water is scarce (Maestre et al., 2011). At a fine scale, soil crusts can be considered as ecological boundaries, because they control the flux of materials and energy in the interface between the atmosphere and the soil surface and between bulk soil and plant roots (Belnap et al., 2003b). Crusts influence different soil surface properties, such as texture, porosity, cracking and roughness, which affect water movement in soils and thereby condition water, sediment, and nutrient redistribution in ecosystems. Various studies have investigated the influence of physical crusts and BSCs on runoff and infiltration at the plot scale but, whereas there is general agreement regarding the negative impact of physical crusts on infiltration from reducing hydraulic conductivities and infiltration rates (Römkens et al., 1990; Singer and Le Bissonnais, 1998; Neave and Rayburg, 2007), the role of BSCs in regulating water flow into soils is not well understood (Eldridge and Greene, 1994a). Some studies indicate that the presence of BSCs increases infiltration, and consequently, decreases runoff (e.g., Harper and St. Clair, 1985; Greene and Tongway, 1989; Eldridge, 1993), whereas others have found that it has no effect on either of them (e.g., Eldridge et al., 1997). Still other studies suggest that both physical crusts and BSCs decrease infiltration and increase runoff (e.g., Solé-Benet et al., 1997; Eldridge et al., 2000; Cantón et al., 2002). Part of this controversy was interpreted by Warren (2003a), who concluded from the literature that BSCs decrease infiltration on soils where the sand content exceeds 80% and do not frost, due to blocking of soil pores by filaments of BSCs, but increase infiltration on soils up to approximately 80% sand, due to the aggregation of fine soil particles, promoted by the polysaccharide secretions and anchoring structures and filaments of BSCs, and the consequent improvement in porosity. According to a review by Belnap (2006), the contradicting results on the hydrological role of the BSCs are due to the interaction of several causes. First, the absence of information about crust characteristics and surface and sub-surface soil properties makes it difficult to separate the relative contribution of crusts to infiltration and runoff relative to other soil factors. Second, comparisons are made between undisturbed crusted soils and soils where the crust is disturbed by different methods, so that the structure of the original surface and sub-surface soil is lacking. Finally, the utilization of different instruments and methodologies or the measurement of different variables makes it difficult to compare results of different studies. Furthermore, the existing studies usually consider different crust types, making comparisons among them difficult and therefore the use of gradients of crust types (e.g. from early to late successional BSCs) existing at a site is advisable (Belnap, 2006). Another important factor that influences the response of open areas to rainfall is antecedent soil moisture, which affects soil cracking and soil water storage capacity. The ability of BSCs to swell upon wetting can cause pore clogging (Kidron et al., 1999; Fischer et al., 2010) and induce important differences in runoff generation. Furthermore, BSCs are not resilient to physical disturbances (Belnap, 2002) and increasing human activities in dry areas such as livestock grazing, off-road vehicles, and trampling usually cause the loss of BSCs or convert late-successional BSCs into early ones (Barger et al., 2006; Belnap, 2006). These crust disturbances have important consequences on infiltration processes as well as on a large number of ecological processes including soil stability, dust emission, and nutrient losses (Eldridge and Greene, 1994a; Mazor et al., 1996). However, there are also conflicting results related to the effects of BSC disturbance on infiltration and to understand this effect, it has been suggested that studies should include more than one treatment, such as a combination of crust removal and trampling (Herrick et al., 2010).

Derived from the reasons mentioned above, we designed an experiment to analyse the interactions between spatial (site properties, type of crust, or developmental stage of the crust and soil disturbances) and temporal (antecedent soil moisture) variations in infiltration of soil crusts. To do this, infiltration of physical crusts and BSCs was investigated by rainfall simulation in two Mediterranean ecosystems in SE Spain. The two selected study sites were suitable to conduct our research because: 1) they are representative of the most common habitats and spatial distributions of ground covers in the Mediterranean semiarid region, characterised by disperse patches of vegetation and interplant spaces occupied by soil crusts; 2) successional dynamics of BSCs (i.e. from poorly developed BSCs as cyanobacteria to well-developed BSCs as lichens and mosses) are well represented in both sites. Moreover, through the selection of a variety of crust types, the heterogeneity in the hydrological behaviour of crusted soils within a site is incorporated; and 3) the two experimental sites provide the possibility of examining comparable crust types under different lithology, topography and land-use conditions, under similar climate conditions. Furthermore, although physical crusts and BSCs are interspersed in many semiarid ecosystems, few studies have considered both jointly (e.g., see Solé-Benet et al., 1997; Cantón et al., 2002).

The specific objectives of this paper were to: 1) analyse the influence of different crust types, representing a development gradient, on infiltration, 2) analyse the importance of antecedent soil moisture on the hydrological response of the crust, and 3) examine how disturbance of the crust (trampling and crust removal) affects infiltration rates. Our working hypothesis was that infiltration would be lower in the physical crusts than in the BSCs and within these, infiltration would increase from the least to the most developed BSCs, as a result of increased biomass and roughness with the higher development of the BSC (Belnap, 2006). As far as we know, this is the first time the effect of soil crusts on infiltration is tackled from a developmental stage perspective, including both physical crusts and BSCs, on two different soil types and also considering different crust disturbance conditions.

MATERIAL AND METHODS

Experimental design

To examine the influence of different crust types on infiltration and how crust disturbance and soil moisture could affect this response, rainfall simulations were conducted in microplots (0.25 m^2) containing the most representative soil crust types at each study site. The selection of the crust types was done according to Lázaro et al. (2008), who classified the main types in our study areas based on the crust development stage, using crust composition and colour as indicators. The most representative crust types in El Cautivo area, on fine-textured soils (indicated by subscript F), were (Fig. 1a): 1) physical soil crust (P_F), formed by raindrop impact (structural crust) and which usually develops over the bare marl surfaces, 2) incipient-cyanobacterial crust (IC_F), 3) cyanobacterial crust (C_F), which represents an intermediate-successional stage between the incipient-cyanobacterial and lichen crust, and often includes a considerable amount of small pioneer lichen species, and 4) lichen crust (L_F). In Las Amoladeras area, on coarse-textured soils (indicated by subscript C), the most representative crust types were (Fig. 1a): 1) cyanobacterial crust (C_C), 2) lichen crust, (L_C) and 3) cyanobacterial crust with abundant moss (M_C). The cyanobacterial crust represents an early-successional stage of BSCs, whereas the lichen and moss crusts represent late-successional stages.

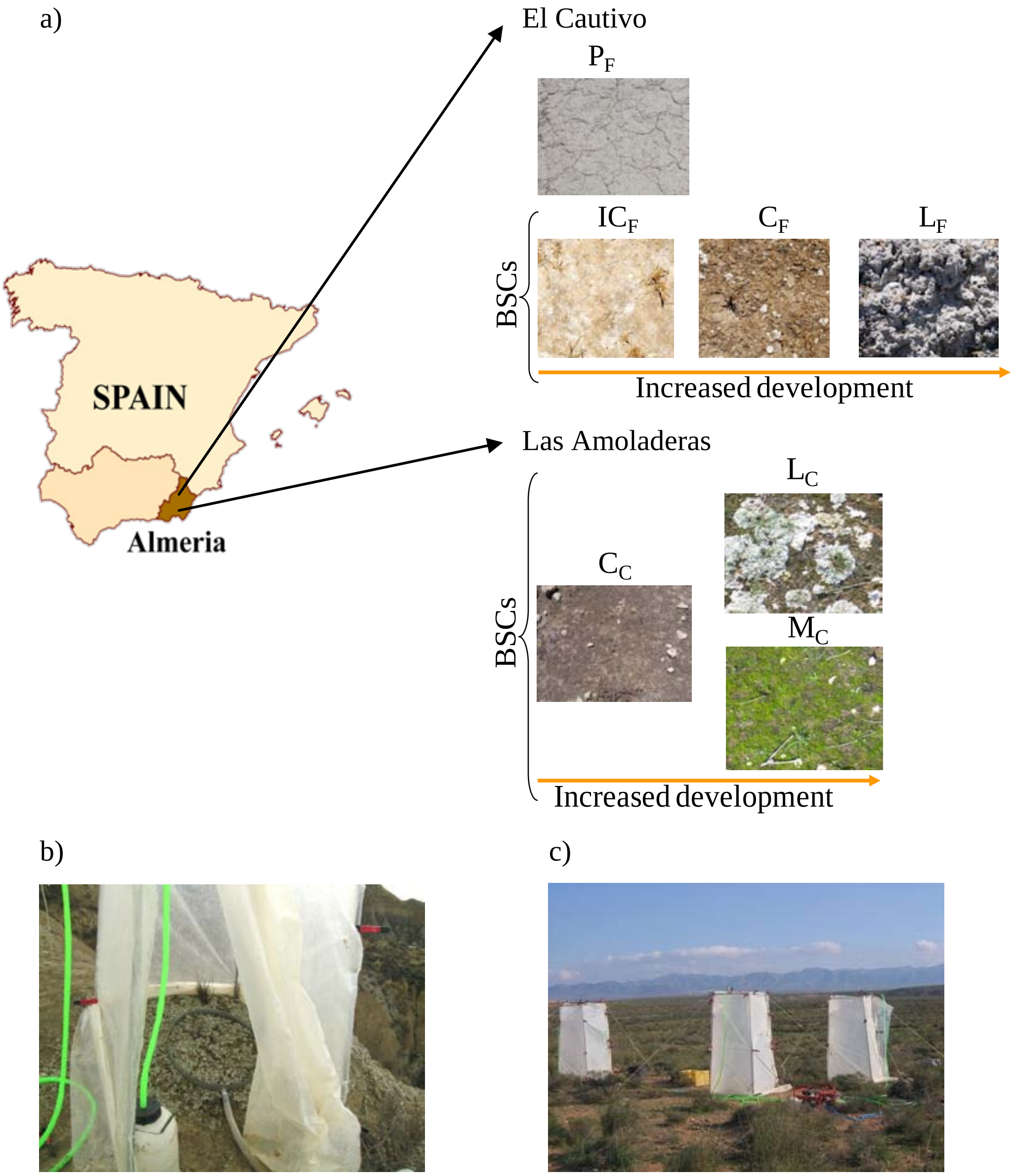

Fig.1. Location map and photographs of the most representative soil crusts at each site. Fig.1a. The different crust types in the two study sites. P: Physical soil crust; IC: Incipient-cyanobacterial crust; C: Cyanobacterial crust; L: Lichen crust; M: Moss crust. The subscripts indicate the soil texture below the crust: F: fine and C: coarse. Fig. 1b. Rain simulation microplot bounded by a metal ring and the pipe to collect water runoff. Fig.1c. The three rainfall simulators, one for every treatment, running simultaneously. Rainfall simulations were done on every soil crust type.

Before the rainfall simulations were conducted, soil characteristics that were expected to influence infiltration, such as slope, cover, and roughness were measured in the microplots containing the undisturbed crust types. Slope was measured with a clinometer, placing it on a stick over the microplot. A photograph was taken in each microplot and surface cover was estimated using Idrisi software and applying a supervised classification, selecting several training areas from the main cover types: physical, cyanobacterial, lichen and moss crusts, annuals, and stones. Crust roughness was measured using the chain method described by Saleh (1993), which consists of measuring the difference between the full length of the chain and the horizontal distance between its ends when placed on the soil. To do this, we used a 0.5-m long chain with 0.03-m long links. Three roughness transects were made in the direction of the maximum slope and another three transects, perpendicular to the previous one. Transects in each direction were averaged (“vertical” and “transversal” roughness, respectively).

Rainfall simulations were carried out after summer when soils were completely dry. We used rainfall simulations because, unlike the cylinder infiltrometer, they reproduce the crusting process that occurs under natural rain conditions (Cerdá, 1999a), and therefore can be considered a more suitable method for hydrological studies. Two months before the rainfall experiments, 0.56-m diameter circular steel rings with a tube at the bottom to drain runoff and sediments were fitted into previously wetted soil to prevent the physical disruption (cracking) of the crusts along the edges of the ring at the time it was inserted (Fig. 1b). The experiments were carried out at the microplot scale (area ~0.25 m^2) to find representative plots of each crust type and to maximize the effect of the cover (crust) compared to other factors, such as vegetation or slope angle (Cerdá, 1999b). A total of 48 microplots were prepared in El Cautivo, including the 4 crust types and 3 disturbance treatments with 4 repetitions, and 36 microplots in Las Amoladeras, including the 3 crust types, each subjected to 3 disturbance treatments and replicated 4 times. The treatments applied to each crust type were: 1) undisturbed crust or control; 2) trampling, treading the microplot 100 times (five rounds and 20 steps per round), and 3) removing the crust from the soil surface by scraping. The last two treatments were applied just before rainfall simulation.

To examine the influence of antecedent soil moisture on the hydrological response of intact and disturbed crusts, two consecutive 30-min rainfall simulations were carried out over each microplot, the first one on dry soil and the second one, 30 min after the first one ended, on wet soil. Thus, 96 rainfall simulations were performed in El Cautivo (4 crust types x 3 treatments x 2 antecedent soil moisture conditions x 4 repetitions) and 72 in Las Amoladeras (3 crust types x 3 treatments x 2 antecedent soil moisture conditions x 4 repetitions). The rainfall simulator used, described by Calvo-Cases et al. (1988) and Cerdá et al. (1997), has been successfully applied in numerous studies of the effect of surface on infiltration (Solé-Benet et al., 1997; Cerdá 1999a,b; Mayor et al., 2009). It has a sprinkler nozzle for rain over a 1-m^2 area, but we only considered the 0.25-m^2 circle in the centre delimited by the ring, where rainfall is uniform. The rain (deionised water) was applied at a constant intensity averaging 50 mm h^{-1}, which corresponds to rainfall intensity with a return period of 5 years (García-Bartual, 1986). To speed up the process, 3 rainfall simulators worked at the same time, placed over the control, trampled, and scraped microplots, respectively, and repeated on each crust type (Fig. 1c). Water pressure and rain intensity were regulated and monitored by pressure gauges located in the hosepipe that carried the water to the nozzle. Before each rainfall experiment, a waterproof cover was put over the microplots and 8 rain gauges were regularly distributed on that cover to detect any irregularities in rain distribution (which were corrected by cleaning the nozzle), and to verify that deviation of the average rain intensity never exceeded 10-15%. Rain intensity of every specific experiment was recorded and used to determine infiltration rates.

In each microplot for both events (dry and wet), once runoff started, runoff volume was recorded every minute for the first 7 min, every 2 min from 7 to 17 min, every 3 min from 17 to 29 min, and also during the last minute. These intervals were set in an attempt to acquire the maximum information with the least effort based on experience in previous rainfall experiments (Solé-Benet et al., 1997).

Data treatment

Differences in cover and roughness among crust types were tested using one-way ANOVAs and the post hoc LSD test.

Infiltration was determined as the difference between rainfall and runoff volume, considering evaporation during the experiment to be negligible. Previous studies have found that the Hortonian overland flow model explains the mechanism responsible for runoff generation in our study areas (Solé-Benet et al., 1997; Cantón et al., 2002). Steady-state infiltration rates (fc), for each crust and treatment, were estimated by fitting the infiltration rates to an exponential decay function based on the Horton equation (Horton, 1933).

Generalized Linear Models (GLMs) were used to test for differences in the dependent variables: total infiltration rate (In, mmh^{-1}) and steady-state infiltration rate (fc, mmh^{-1}). First, a series of GLMs (one analysis for each dependent variable) was performed to test the influence of the characteristics of the underlying material using the data from both sites, but including only the crusts common to both. Then, as the same crust types were not present at both sites, a series of GLMs was done separately for each study site. The factors (categorical predictors for the dependent variables) were crust type (P_F, IC_F, C_F, and L_F in El Cautivo and C_C, L_C, and M_C in Las Amoladeras), treatment (control, trampling, and scraping), antecedent soil moisture (dry and wet) and the study site (only in the first series of models). Because antecedent soil moisture has little impact on steady-state infiltration rate (Warren, 2003a) and this was reached during the second rain event in some of the Las Amoladeras microplots, antecedent soil moisture was not included in the GLM analysis as a factor influencing fc. All factors were considered fixed. All possible interactions among factors, both first order (between pairs of factors) and second order (combinations of three factors) were considered, and slope (in degrees) was included in the analysis as a continuous predictor. Total infiltration rates at both sites and fc in Las

Amoladeras fit a normal distribution and fc in El Cautivo fit a gamma distribution. GLM analyses were applied selecting these distribution functions. Statistical analyses were conducted using STASTISCA 8.0 (StatSoft, Inc., Tulsa, Oklahoma).

RESULTS

Crust type characteristics

Table 1 shows the average cover and roughness for the different crust types at both study sites. The most abundant cover in each crust type, together with other characteristics associated to increased crust development as roughness (Belnap, 2006), supports our selection of the crust types according to their developmental stage. There were significant differences in roughness among crust types on the fine-textured soils, where roughness increased with BSC development. The physical crust showed similar roughness to the cyanobacterial crust. On the coarse-textured soils, all the crusts were quite smooth and there were no significant differences in roughness.

Factor influences on infiltration

Effects of site characteristics

According to the first series of GLMs testing the influence of the underlying material, there were significant interactions between this factor and the others (crust type, disturbance and antecedent soil moisture) for the infiltration variables (Table 2). Slope, included in the models as a continuous predictor, only marginally influenced total infiltration (P=0.07) and steady-state infiltration rate (P=0.10) on fine-textured soils (El Cautivo badlands area).

Table 1. Mean and standard deviation of each cover type: physical, cyanobacterial, lichen, and moss crusts, annuals and rock fragments (expressed as percentages) and of surface roughness (expressed by a dimensionless index calculated as the ratio between the measured profile length in cm and the projected length in cm) for all crust types. Different letters within each column indicate significant differences (at 90% confidence interval) among crust types on fine- (small letters) and coarse-textured soils (capital letters).

Crust type	Physical crust (%)	Lichens (%)	Cyanobacteria (%)	Moss (%)	Annuals (%)	Rock fragments (%)	Vertical roughness	Transversal roughness
P_F	^{a}99.8 ± 0.2	^{b}0	^{c}0	0	^{a}0	^{a}0.1 ± 0.2	^{b}1.09 ± 0.03	^{bc}1.10 ± 0.06
IC_F	^{b}66.5 ± 19.1	^{b}4.0 ± 0.1	^{b}27.5 ± 17.7	0	^{b}0.7 ± 1.1	^{a}1.2 ± 0.3	^{c}1.04 ± 0.00	^{c}1.04 ± 0.00
C_F	^{c}7.7 ± 1.5	^{b}5.8 ± 5.1	^{a}84.7 ± 4.3	0	^{ab}0.8 ± 0.6	^{a}0.7 ± 0.8	^{b}1.09 ± 0.04	^{b}1.12 ± 0.07
L_F	^{c}3.4 ± 3.8	^{a}77.7 ± 10.8	^{b}15.5 ± 10.1	0	^{b}1.7 ± 1.3	^{a}1.6 ± 2.9	^{a}1.18 ± 0.01	^{a}1.22 ± 0.01
C_C	^{A}14.0 ± 5.6	^{B}1.3 ± 1.4	^{A}67.3 ± 17.5	^{B}12.5 ± 11.8	^{A}4.0 ± 1.0	^{A}0.8 ± 0.3	^{A}1.03 ± 0.00	^{A}1.03 ± 0.00
L_C	^{B}2.5 ± 1.7	^{A}54.2 ± 10.7	^{C}7.5 ± 5.3	^{B}27.5 ± 20.2	^{A}8.0 ± 6.2	^{A}0.2 ± 0.5	^{A}1.04 ± 0.00	^{A}1.05 ± 0.00
M_C	^{A}10.0 ± 2.8	^{B}0.5 ± 0.7	^{B}23.5 ± 9.2	^{A}54.5 ± 0.7	^{A}10.0 ± 7.1	^{A}1.5 ± 0.7	^{A}1.04 ± 0.01	^{A}1.04 ± 0.00

P_F: Physical soil crust over fine soil; IC_F: Incipient-cyanobacterial crust over fine soil; C_F: Cyanobacterial crust over fine soil; L_F: Lichen crust over fine soil; C_C: Cyanobacterial crust over coarse soil; L_C: Lichen crust over coarse soil; M_C: Moss crust over coarse soil.

Table 2. P-values from the Generalized Linear Models (GLMs) to test the influence of the categorical predictors and their interactions (rows): site (only in the first series of GLMs, considering both study sites together), crust type, antecedent soil moisture, and disturbance, on the dependent variables (columns): total infiltration rate and steady-state infiltration rate (fc). Third order interactions were not significant and are not shown in the table. Significant p-values at **95% and * 90% confidence interval.

	Both areas		Badlands area		Caliche area	
	In (mmh^{-1})	fc (mmh^{-1})	In (mmh^{-1})	fc (mmh^{-1})	In (mmh^{-1})	fc (mmh^{-1})
Slope	*0.07	*0.10	*0.07	0.26	0.14	0.20
Site	0.34	0.47				
Crust type	0.56	0.46	**0.00	**0.00	**0.00	**0.00
Antecedent soil moisture	**0.00	-----	**0.00	-----	**0.00	-----
Disturbance	**0.00	**0.00	**0.00	**0.00	0.46	*0.06
Site*Crust type	**0.00	**0.00				
Site*Disturbance	*0.09	**0.04				
Crust type*Antecedent soil moisture	0.38	-----	0.83	-----	0.38	-----
Site*Antecedent soil moisture	*0.06	-----				
Crust type*Disturbance	**0.01	**0.02	**0.04	**0.05	**0.00	**0.00
Disturbance*Antecedent soil moisture	0.55	-----	0.68	-----	0.57	-----

Table 3 shows total infiltration rates and steady-state infiltration rates in the undisturbed and disturbed crusts on fine and coarse-textured soils. Total and steady-state infiltration rates were, in general, low in the crusted surfaces, although there were marked differences depending on topography and soil texture. Total infiltration rates and steady-state infiltration rates were higher on coarse-textured soils with a flat topography than on fine-textured soils over relatively steep slopes. For crusts on fine-textured soils, only from 1.17 mm to 3.84 mm of rain (1.4-5 min) were needed to generate runoff on dry soil, and average total and steady-state infiltration rates (mm h^{-1}) were 17.9 ± 7.9 and 12.6 ± 8.2, respectively, whereas for crusts on coarse-textured soils, from 2.25 to 10.26 mm (2.3-13.2 min) were needed to generate runoff on dry soil, and average total and steady-state infiltration rates (mm h^{-1}) were respectively 31.8 ± 9.0 and

21.6 ± 7.6. Steady-state infiltration rates (fc) at both sites were reached during the first 30 min of rain in most cases.

Table 3. Mean infiltration rates (after 1 hour-simulated rainfall) and steady-state infiltration rate (average of the four plots) with their standard deviations in the crust types under the different disturbance conditions. Different letters at the left of the number within each column indicate significant differences (at 95% confidence interval; LSD test) among crust types, on fine- (small letters) and coarse-textured soils (capital letters). Different letters at the right of the number within each row indicate significant differences (at 95% confidence interval; LSD test) among disturbance conditions of crusts, for total infiltration rates (small letters) and for steady-state infiltration rates (capital letters).

	Total infiltration rates (mm h^{-1})			Steady-state infiltration rates (mm h^{-1})		
Crust type	Undisturbed	Trampled	Scraped	Undisturbed	Trampled	Scraped
P_F	$^{b}13.3 \pm 0.8^{ab}$	$^{b}9.9 \pm 2.5^{b}$	$^{b}16.7 \pm 4.0^{a}$	$^{bc}8.8 \pm 4.9^{AB}$	$^{bc}4.0 \pm 2.3^{B}$	$^{b}11.0 \pm 4.1^{A}$
IC_F	$^{b}18.5 \pm 4.1^{a}$	$^{ab}16.5 \pm 3.9^{a}$	$^{b}20.8 \pm 3.8^{a}$	$^{b}14.7 \pm 6.2^{A}$	$^{b}10.7 \pm 4.0^{A}$	$^{b}16.5 \pm 5.0^{A}$
C_F	$^{a}23.2 \pm 7.9^{b}$	$^{a}19.6 \pm 2.1^{b}$	$^{a}34.1 \pm 8.8^{a}$	$^{ab}17.7 \pm 8.2^{B}$	$^{ab}14.1 \pm 3.7^{B}$	$^{a}28.2 \pm 10.2^{A}$
L_F	$^{b}13.7 \pm 4.8^{ab}$	$^{b}11.3 \pm 2.1^{b}$	$^{b}17.7 \pm 8.0^{a}$	$^{bc}8.9 \pm 6.2^{A}$	$^{bc}5.3 \pm 1.1^{A}$	$^{b}12.1 \pm 8.3^{A}$
C_C	$^{A}20.1 \pm 3.1^{b}$	$^{A}21.9 \pm 4.2^{b}$	$^{A}28.6 \pm 3.6^{a}$	$^{C}13.2 \pm 1.9^{B}$	$^{B}14.4 \pm 3.3^{B}$	$^{A}19.6 \pm 3.7^{A}$
L_C	$^{B}33.5 \pm 10.6^{a}$	$^{A}30.0 \pm 1.9^{a}$	$^{A}32.3 \pm 7.0^{a}$	$^{B}25.3 \pm 8.3^{A}$	$^{B}20.0 \pm 3.9^{A}$	$^{A}19.7 \pm 8.4^{A}$
M_C	$^{C}44.4 \pm 3.0^{b}$	$^{B}41.6 \pm 3.7^{ab}$	$^{A}34.1 \pm 9.4^{a}$	$^{A}35.8 \pm 8.2^{A}$	$^{A}25.4 \pm 3.4^{B}$	$^{A}22.1 \pm 4.8^{B}$

P_F: Physical soil crust over fine soil; IC_F: Incipient-cyanobacterial crust over fine soil; C_F: Cyanobacterial crust over fine soil; L_F: Lichen crust over fine soil; C_C: Cyanobacterial crust over coarse soil; L_C: Lichen crust over coarse soil; M_C: Moss crust over coarse soil.

Effects of the crust type

The crust type significantly influenced infiltration and steady-state infiltration rates at both study sites (Table 2). As can be seen in table 3, the physical crust showed the lowest infiltration rates. Within BSCs, infiltration increased with BSC development (IC_F-C_F and C_C-L_C-M_C), except for the lichen BSC, which showed different responses to infiltration depending on the site. In the area with coarse-textured soils, lichens had high infiltration rates, whereas in the area with fine-textured soils, lichens showed lower infiltration than the other BSCs and infiltration rates similar to the physical crusts. The steady-state infiltration rates (fc) followed the same pattern as total infiltration rates, i.e., higher as BSC development increased, except for the lichen BSC on fine-textured soils, which generated steady-state infiltration rates similar to the physical crusts.

Effects of antecedent soil moisture

Infiltration rates significantly varied depending on antecedent soil moisture (Table 2). Fig. 2 shows total infiltration rates on dry and wet soil in the undisturbed crusts on fine and coarse-textured soils. Infiltration rates were nearly two times greater when soil was dry (17-26 mm h^{-1} on silty soil and 27-46 mm h^{-1} on sandy soil) than when it was wet (9-20 mm h^{-1} on silty soil and 15-40 mm h^{-1} on sandy soil).

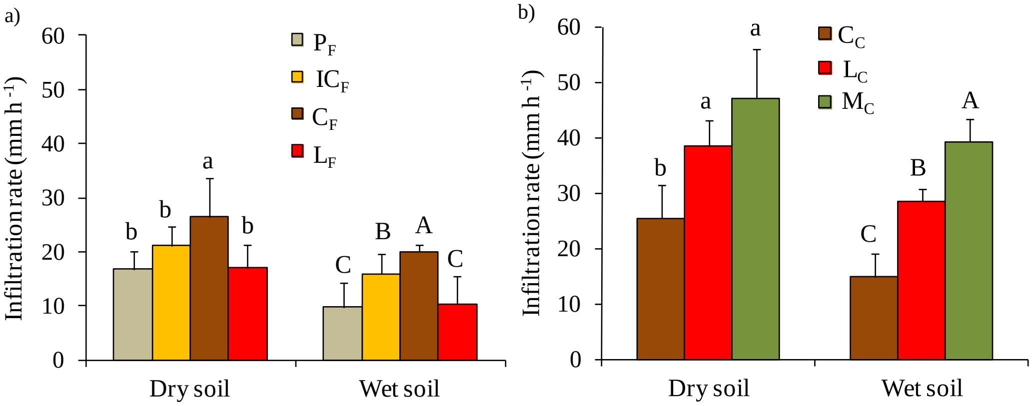

Fig. 2. Mean (± sd) infiltration rates (average of the four plots) in the different crust types on fine-textured soil (El Cautivo) (a): P_F, Physical soil crust; IC_F, Incipient-cyanobacterial crust; C_F, Cyanobacterial crust; L_F, Lichen crust; and on coarse-textured soil (Las Amoladeras) (b): C_C, Cyanobacterial crust; L_C, Lichen crust; M_C: Moss crust), under dry and wet antecedent soil conditions. Different letters within a graph indicate significant differences (at 95% confidence interval; LSD test) among crust types on dry (small letters) and wet soil (capital letters).

The infiltration curves for the different crust types during both rainfall events, the first on dry soil and the second on wet soil, are shown in Fig. 3. It may be observed that steady-state infiltration (fc) was reached more rapidly on wet (less than 10 min) than on dry soil, and on fine (after 15-20 min from the beginning of rain on dry soil) than on coarse-textured soils (after around 25-30 min), where fc in some microplots was reached during the second rain event on wet soil (see for instance the lichen BSC in Fig. 3b).

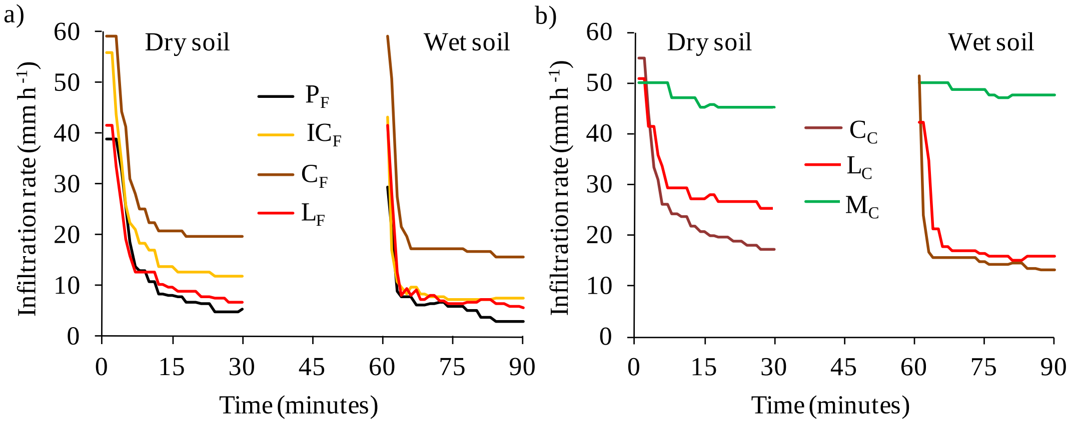

Fig. 3. Infiltration curves in plots of each undisturbed crust type under dry and wet antecedent soil moisture, on fine- (El Cautivo) (a) and coarse-textured (Las Amoladeras) (b) soil.

Effects of crust disturbance

Disturbance significantly affected infiltration rates and steady-state infiltration rates of crusts, but on coarse-textured soil, the effect of the disturbance treatment depended on the crust type (Table 2). Trampling caused a reduction in infiltration, however the difference in infiltration rate after the 1-hour simulated rain between the trampled and the respective undisturbed crust type was not statistically significant (Table 3). As shown in Fig. 4, the reduction in infiltration due to trampling was especially marked during the second rain event. Removal of the crust led to higher infiltration rates than the undisturbed crusts, except in the moss BSC, where BSC removal decreased infiltration (Table 3). But the enhancement in infiltration after scraping the crust decreased after the first minutes of rain, and during the second rain event, infiltration rates in the scraped crusts approached those recorded in the respective undisturbed crust types (Fig. 4). Hence, differences in infiltration between the undisturbed and the respective scraped crusts after the 1-hour simulated rain were only significant in some of the crust types (Table 3). Steady-state infiltration rates generally followed the same pattern as total infiltration rates, with the highest values in the scraped microplots and the lowest in the trampled ones (Table 3).

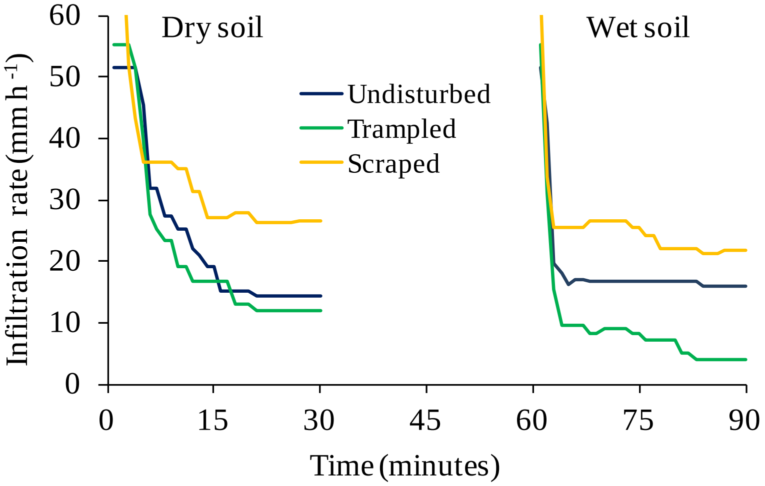

Fig. 4. Infiltration curve of a lichen microplot on fine-textured soil (El Cautivo), for the three disturbance conditions and under dry and wet antecedent soil moisture.

DISCUSSION

The role of BSCs in infiltration and runoff has been examined by several works in arid and semiarid environments around the world, but none of the previous works have simultaneously analysed the influence on these processes of various crust types, including physical crusts and different developmental stages of BSCs, subjected to different disturbance conditions and on two different soil types, in addition to accounting for dry and wet antecedent conditions of soil moisture. Our results demonstrate that the soil type and the antecedent soil moisture greatly affect the infiltration response of crusts. Under homogeneous soil and moisture conditions, infiltration significantly varies depending on the crust type (physical or biological) and the developmental stage of the BSC. Disturbance alters infiltration of the crust, but its effect differs depending on the crust type and the type of disturbance applied. The influence of these factors on the infiltration response of crusts is explained below, as well as the implications for ecosystems where crusts constitute a key component.

Factors influence on infiltration of soil crusts

Sandy soils are generally characterised by large pores and rapid infiltration, whereas fine-textured soils are characterised by narrow pores that lessen the movement of water through them (Warren, 2003a). Thus, infiltration rates and steady-state infiltration rates of crusts were higher on coarse-textured than on fine-textured soils (Table 3). We found that the presence of BSCs increased infiltration compared to physical crusts, and that infiltration generally increased with greater development of the BSC (Table 3, Fig. 2). These results agree with the hypothesis suggested by Warren (2003a) regarding the positive effect of BSCs on infiltration in soils with a sand content less than 80%, where pore formation by BSCs have a larger impact on infiltration rates than pore blocking by them.

Physical crusts are known to reduce infiltration by blocking soil matrix pores (Römkens et al., 1990). Miralles-Mellado et al. (2011) reported these crusts to be characterised by small rounded pores, most of them vesicles formed by splash, which together with the fine texture and low organic matter of the soils contribute to a dense low-porosity layer that limits infiltration. BSCs can also reduce infiltration by clogging soil pores (Greene and Tongway, 1989) or swelling of cyanobacteria in the crust (Eldridge, 2003). But on the other hand, BSCs can enhance infiltration by their effect on microtopography (Eldridge and Greene, 1994a) or by improving macroporosity due to the formation of soil aggregates promoted by the filaments and anchoring structures of biological crust organisms and polysaccharides secreted by them (Warren, 2003a,b). The incipient-cyanobacterial BSC had low biotic crust biomass and little roughness (Table 1) and also low porosity due to the predominance of vesicle pores (Miralles-Mellado et al., 2011), explaining the lower infiltration rates than the cyanobacterial BSC, which was rougher (Table 1) and has higher meso- and macroporosity (Miralles-Mellado et al., 2011), thus promoting higher infiltration rates (Table 3, Fig. 2). The lichen BSC, although more developed and, consequently, rougher than the other crust types (Table 1), showed similar infiltration rates to physical crusts (Table 3, Fig. 2). These low infiltration rates in the lichen BSCs are consistent with the results found by other authors. Alexander and Calvo (1990) reported an inverse relationship between time-to-ponding, time-to-runoff and runoff rates, and cover of crustose and squamulose lichens on soil. Eldridge et al. (2010) also found that infiltration decreased proportionally as the cover of the *Fulgensia subbracteata, Squamarina lentigera,* and *Diploschistes diacapsis* lichens increased. Lichens may reduce infiltration by blocking access to the soil pores (Warren, 2003a). Our lichen BSC mainly consisted of *Diploschistes diacapsis* and *Squamarina lentigera* that have been described as having hydrophobic features in the soil interface (Souza-Egipsy et al., 2002). Souza-Egipsy et al. (2002) pointed out that only when the lichen's fungal material is in contact with calcium oxalate crystals or minerals, water is able to filter through the thallus into the soil. However, when the crust is not in contact with the soil below, water is retained by the thallus, thereby reducing infiltration and enhancing runoff. Similarly, Miralles-Mellado et al. (2011) reported for these lichen BSCs that, despite having high porosity due to the predominance of elongated pores, most of them are between the detached lichen and the underlying substrate, thus originating a disconnect pore system between the surface and the soil underneath it which does not favour infiltration. Hydrophobicity in BSCs can be generated also chemically, due to metabolites of some fungi and polysaccharide secretions of some algae and cyanobacteria (Mazor et al., 1996; Kidron et al., 1999; Warren, 2003a; Fischer et al., 2010). As shown in Table 3, infiltration remained low even after removal of the lichen BSC, which seems to suggest that these reduced infiltration rates could be caused by hydrophobic chemical components synthesized by the lichen species. However, more research would be necessary to gain an insight into the apparently hydrophobic conditions created by some crust species.

The area with coarse-textured soil is subjected to frequent trampling by livestock, and all the crusts showed very little roughness (Table 1). At this site, lichen BSCs usually appear mixed with an important cover of moss (Table 1), which can greatly enhance water retention and increase infiltration in the discontinuities between lichens (Bowker et al., 2010) and, along with frequent cracks in the lichens from trampling, explains the higher infiltration rates compared to the cyanobacterial BSCs. Mosses are highly permeable and have high water-holding capacity and micro-roughness which slows runoff flux, thus lengthening the beginning of runoff by absorbing large amounts of water after a rain (Maestre et al., 2002; Eldridge, 2003). Moss BSCs therefore showed the highest total and steady-state infiltration rates, which is in agreement with other studies that have found higher infiltration rates in moss BSCs than in lichens or cyanobacterial BSCs (Brotherson and Rushforth, 1983; Eldridge et al., 2010).

It is known that high soil moisture content at the beginning of a rainfall retards the initial rate of infiltration and enhances the amount of runoff (Warren, 2003a). Thus, when antecedent soil moisture was high, total infiltration rates of crusts were lower (Fig. 2) and steady-state infiltration rates were reached sooner (Fig. 3).

Effects of crust disturbance on infiltration

Given the vulnerability of BSCs to disturbance, in addition to analyzing the role of different developmental stages of BSCs on infiltration, disturbance treatments were included to provide information on the consequences of a possible land-use change (e.g., designation of undisturbed/protected areas for grazing, hunting, or recreational uses) on the infiltration response of crusts. According to our results, disturbances altered infiltration in the crust, but their effect differed depending on the type of disturbance. Trampling caused infiltration to decrease (Table 3), however the difference with respect to the undisturbed crust was only remarkable during the second rain event (Fig. 4), explained by the progressive sealing of the soil due to raindrop impact and clogging of soil pores by crust fragments. Moreover, trampling compacts the soil aggregates into an impermeable surface layer, especially when soil is wet, thus reducing infiltration (Warren et al., 1986). Some studies conducted in North-American deserts have also found reductions in infiltration rates when the crust is subjected to trampling or tracked vehicle traffic (reviewed in Warren, 2003b). Trampling caused a higher reduction in infiltration in the ungrazed area with fine-textured soils than in the area subjected to frequent trampling by livestock and with coarse-textured soils. At this latter site, trampling mainly impacted on well-developed lichen and moss

BSCs, but not on the earlier cyanobacterial BSCs (Table 3). In contrast, Herrick et al. (2010) found reduced infiltration on trampled coarse soils with low cyanobacterial biomass.

The removal of the crust by scalping resulted in increased water infiltration in all crust types except in the lichen and moss BSCs on coarse-textured soil, probably because these BSCs promoted the highest infiltration rates (Table 3). Unlike them, the cyanobacterial BSC on coarse soil presented low infiltration rates and its removal caused infiltration to decrease (Table 3). Some authors have reported an increase in infiltration after removing the crust (Greene and Tongway, 1989; Eldridge et al., 2000; Barger et al., 2006). However, other researchers have found higher infiltration rates in soil with undisturbed crusts than where the crust was removed (Brotherson and Rushforth, 1983; Harper and St. Clair, 1985; Harper and Marble, 1988). Although it might seem that scraping the crust enhances infiltration, it should be mentioned that the enhancement in infiltration after removing the crust decreased over time and, after just one intense rain, the scraped soils sealed again from raindrop impact, making infiltration rates in these surfaces approach those recorded in the respective undisturbed crust types (Fig. 4). Besides, the formation of physical crusts occur more rapidly on unvegetated (uncovered) surfaces than on vegetated (covered) surfaces, and unvegetated surfaces also develop stronger crusts (Neave and Rayburg, 2007). Therefore, after successive rain events, the formation of a well-developed physical crust in the scraped soils is likely to generate higher runoff than the biologically crusted soils. Moreover, both trampling and especially crust removal dramatically increased erosion. Table 4 shows average erosion rate after the 1 hour-simulated rainfall on the undisturbed and disturbed crust types, at both sites. Sediments yield strongly decreased from the physical to cyanobacterial and to lichen and moss crusts and was much lower on the flat coarse soil than on the steeper fine soil. It is important to emphasize that, despite the lichen BSCs on fine soil generated similar infiltration rates to physical crusts, there were marked differences in erosion rates between them. The lichen BSCs generated the lowest erosion rates whereas the physical crusts exhibited the highest. The removal of the lichen BSCs also induced the highest increase in erosion.

Table 4. Mean erosion rate and standard deviation (g m^{-2}), after 1 hour-simulated rainfall on the undisturbed, trampled, and scraped crust types. Different letters at the left of the number within each column indicate significant differences (at 95% confidence interval; LSD test) among crust types, on fine (small letters) and coarse-textured soils (capital letters). Different letters at the right of the number within each row indicate significant differences (at 95% confidence interval; LSD test) among disturbance conditions of crusts.

	Erosion rate (g m^{-2})		
Crust type	Undisturbed	Trampled	Scraped
P_F	^{a}647.8 ± 230.5	No data	No data
IC_F	^{b}150.6 ± 136.2^{a}	^{a}118.3 ± 109.4^{a}	^{b}274.8 ± 182.3^{a}
C_F	^{c}26.0 ± 23.4^{b}	^{a}108.3 ± 67.7^{ab}	^{b}128.8 ± 92.48^{a}
L_F	^{c}10.7 ± 3.1^{b}	^{a}222.1 ± 157.5^{ab}	^{a}744.6 ± 19.3^{a}
C_C	^{A}15.3 ± 12.9^{b}	^{A}52.5 ± 44.3^{ab}	^{A}79.4 ± 41.2^{a}
L_C	^{B}2.0 ± 1.5^{b}	^{B}5.5 ± 3.9^{ab}	^{B}14.6 ± 4.0^{a}
M_C	^{B}0.8 ± 0.1^{a}	^{B}2.0 ± 1.0^{ab}	^{B}11.4 ± 1.7^{b}

P_F: Physical soil crust over fine soil; IC_F: Incipient-cyanobacterial crust over fine soil; C_F: Cyanobacterial crust over fine soil; L_F: Lichen crust over fine soil; C_C: Cyanobacterial crust over coarse soil; L_C: Lichen crust over coarse soil; M_C: Moss crust over coarse soil.

Implications for the ecosystem

Infiltration is fundamental for many ecosystem processes such as water and nutrient fluxes, nutrients cycling, productivity, and erosion dynamics in drylands. Bautista et al. (2007) reported that soil surface crusting, along with functional diversity of perennial vegetation, condition spatial pattern and hydrological functioning in semiarid areas. Our work clearly demonstrates that the presence of crusts and crust composition exert an important influence on infiltration. In general, intershrub patches dominated by communities of well-developed BSCs contribute to increased water infiltration (Table 3) and reduced erosion (Table 4) compared to physical crusts or poorly-developed BSCs. This absorbed water triggers microbial activity and stimulates C and N fixation by BSCs that is used to produce more BSC biomass (Belnap et al., 2005). Increased biomass contributes to increase soil aggregation and soil stability, thus increasing organic matter and water retention (Tongway and Ludwig, 1997). Water availability also promotes biological activity by soil invertebrates, which increase the formation of macropores in the soil, thereby enhancing infiltration (Ludwig et al., 2005). Nevertheless, infiltration rates found in the BSCs are lower than those commonly reported for vascular plants (Cantón et al., 2011), which highlights the relevance of BSCs as runoff sources in arid and semiarid areas. This additional runoff can serve as an important water resource for adjacent vegetation patches. If runoff is effectively obstructed by vegetation patches, the water infiltrated results in a pulse of plant growth, which contributes to increased plant productivity, thus increasing the capacity of the vegetation patch to trap runoff in future rainfall events (Ludwig et al., 2005). The transmission of resources from the crust to the vegetation patches can be especially important under wet conditions of antecedent soil moisture, where runoff generation in the crusts can be almost two times greater than when soil is dry (Fig. 2). Moreover, unlike physical crusts, BSCs strongly contribute to reduction of soil erosion and thus, to nutrient retention and maintaining of fertility in the interplant spaces, also creating a more favourable habitat for soil microbiota (Belnap, 2003) and vascular vegetation (Belnap et al., 2003c).

The scenarios for future climate change have predicted warmer temperatures and modifications in the amount and timing of precipitation. However the direction in which precipitation regimes will be modified is uncertain. Changes in temperature and precipitation are likely to alter cover and composition of BSCs. Belnap et al. (2004) reported that alterations in precipitation frequency could reduce the cover of late-successional BSCs. The expected consequences of a replacement of late-successional by early-successional BSCs, on the basis of our results, are the enhancement of runoff production and sediment loss, which would lead to increased nutrient leaching losses, a reduction of C and N inputs into the ecosystem and a reduction of their stocks in the soil.

Impacts caused by increasing human activities as grazing, hunting, or recreational uses in private and public lands have the potential to cause the deterioration or destruction of BSCs (Barger et al., 2006), leaving the soil surface unprotected and, as shown by our results, facilitating the formation of physical crusts, which increase runoff and erosion (Table 3, Table 4). The loss of BSCs would be implicated in a decrease of soil stability, an increase in water and wind erosion (Eldridge and Greene, 1994b) and a reduction in the capacity of soils to trap nutrient-enriched dust (Reynolds et al., 2001). Intensive anthropogenic disturbances in semiarid areas can also reduce the cover and size of vegetation patches, which decreases their ability to retain resources in future rainfall events, thereby increasing runoff and erosion (Calvo-Cases et al., 2003; Ludwig et al., 2005; Li et al., 2008). This diminishing ability of vegetation patches to absorb the fluxes of water, sediments, and nutrients generated in the crust patches together with the enhancement of such fluxes induced by an increased cover of physical crusts as a result of disturbance, might lead to the discharge of resources out of the system. The ultimate consequence would be the conversion of a conserving system to a leaky and dysfunctional system, where losses of materials exceed gains (Belnap et al., 2005; Ludwig et al., 2005). Therefore, it can be expected that disturbance of ecosystems where BSCs are predominant soil surface covers leads to changes in C and N cycling, spatial redistribution of water and nutrients and their availability for plants, and affects plant distribution. Consequently, BSCs acquire a relevant role in the maintenance of ecosystem functioning.

We examined the effects of different factors (crust type, antecedent soil moisture, and disturbance) on infiltration parameters at two different sites, and found significant interactions between the site characteristics and these factors (Table 2). This highlights the importance of spatial and temporal variability in the infiltration response of crusted surfaces and the necessity of accounting for site characteristics as soil properties, topography, or land uses.

CONCLUSIONS

Crust infiltration rates greatly depended on the site characteristics, thus we found higher infiltration rates in the crusts in a flat area with coarse-textured soils than in an area with highly variable topography and fine-textured soils. Infiltration rates were higher in BSCs than in physical crusts. Within the BSCs, infiltration increased as cyanobacterial biomass increased and was the highest in the late-successional moss BSCs, but late-successional crustose and squamulose lichen BSCs showed very low infiltration rates. Therefore, infiltration does not always linearly increase with BSC development and is strongly determined by other factors, such as the specific characteristics of the species that compose the crust. Disturbance of the crust affected infiltration rates. Trampling resulted not only in crust disruption, but also in soil compaction, causing infiltration to decrease, especially on the wet soil. The removal of soil surface crusts (by scraping) initially increased infiltration but this enhancement decreased over time as a physical crust formed again from raindrop impact. Even in further rainfall events the formation of a new well-developed physical crust over the scraped surfaces may generate higher runoff than over undisturbed biologically crusted surfaces. Moreover, destruction of BSCs dramatically increased erosion. Therefore, the conservation of crust patches is crucial for soil stability, water, sediment, and nutrient distribution within the landscape and, ultimately, to maintain ecosystem functioning.

CHAPTER III

Runoff at contrasting scales in a semiarid ecosystem: A complex balance between biological soil crust features and rainfall characteristics

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ABSTRACT

Runoff in arid and semiarid areas is characterised by high spatial and temporal variability. The spatial component is largely associated with the high spatial heterogeneity of soil surface attributes, such as vegetation and rock fragment covers, topography, and soil crust typology. Biological soil crusts (BSCs) are a common soil cover in arid and semiarid areas, and they play an essential role in local hydrological processes, since they affect many soil surface attributes associated with hydrologic properties. Although several publications have reported on the influence of BSCs on runoff at microplot spatial scales, only a few have examined their influence on larger spatial scales. Moreover, very few studies have analysed the effect of BSCs on runoff under natural rain conditions. This is difficult, since a complex pattern of interactions among rainfall properties, BSC characteristics and some local characteristics, such as topography or type of soil is expected. In addition, in order to achieve a realistic model of how BSCs and rainfall affect runoff, it would be necessary to consider the level of human-driven degradation of BSCs. In this study, runoff was analysed in plots with varying cover of cyanobacterial and lichen BSCs at microplot and small hillslope scales for two hydrological years in badlands in SE Spain. Structural equation modelling (SEM) was applied to test both direct and indirect relationships of BSC cover, slope gradient, rainfall characteristics and runoff. Our model showed that rainfall characteristics were the main factors controlling runoff yield. The slope positively affected runoff at small hillslope scales, but did not influence runoff at microplot scales. Runoff decreased at both scales with increased lichen-BSC cover. However, this effect was only significant during low-intensity events. Under high rainfall intensities, neither the BSC cover nor the slope had a causal effect on runoff. Our results suggest that incorporation of BSC-crusted surfaces in models should improve their capabilities for low-intensity rainfall events in semiarid areas similar to ours, but would be less important for high-intensity events. In addition, our approach, which takes direct and indirect relationships of factors affecting runoff into consideration, provides a very accurate picture of the process.

Keywords: cyanobacteria, lichen, runoff, microplot scale, hillslope scale, structural equation modelling.

INTRODUCTION

In arid and semiarid lands, the landscape is structured in a two-phase pattern in which open areas are interspersed with patches of perennial plants. These open areas are usually covered by complex communities of cyanobacteria, microfungi, algae, lichens, and bryophytes known as biological soil crusts (BSCs). It is well known that BSCs have a profound effect on ecosystem functioning and services (Castillo-Monroy and Maestre, 2011; Maestre et al., 2011). They affect many soil properties, such as aggregate stability, soil structure, organic matter, soil nutrient content and microtopography, most of them influencing hydrological processes, such as infiltration-runoff, evaporation and soil water retention. Thus they have an essential role in the local water balance in arid and semiarid areas (Belnap et al., 2005; Chamizo et al., 2012a). Publications on their role in infiltration and runoff have reported contradictory results, with some findings supporting a positive effect on infiltration compared to bare or uncrusted soil surfaces (Greene and Tongway, 1989), others decreased infiltration (Eldridge et al., 2000), and still others neutral effects (Eldridge et al., 1997). We hypothesised that this lack of congruence could be due to the fact that the large number of interacting factors conditioning the hydrological response of BSCs is rarely considered simultaneously, and their direct and indirect effects on runoff never disentangled. Among them, soil type, antecedent soil moisture, crust cover and composition or level of disturbance have been highlighted (Chamizo et al., 2012b). However, there is agreement that BSCs produce more runoff than vegetation-covered soils in semiarid lands, and several studies have pointed out the relevance of this water supply for the survival and maintenance of perennial vegetation downstream (Ludwig et al., 2005; Almog and Yair, 2007; Li et al., 2008; Cantón et al., 2011; Yair et al., 2011).

On the other hand, BSCs are fragile structures vulnerable to disturbance, especially to human-driven impacts, such as trampling by livestock, burning or vehicle traffic, which usually causes the loss of mature BSCs and reversal to early cyanobacterial BSCs (Barger et al., 2006; Housman et al., 2006). These disturbances simultaneously reduce soil surface roughness promoted by typical well-developed BSCs, causing soil compaction, and often sealing the soil surface (Chamizo et al., 2012b). This leads to increased overland flow and reduced storage capacity for water and sediments (Abrahams et al., 1995). Therefore, to form a more realistic picture of runoff generation, it would be necessary to examine the hydrological response of different types of BSCs linked to BSC dynamics and disturbance.

An additional critical factor for understanding runoff and infiltration in semiarid areas better is the necessity for explicitly considering the spatial scale of the survey. Runoff processes are characterised by high spatial and temporal variability, which results from the interaction of different factors acting at each scale (Puigdefábregas et al., 1999; Cammeraat, 2002; Calvo-Cases et al., 2003; Mayor et al., 2011). Whereas temporal variability mostly depends on the variation of rainfall and antecedent moisture (Gómez-Plaza et al., 2001), the spatial variability of hydrological processes is largely associated with the high spatial variability of soil surface characteristics such as vegetation and rock fragment covers, position of rock fragments, topography and types of soil crusts (Alexander and Calvo, 1990; Solé-Benet et al., 1997; Lavee et al., 1998; Arnau-Rosalén et al., 2008; Cantón et al., 2011). In this sense, there is no doubt that the presence and development of soil surface crusts constitute critical factors in explaining the spatial variability of soil infiltration capacity and runoff generation (Yair, 2003; Greene and Hairsine, 2004). However, most research on the effect of BSCs on runoff and infiltration processes has focused on the so-called mini plot scale (<1 m^2) (e.g., Alexander and Calvo, 1990; Herrick et al., 2010; Chamizo et al., 2012b), and few studies have examined responses at coarser spatial scales, such as hillslopes (e.g., Yair, 2003; Almog and Yair, 2007; Yair et al., 2011) and catchments (e.g., Cantón et al., 2001). Moreover, while most studies have used rainfall simulations or disk infiltrometers to examine the influence of BSCs on infiltration and runoff, only a few studies have analysed their influence under natural rain conditions (e.g., Kidron and Yair, 1997; Cantón et al., 2001, 2002; Almog and Yair, 2007; Yair et al., 2011).

Therefore, for a clearer understanding of the role of BSCs in infiltration-runoff processes, the factors above and interaction among them need to be explicitly considered. To build realistic models improving the prediction of runoff in arid and semiarid areas, the influence of BSCs on infiltration and runoff should be studied at different spatial scales, incorporating the effect of disturbance, and taking into consideration different rainfall conditions, as these will ultimately control runoff generation mechanisms in arid and semiarid areas (Calvo-Cases et al., 2003; Mayor et al., 2011). We think that discrepancies reported in the role of BSCs in runoff could be clarified by a more detailed analysis in which scales and BSC disturbance, along with direct and indirect relationships among controlling factors are incorporated in current models.

In this study, we examined the relationships of BSC cover and composition, antecedent soil moisture, topography, rainfall characteristics, and runoff yield at two different spatial scales (microplot and small hillslope) in a semiarid badlands area of SE Spain in order to identify the variables or interactions among them that mainly drive runoff yield. We also wanted to know whether these interactions changed with the spatial scale. With this aim, runoff was monitored under natural rainfall for over two years in open plots with different contributing areas, over undisturbed soils covered by two main types of BSCs (cyanobacteria and lichen-dominated BSCs) and soils where these BSC types had been removed in two different previous years and now had a differing degree of colonization by BSCs. We hypothesised that runoff yield would decrease with increased BSC cover, that this effect would be more significant at a coarser spatial scale, and that runoff would be lower in soils predominantly covered by cyanobacterial than by lichen BSCs, due to reported blocking of soil pores and creation of hydrophobic soil conditions by some lichen BSCs (Alexander and Calvo, 1990; Cantón et al., 2001; Warren, 2003a; Eldridge et al., 2010; Chamizo et al., 2012b). We also tested the hypothesis that BSCs would have a more significant effect on runoff in low-intensity rainfalls than high-intensity rainfalls, as the role of BSCs in increasing roughness and surface storage capacity would be overridden by the effect of rainfall intensity (Rodríguez-Caballero et al., 2012). Our final hypothesis was that the amount of rainfall would influence runoff more during low-intensity events, whereas rainfall intensity would be more influential during high-intensity events, as suggested in previous studies (Mayor et al., 2011). Thus, the main objectives of this paper were to: i) explore whether increased cover of BSCs, as well as the type of BSC, affect runoff; ii) examine how factors such as antecedent soil moisture and the slope gradient affect runoff; iii) find out whether the interaction of BSC cover and composition, antecedent soil moisture and slope gradient affect runoff differently depending on rainfall characteristics and the spatial scale under study (microplot and small hillslope).

MATERIAL AND METHODS

Runoff plots

Open microplot (around 1 m^2 area) and small hillslope (6.7 ± 1.9 m^2) scale plots containing two types of BSCs, cyanobacteria and lichen-dominated crusts, each in three different stages of development, were set up at the El Cautivo experimental site. The cyanobacteria-dominated plots, apart from high cyanobacteria cover, contained significant amounts of pioneer nitrogen-fixing lichens, such as *Collema spp* with cyanobacteria symbionts. The lichen-dominated plots consisted mostly of *Diploschistes diacapsis* and *Squamarina lentigera* species of lichens (from 35 to 55% cover) though there was also significant cyanobacteria cover (from 15 to 35%). The three development stages considered for each BSC type were: 1) Undisturbed BSC, 2) BSC-removal in 2005 (intermediate between undisturbed and recently removed BSCs) and 3) BSC-removal in late 2007 (physical crust with very early colonization by cyanobacteria). Three and two plots per development stage of each BSC type respectively were set up at microplot and small hillslope scales, thus totalling 18 microplots and 12 small hillslope plots. All the plots were set up on the same type of soil and separated from each other by a distance of 10 to 100 m. The microplots were bounded at the lower edge by a 0.5-m-long steel separator with a hole in the middle connected by a hose to a 20-l deposit (Fig. 1a). Total runoff was measured manually after each rainfall event. The larger plots were limited at the bottom with a 0.7-m-long steel separator connected by a 0.04-m-diameter pipe to a 50-l tank (Fig. 1b). Each tank was equipped with a 0.5-l tipping-bucket rain gauge connected to a data logger (HOBO Pendant, Equipos Instrumentación y Control S.L., Madrid, Spain). Rainfall was recorded by another tipping-bucket gauge with a 0.20-mm resolution in an area next to the plots. From the data recorded by the gauge, total rainfall, maximum 5-min rainfall intensity (I_5max) and rainfall duration were calculated for each event. A period of 6 hours without rainfall separated single rain events (Mayor et al., 2011). Fewer rainfall events were recorded for the microplots, as in some cases total runoff in these plots was collected after consecutive events (several consecutive days of rain). Runoff coefficients for each plot after each rain event were determined from the rainfall recorded by the gauge. Runoff was measured from September 2008 to December 2010.

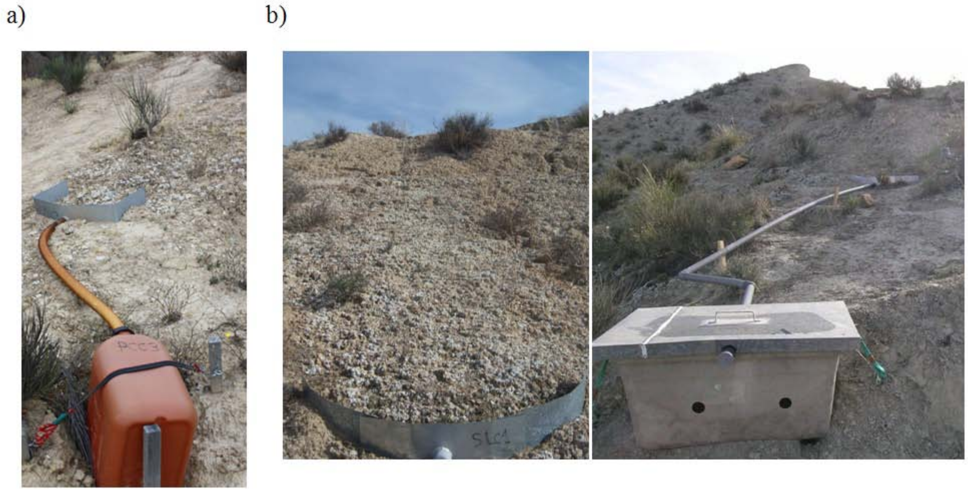

Fig. 1. a) Microplot on a BSC-crusted surface, connected to a 20 l deposit to collect total runoff. b) Hillslope plot on a BSC-crusted surface, connected to a tank provided with a 0.5 l tipping-bucket rain gauge to register runoff at high temporal resolution.

As the plots were open, the contributing area to each plot was estimated from a 0.01-m-resolution digital elevation model of the hillslope the plot was on. Each model was built up from height points of the plot surface recorded with a Leica

ScanStation 2 (Leica Geosystems AG, Heerbrugg, Switzerland) terrestrial laser scanner mounted in the field. The topography of each plot was scanned from different angles for a complete topographical description of the plot and to avoid shading. Then the individual scans were combined in the laboratory, and the resulting point cloud was filtered to remove plants and annuals. After filtering, areas with no data were filled in by interpolation based on inverse distance weighting. Finally, the DEM was georeferenced using reference points (i.e. targets) at the study site. The contributing area was determined using ArcGis 10.0 software.

A mosaic of georeferenced pictures covering the entire surface of each plot was used to estimate the cover of bare soil/physical crust, cyanobacterial BSC, lichen BSC and vegetation in each plot by applying multiresolution segmentation followed by automatic maximum likelihood classification using Ecognition software (Trimble GeoSpatial, Munich, Germany). Multiresolution segmentation groups neighbouring pixels with similar spectral response into coarser homogenous areas (known as objects). After segmentation, training areas of the different cover types were selected for maximum likelihood classification. This classification was then validated by using points from the pictures for which cover type was known.

Soil moisture was recorded by probes (EC-5 soil moisture sensors, Decagon Devices, Inc., Pullman, Washington, USA) permanently located in the area at a soil depth of 0.03 m under bare soil (physical crust), cyanobacteria, and lichen-dominated BSCs.

Structural equation modelling

The relationships among rainfall characteristics (intensity, duration and amount), soil surface characteristics (antecedent moisture, slope gradient and BSC cover) and runoff coefficients were tested using structural equation modelling (SEM). We used this modelling tool because, unlike most linear models, SEM allows the direct and indirect effects that one variable may exert on another to be separated, and estimates the strength of these multiple effects (Iriondo et al., 2003; Grace, 2006). Moreover, this tool has rarely been used in hydrology or ecohydrology. To our knowledge, only one study, which explored the interactive effects of *Stipa tenacissima*, BSCs and rabbits on infiltration, has used this technique (Eldridge et al., 2010).

SEM modelling evaluates complex multivariate causal relationships which are represented in a causal diagram. The researcher formulates a possible complex causal framework underlying a multivariate relationship, and confronts it with the field data. The SEM tests whether the data are supported by the underlying mechanisms that the specific model and causal relationships describe (Shipley, 2000). This is done by comparing the covariance structure of data implied by the model with the observed covariance structure of the data (Bollen, 1989; Grace and Pugesek, 1998; Shipley, 2000; McCune and Grace, 2002). We formulated our path diagram based on our *a priori* hypotheses of causal links among variables. Our working model proposed that rainfall duration and intensity would determine total rainfall and that all these rainfall characteristics would exert a causal effect on runoff yield (Fig. 2). We used the maximum 5-min rainfall intensity (I_5max), which is related to the maximum runoff peak in this system (Cantón et al., 2001). Topography and soil surface properties such as antecedent soil moisture and BSC cover and type were expected to determine runoff yield. As physical, cyanobacterial and lichen crust covers accounted for 100% of the soil surface cover in the plot and these cover types were correlated, only the cover of the two types of BSC were included in the SEM model. At small hillslope scale, we considered slope a factor controlling lichen and cyanobacterial BSC cover in addition to the direct effect of the slope gradient on runoff, as a previous study in the Tabernas badlands had shown that ground cover is strongly controlled by topography, and crustose lichen BSCs generally occupy moderate to high steep slopes (Cantón et al., 2004a). The input data in our models were the runoff coefficients measured in each plot after every rainfall event. The proposed model was evaluated separately for each spatial scale and for the whole data set (hereafter referred as the “general model”). An unsupervised K-means classification was used to separate high and low-intensity rainfall events, by explicitly searching for an “objective” two-group classification based on the I_5max. Our working hypothesis at this point was that controlling factors clearly shift from high to low rainfall events.

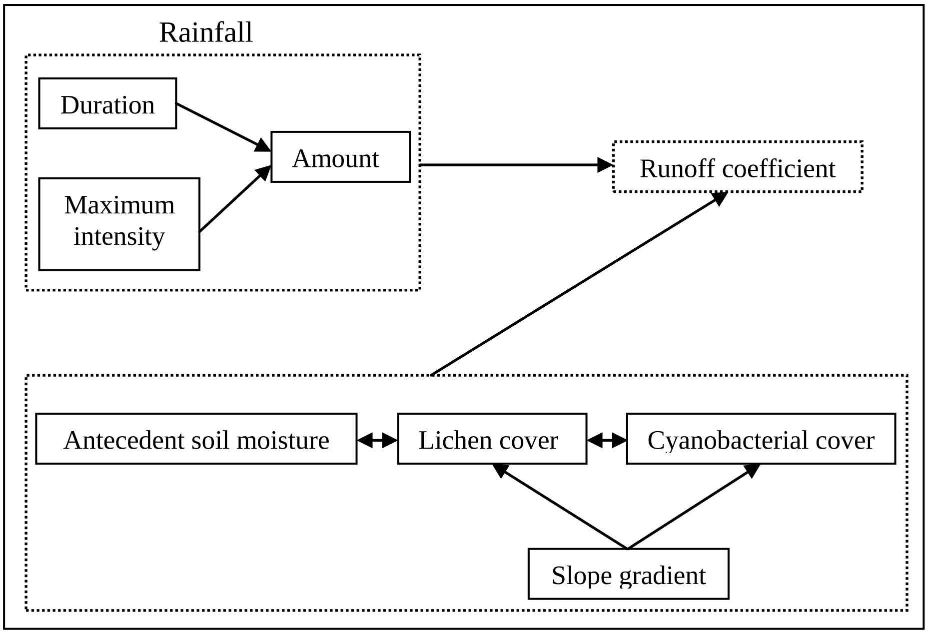

Fig. 2. *A priori* model representing the hypothesised causal relationships among rainfall characteristics, soil surface properties and runoff.

The degree of fit between observed and predicted covariance structures was first assessed with a maximum-likelihood goodness-of-fit test, which is the best method for severe deviations from multivariate normality in rather small sample sizes (Finch et al., 1997). The null hypothesis of the model is that observed and predicted covariances are the same. Thus contrary to most statistical tests, in this test $P < 0.05$ indicates a significant lack of fit, and a significant χ^2 indicates that the model does not properly fit the data. We used two alternative fit indices that provide an accurate fit and are independent of sample size: the comparative fit index (CFI) (Bentler, 1989) and the nonnormed fit index (NNFI) (Bentler and Bonet, 1980). Values over 0.90 and 0.81, respectively, indicate good fit compared to a null model that assumes that all variables are independent (Hatcher, 1994). As satisfactory goodness of fit is often not found at first, our model was tested iteratively and modified by exploring some suggestions coming from the use of modification indices (e.g., removing a variable from the model) until fit with the data was satisfactory (Bollen and Stine, 1992). Finally, we removed uninformative weak pathways to conserve parameters and simplify, and retested the resulting final model. The significance of each individual path coefficient was subsequently assessed by a multivariate Wald test ($P<0.05$). This test locates the path coefficients that can be eliminated without significantly increasing the χ^2 of the model. The structural equations were processed using AMOS 5.0 (SPSS Inc., 2003).

RESULTS

Plot characteristics and rainfall and runoff patterns

Cyanobacterial and lichen BSC cover varied widely from the undisturbed crusted plots to the more recently BSC-removed plots. In all plots, BSC cover was homogeneously distributed along the plot and not concentrated at specific points (at the top or the bottom of the plot). Patches of BSCs were interspersed with patches of physical crust. Mean cyanobacterial, lichen and physical crust cover (%) were, respectively, 56 ± 14, 10 ± 7 and 24 ± 16 in the undisturbed cyanobacteria-dominated plots, and 23 ± 12, 39 ± 11 and 25 ± 19 in the lichen-dominated plots. Regarding the plots where the BSC was removed, mean cyanobacterial, lichen and physical crust cover (%) were, respectively, 42 ± 17, 7 ± 8 and 40 ± 13 in the plots where the BSC was removed in 2005, and 23 ± 9, 3 ± 3 and 65 ± 14 in the plots where the BSC was removed in 2007. The slope ranged from 5º to 14º in the microplots and from 10º to 24º in the small hillslope plots.

Annual rainfall during hydrological year 2008 (1st October)-2009 (30th September) was 247 mm, which is close to the mean annual rainfall in the study site (235 mm; 30-year average recorded in Tabernas, Almería Province (Lázaro et al., 2001)). The hydrological year 2009 (1st October)-2010 (30th September) was atypically rainy and the annual rainfall recorded was 384 mm. Around 43% of the rainfall events recorded during the two-year period were under 10 mm, 20% from 10 to 20 mm, 20% from 20 to 30 mm and only 17% exceeded 30 mm. Most rainfall events (85%) were low-intensity, with a mean maximum 5-min rainfall intensity (I_5max) of 10.9 mmh^{-1}, and minimum and maximum of 5.4 and 19.8 mm h^{-1}, respectively. Only 15% of the rainfall events registered during the study period was high-intensity. The lowest and highest I_5max in these events were 27.9 mmh^{-1} and 57 mmh^{-1} (mean 36 mm h^{-1}), with rainfall ranging from 11.9 to 27.7 mm. Mean runoff coefficients (%) in the microplots and small hillslope plots were 18.4 ± 15.3 and 19.9 ± 17.1, respectively, for low-intensity rain, and 40.6 ± 26.6 and 28.0 ± 18.4, for high-intensity rain.

Fig. 3 shows hydrographs of plots with different proportions of physical, cyanobacterial and lichen covers. During low-intensity rain, runoff started earlier in the plot where physical crust cover was predominant, followed by the plot with predominant cyanobacterial cover, and last in the plot with the most lichen cover (Fig. 3a). Runoff peaks decreased from the physical crust-dominated plot, to the cyanobacteria-dominated plot and to the lichen-dominated plot. During high-intensity rain, the start of runoff was rather similar in all plots (Fig. 3b).

Microplot runoff SEM model

The microplot runoff model is presented in Fig. 4. Antecedent soil moisture did not show a causal relationship with runoff, and because of this, it was removed from our *a priori* models to improve fit. This was also the case of slope gradient, which did not have a causal effect on runoff coefficients either. The final models taking into account all, high or low-intensity rainfall events showed good overall fit, with both NNFI and CFI over 0.90. 32% of variance in runoff was explained in the general model (Fig. 4a). Rainfall characteristics had the strongest influence on runoff response. Whereas rainfall duration had a direct negative effect on runoff coefficients, it had an indirect positive effect on runoff coefficients because of its positive causal effect on amount. Rainfall intensity (I_5max) also had an indirect positive effect on runoff due to the same causal path. Both intensity and amount of rainfall had a direct positive effect on runoff coefficients. The cyanobacterial BSC cover did not have a causal effect on the runoff coefficient, whereas the lichen cover had a negative effect. The two types of BSC cover were negatively correlated.

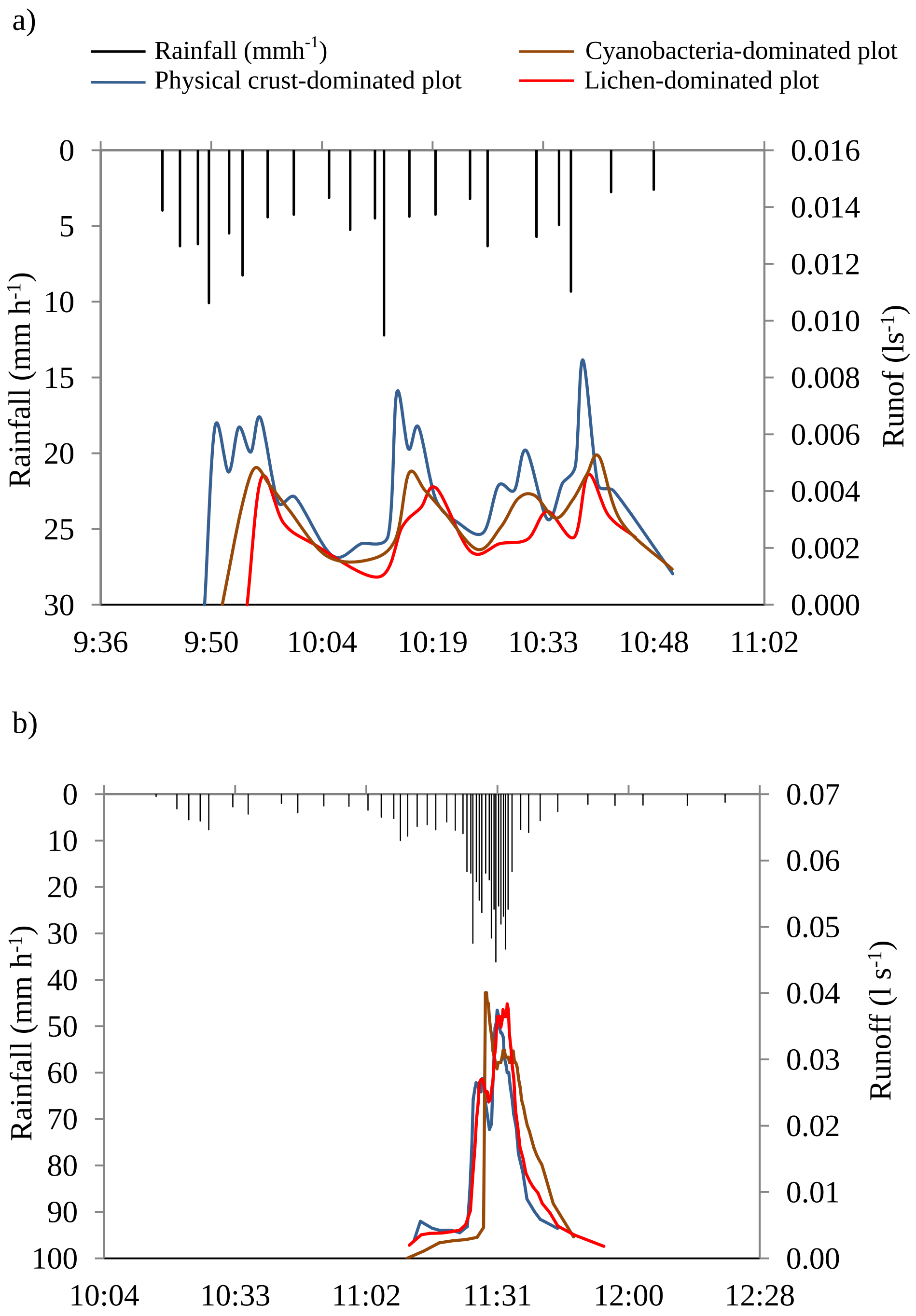

Fig. 3. Hydrograph of a physical-dominated, cyanobacteria-dominated plot and lichen-dominated hillslope plot, for a low intensity-rainfall (I_5max=9.8 mmh^{-1}; rainfall amount=7.5 mm) (a) and a high intensity rainfall (I_5max=27.9 mmh^{-1}; rainfall amount=19.8 mm) (b).

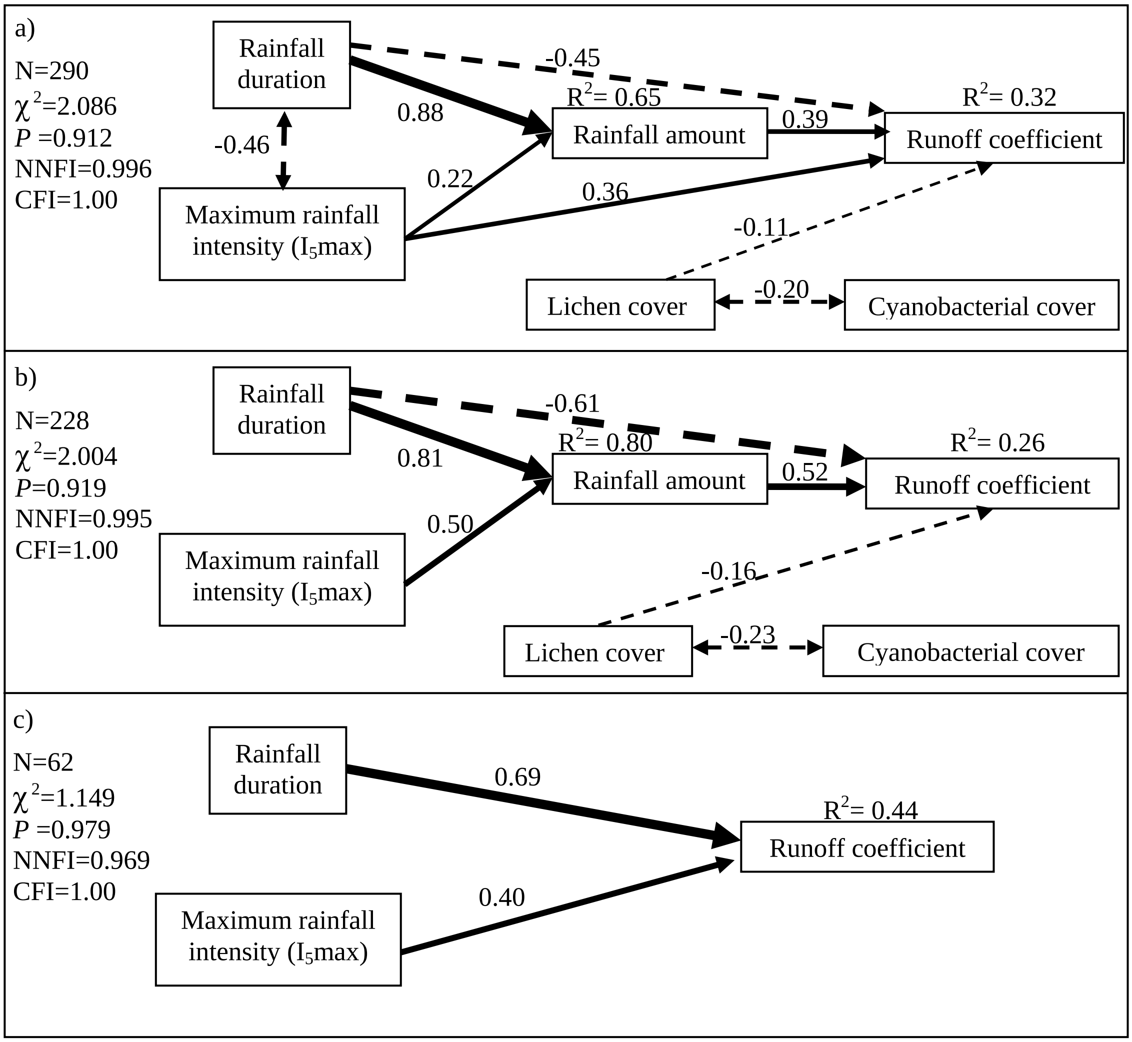

Fig. 4. Microplot runoff SEM model, including a) all the events registered during the study period (September 2008-December 2010), b) low-intensity events, and c) high-intensity events. Continuous lines show positive effects. Dashed lines show negative effects. Arrow widths are proportional to adjacent standardized path coefficients. Non significant paths are omitted (see Fig. 2 for our *a priori* model). Fit statistics (nonnormed fit index, NNFI; comparative fit index, CFI; *P*; χ^2) and sample size (*N*) are given at the upper-left corner of each model.

*I_5max is the maximum 5-min rainfall intensity.

The same relationships among variables were found in low-intensity rainfall events (Fig. 4b), with the exception that in this case, rainfall intensity (I_5max) did not have a significant direct effect on runoff, and the path coefficient estimate of lichen cover on runoff increased slightly from 0.11 to 0.16. Under intense rainfall events (Fig. 4c), rainfall duration and intensity (I_5max) showed a significant positive effect on runoff coefficients, and contrary to the low-intensity events, the relationship between amount of rainfall and runoff coefficients was not significant. Neither BSC cover nor type had a significant causal effect on runoff. Variance in runoff explained was higher in these high-intensity events (44%) than in low-intensity events (26%), which suggests that a significant fraction of runoff was not properly captured by our predictors in low-intensity rainfall.

Small hillslope runoff SEM model

The final hillslope runoff model is shown in Fig. 5. Antecedent soil moisture did not show a causal relationship with runoff, and was removed from the *a priori* model to improve model fit. All models, including the general model and those for low and high-intensity rainfall events, showed good fit (NNFI and CFI over 0.90). Variance explained for runoff in the general model was 35% (Fig. 5a), and slightly increased in the model for low (37%) and high (36%) intensity rainfall. The same relationships between rainfall characteristics and runoff coefficients found at microplot scale were also found at this scale in the general, low and high-intensity rainfall models, but I_5max also had a significant runoff path in low-intensity events (Fig. 5b). Nevertheless, this pathway was much weaker than in high-intensity events (Fig. 5c). Our model confirmed the positive relationship between the slope gradient and lichen cover. Under low-intensity rainfall (Fig. 5b), the slope gradient had a positive causal effect on runoff. Lichen cover had a significant negative effect on runoff, while cyanobacterial cover did not show a significant effect on runoff. Under high-intensity rains, neither the slope nor the BSC cover had a causal effect on runoff (Fig. 5c).

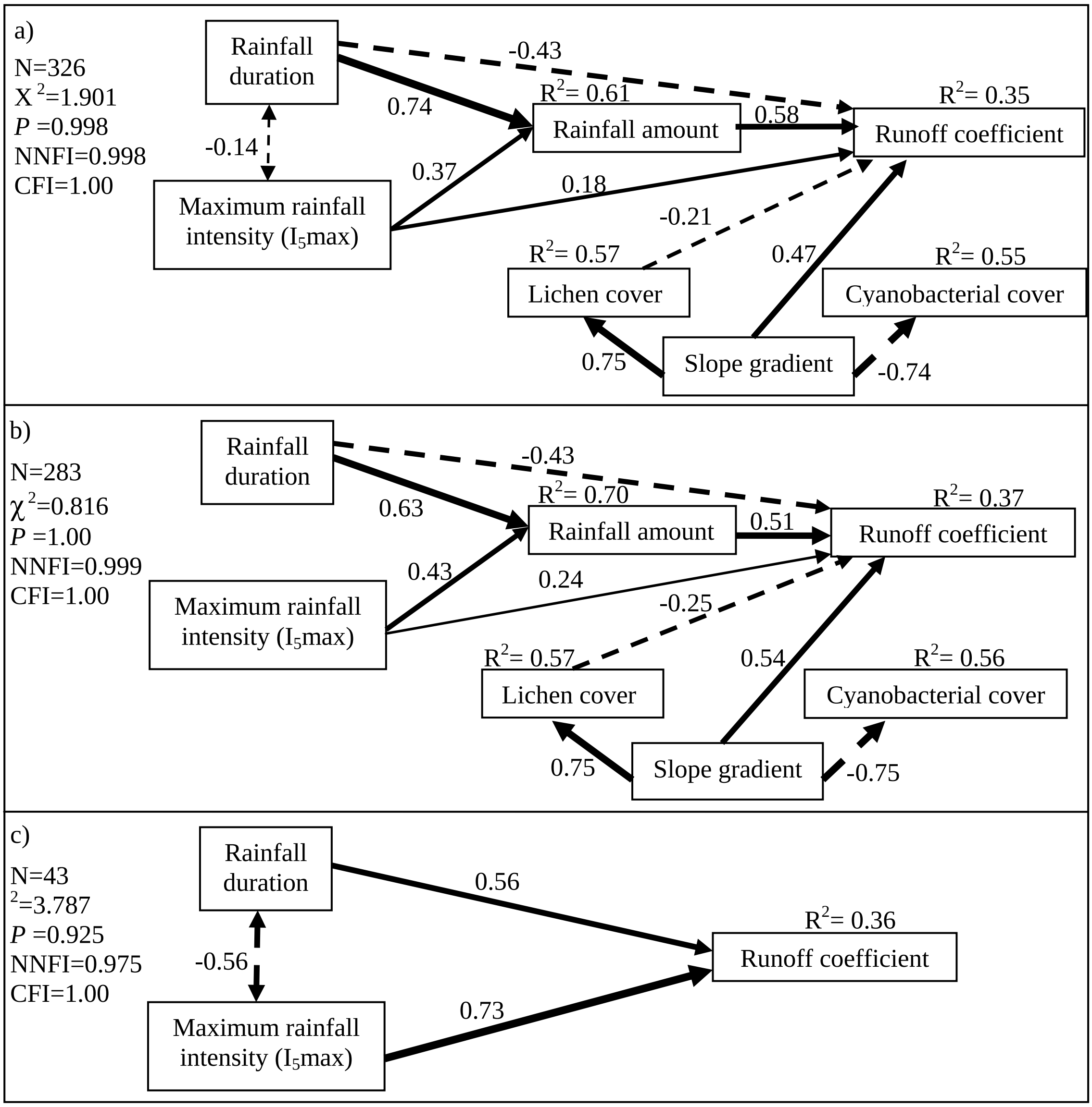

Fig. 5. Small hillslope scale runoff SEM model, including a) all the events registered during the studied period (September 2008-December 2010), b) low-intensity events and c) high-intensity events. Continuous lines show positive and significant effects. Dashed lines show negative effects. The strength of the path is represented by the line thickness. Non significant paths are omitted (see Fig. 2 for our *a priori* model). Fit statistics (nonnormed fit index, NNFI; comparative fit index, CFI; *P*; $\chi 2$) and sample size (*N*) are given at the upper-left corner of each model.
*I_5max is the maximum 5-min rainfall intensity.

DISCUSSION

The good fit of our models on both spatial scales confirms that our hypotheses about the causal relationships controlling runoff on biologically crusted soils are supported by the data observed. Soil surface-related components, such as BSC cover and topography, rainfall characteristics, particularly rainfall intensity, and the spatial scale at which these factors interact, condition runoff yield in this type of semiarid ecosystem. As expected, rainfall characteristics were the main factors driving runoff generation followed to a lesser extent by the presence and composition of BSCs. The influence of this biological component was conditioned by the interaction between the type of BSC and the type of rain event.

Relationship between biological soil crusts and runoff

It has been suggested that the spatial variability in runoff is mainly determined by the spatial patterns of soil surface properties (Arnau-Rosalén et al., 2008; Cantón et al., 2011). Among these properties, the presence of BSCs is a critical factor influencing water redistribution in semiarid areas (Alexander and Calvo, 1990; Li et al., 2008; Cantón et al., 2011; Maestre et al., 2011). After monitoring runoff under natural rainfall in plots with varying cover of lichens and cyanobacteria for over two years, we found that runoff decreased with increased lichen cover at both microplot and small hillslope scales, when rainfall intensity was low (Figs. 4b and 5b). A negative relationship was found between lichen and cyanobacterial cover (Fig. 4a) which can easily be explained by BSC dynamics in semiarid ecosystems. As BSC succession advances, later successional species like lichens become established and replace the pioneer cyanobacterial component (Lázaro et al., 2008).

Several authors have documented the influence of the type of BSC on the infiltration and runoff response of biologically crusted surfaces (Alexander and Calvo, 1990; Warren, 2003a; Eldridge et al., 2010; Chamizo et al., 2012b). Previous high- intensity rainfall simulations (50 mmh^{-1}) conducted in the same study area in microplots (0.25 m^2) with different types of BSCs showed that infiltration increased with cyanobacterial biomass and as later-successional species colonised the BSC, but that late-successional BSCs of crustose and squamulose lichens generated low infiltration rates and runoff levels similar to those of physical soil crusts (Chamizo et al., 2012b). Other authors have also found reduced infiltration with increased cover of crustose and squamulose lichens in experiments using rainfall simulations (Alexander and Calvo, 1990) or infiltrometers (Eldridge et al., 2010). These low infiltration rates are attributed to the hydrophobic properties of such lichens (Souza-Egipsy et al., 2002) and to their ability to block soil pores when wet (Warren, 2003a). Despite their hydrophobic properties, these BSCs can reduce runoff by two mechanisms: 1) lichen surfaces are discontinuous, and when they dry, they crack, allowing water to infiltrate. This effect would be enhanced at coarser spatial scales, as the possibility for runoff infiltration along the soil surface increases (Puigdefábregas et al., 1998; Wilcox et al., 2003; Cantón et al., 2011; Mayor et al., 2011). This could be the reason why we found a stronger negative relationship between lichen cover and runoff at small hillslope (path coefficient = -0.21) than at microplot scale (path coefficient= -0.11) (Figs. 4a and 5a); 2). Infiltration is controlled by the interaction of water residence time on a soil surface and the permeability of that surface (Eldridge and Greene, 1994a). In this sense, lichen BSCs could enhance infiltration by increasing soil surface roughness and water storage capacity (Rodríguez-Caballero et al., 2012). Since lichens generate rougher surfaces than cyanobacteria (Rodríguez-Caballero et al., 2012), they are expected to be more effective in reducing runoff than the smoother cyanobacterial BSCs. This seems especially feasible in the case of squamulose and foliose lichens such as *Squamarina lentigera* or *Cladonia convoluta* which present an extremely rough surface. In addition, surface microtopography is a scale-dependent variable. Álvarez-Mozos et al. (2011) showed that surface storage, which depends on soil surface roughness, significantly depends on the length of the profile, the size of the plot being positively correlated with storage values found. We found a greater reduction in infiltration with increased lichen cover in the small hillslope plots (Fig. 5a) than in the microplots (Fig. 4a). It is therefore possible that at very small spatial scales, the effect of BSC microtopography on runoff is underestimated, and other factors, such as BSC hydrophobicity or reduction of porosity due to pore clogging when BSCs get wet become more relevant, or even negate the effect of microtopography. But as the scale becomes larger, microtopography induced by BSCs, especially well-developed BSCs, such as lichens, gains importance and becomes the key factor determining infiltration in BSCs (Rodríguez-Caballero et al., 2012). This would also explain the lower variance in runoff explained at microplot (26%) than at small hillslope scales (37%) in low-intensity rainfalls. Moreover, Rodríguez-Caballero et al. (2012) reported a significant negative relationship between soil surface water storage and runoff coefficient that decreased as rainfall intensity increased. Probably because of this, we found a negative effect of lichen cover on runoff in low-intensity rainfall (Fig. 4b and 5b), but no significant effect on runoff in high-intensity rainfall (Fig. 4c and 5c). When rain is intense, water storage in soil depressions lasts for a very short time before overland flow runs downslope. Thus, the role of soil surface roughness promoted by BSCs might be overridden by the effect of rainfall intensity. Similarly, Cantón et al. (2004b) suggested that the hydrological behaviour of crustose and squamulose lichens could depend on rainfall intensity: at low intensities, they appeared to favour infiltration and increase soil moisture, whereas at high intensities, they appeared to favour runoff. Faust (1970), studying the effect of rainfall intensity on infiltration of cyanobacteria-dominated BSCs, found that after applying high rainfall intensities of 25 mm h^{-1} and 50 mm h^{-1}, the last slightly increased runoff regardless of the presence of BSCs and that the increase in runoff was higher in fine than in coarse-textured soil. These results were attributed to disruption of the BSC and detachment of soil particles under very intense rain, which would lead to clogging soil pores and consequent reduction in infiltration (reviewed in Warren, 2003b).

Relationship between the slope gradient and runoff

The influence of slope gradient on runoff depended on the spatial scale analysed. It had a significant influence on runoff at small hillslope scales (Fig. 5), but did not influence runoff at the microplot scale (Fig. 4). Other authors have also reported no effect of slope on runoff at microplot spatial scales (Calvo-Cases et al., 1991; Solé-Benet et al., 1997; Chamizo et al., 2012b). In the hillslope plots, increased slopes significantly increased runoff. It is well known that steeper slopes reduce the time water is stored in soil depressions and increase overland flow rates, thereby increasing runoff yield. It should be pointed out that the slope gradient between the microplots and the small hillslope plots might span the threshold separating hillslopes and pediments (see Section 3.1), thus suggesting that, while the slope gradient would represent a key factor controlling overland flow on hillslopes, it would have a minor effect in pediments, where other factors would have a more important role in controlling runoff yield. On the other hand, although having a direct positive effect on runoff, the slope gradient had an indirect negative effect on runoff through its positive causal effect on lichen cover (Fig. 5). Cantón et al. (2004a) found that topography strongly controlled ground cover in this area and the occurrence of white terricolous crustose lichens on relatively steep slopes. Nevertheless, the positive relationship between slope and runoff in the hillslope plots disappeared with high rainfall intensities (Fig. 5c), suggesting that under intense events, the effect of the slope gradient on runoff could also be overridden by the effect of rainfall intensity.

Relationship between rainfall characteristics and runoff

As expected, rainfall characteristics were the main factors explaining runoff variance. Most rainfall events recorded during our study period were light and low intensity, as reported by previous studies which describe two main types of rainfall events at this site: brief, high-intensity storms and longer, low-intensity rain lasting several hours (Cantón et al., 2002). Thus, when the SEM model was applied to all events or only to low-intensity events, which were the majority during the study period, the relationship between rainfall duration and runoff coefficients was negative (Figs. 4a and 4b, Figs. 5a and 5b), since longer events were less intense and generated less runoff than shorter but more intense events. Also because of this, rainfall duration was negatively correlated with the maximum 5-min-rainfall intensity (Figs. 4a and 5a), as events with higher rainfall intensities in the study area were usually related to shorter-duration events. Increased rainfall intensity and duration increased the amount of rainfall (Figs. 4 and 5), thus increasing runoff generation. In low-intensity events, rainfall intensity had little (Fig. 5b) or no effect (Fig. 4b) on runoff and the total amount of rain exerted a stronger influence. Low-intensity events are usually long and characterised by several pulses of different magnitudes within the same event with discontinuous runoff (Cantón et al., 2002), so that the main mechanism for runoff generation is the mixed model which combines saturated and Hortonian overland flow (Mayor et al., 2009, 2011). In intense events, the amount did not exert a significant effect on runoff, and rainfall intensity was the main factor controlling runoff (Figs. 4c and 5c), as the main mechanism for runoff generation in these intense events is the Hortonian overland flow or infiltration-excess mechanism (Cantón et al., 2002; Mayor et al., 2011). Within these high-intensity events, longer rainfall duration had a significant positive effect on runoff (Figs. 4c and 5c). In agreement with our findings, Mayor et al. (2011) suggested that amount of rainfall could be a good predictor of runoff in low-intensity events, which are the majority in semiarid areas, whereas rainfall intensity could be a good predictor of runoff in the case of high-intensity rainfalls.

Whereas some studies have reported significant influence of antecedent soil moisture on infiltration-runoff at microplot scales (Mayor et al., 2009; Chamizo et al., 2012b), others have found no relationship between antecedent moisture and runoff at microcatchment scales in this semiarid system (Cantón et al., 2001). Our model did not find a causal relationship between antecedent moisture and runoff coefficients at any of the two scales studied. It is worth noting that lack of causal effect does not necessarily mean that antecedent soil moisture does not influence runoff coefficients. Two possible reasons could explain this unexpected finding: 1) most rain occurred in autumn and winter, and antecedent soil moisture was relatively high in all events (between 14 and 22%); 2) intense rains, which generated higher runoff, very often occurred after summer when soil was dry.

Consequently, high antecedent soil moisture was not related to high runoff coefficients.

In conclusion, our results support most of our hypotheses and highlight the necessity of simultaneously taking into consideration very different sources of variation, such as BSC cover, topography and rainfall characteristics, and considering direct and indirect causal links among these factors for a complete picture of runoff in semiarid ecosystems. BSC cover and development, the type of rainfall event and the spatial scale at which these factors interact, have been identified as key components in assessing runoff in semiarid ecosystems. In low-intensity rainfall, characteristics such as rainfall amount and some soil surface features, such as lichen BSC cover, are essential factors in determining runoff yield. Moreover, the reduction in runoff with increased BSC development found demonstrates that recovery of BSCs after human disturbances, in terms of increased cover and growth of later-successional species (lichens), has important implications on soil hydrology. In heavy rain, rainfall intensity is the critical factor responsible for runoff yield, and neither BSC cover nor slope have a significant effect on runoff. Our results suggest that the consideration of BSC-crusted surfaces, particularly by well-developed BSCs, should improve runoff modelling in semiarid areas similar to ours for low-intensity rainfall events, but it would be less important when they are high-intensity. However, it should be remarked that this would only be from the point of view of runoff. BSCs are widely recognized as strong protective covers against soil erosion, and thus their influence on erosion dynamics should be assessed under variable rainfall conditions, and especially under high rainfall intensities, as these events are responsible for the most sediment yield in arid and semiarid ecosystems.

CHAPTER IV

Evaporative losses from soils covered by physical and different types of biological soil crusts

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ABSTRACT

Evaporation of soil moisture is one of the most important processes affecting water availability in semiarid ecosystems. Biological soil crusts (BSCs), which are a widely distributed ground cover in these ecosystems, play a recognized role on water processes. Where they roughen surfaces, water residence time and thus infiltration can be greatly enhanced, whereas their ability to clog soil pores or cap the soil surface when wetted can greatly decrease infiltration rate, thus affecting evaporative losses. In this work, we compared evaporation in soils covered by physical crusts, BSCs in different developmental stages, and in the soils underlying the different BSC types. Our results show that during the time of the highest evaporation (Day 1), there was no difference among any of the crust types or the soils underlying them. On Day 2, when soil moisture was moderately low (11%), evaporation was slightly higher in well-developed BSCs than in physical or poorly-developed BSCs. However, crust removal did not cause significant changes in evaporation compared to the respective soil crust type. These results suggest that the small differences we observed in evaporation among crust types could be caused by differences in the properties of the soil underneath the BSCs. At low soil moisture (<6%), there was no difference in evaporation among crust types or the underlying soils. Water loss for the complete evaporative cycle (from saturation to dry soil) was similar in both crusted and scraped soils. Therefore, we conclude that for the specific crust and soil types tested, the presence or the type of BSC did not greatly modify evaporation with respect to physical crusts or scraped soils.

Keywords: physical soil crust, biological soil crust, development, evaporation, microlysimeters.

INTRODUCTION

Water is the primary factor limiting productivity in desert ecosystems (Warren, 2003a). In these ecosystems, evapotranspiration is the key component of the water balance (Domingo et al., 2001; Cantón et al., 2010), such that over 90%

of annual precipitation can be lost by this process (Zhang et al., 2001). Compared to transpiration, evaporation is expected to represent the largest water loss in environments with sparse vegetation cover (Raz-Yaseef et al., 2010). Evaporation in deserts is mainly affected by plant cover and composition and biological soil crusts (Belnap et al., 2005). These crusts consist of an association of soil particles with a complex community formed by cyanobacteria, fungi, algae, lichens, mosses and liverworts. Biological soil crusts (BSCs) have a very wide distribution and provide 40-100% of the ground cover in areas with relatively sparse vascular plant cover (St. Clair et al., 1993) such as hyperarid, arid, semiarid, sub-humid, alpine and polar regions (Belnap, 2006). The establishment of BSCs starts when early-successional cyanobacteria and fungi colonise the soil surface, followed by pioneer lichens and mosses. Once soil conditions are stable enough, later-successional lichens and mosses colonise as well (Johansen, 1993; Lázaro et al., 2008).

The role of BSCs in arid and semiarid areas is widely recognized. They influence different aspects of the soil important to the water regime, including soil porosity, absorptivity, roughness, aggregate stability, soil texture, pore formation and water retention (Campbell, 1979; Brotherson and Rushforth, 1983; Harper and Marble, 1988; Verrecchia et al., 1995; Kidron et al., 1999; Belnap et al., 2005; Belnap, 2006). Their influence on infiltration and runoff is complex and research on this topic show contradictory results. On one hand, BSCs can reduce infiltration through swelling of polysaccharides of cyanobacterial sheaths, thus blocking soil pores (Verrecchia et al., 1995). On the other hand, they can increase infiltration through their effects on microtopography (Eldridge and Greene, 1994a) or by their formation of aggregates, which increases soil macroporosity (Warren, 2003a). Similar to their effect on infiltration and runoff, conflicting hypothesis have been suggested regarding the effect of BSCs on evaporation. Whereas they can reduce evaporation by capping the soil surface and reducing porosity (Kidron et al., 1999), they can alternatively increase evaporation by darkening the surface as well as increasing soil surface roughness and thus the surface area for potential evaporation (Belnap et al., 2005). However, despite the important effects of BSCs on hydrological processes, there are only a few studies directly measuring how they influence runoff generation and infiltration (reviewed in Belnap, 2006) or evaporation (Larson and Kershaw, 1976; Harper and Marble, 1988; George et al., 2003; Xiao et al., 2010).

According to the Intergovernmental Panel on Climate Change report (2007), global average surface temperature will increase 1.8–4.0 ºC and precipitation regimes (intensity and timing) will be modified by the end of this century, both of which will have important consequences in water processes (Niu et al., 2011). Moreover, climate change is likely to alter species composition in BSCs, as increased temperature and/or changed summer precipitation can reduce cover of some species (Bowker et al., 2002; Belnap et al., 2004; Belnap et al., 2006). The consequences of this change in crust composition can greatly affect water processes (George et al., 2003). However, it is not known how different successional stages of BSCs might affect evaporation and this question highlights the importance of considering a gradient from less to more developed BSC types so we may more accurately determine how they affect the evaporative process.

The objective of this study was to determine the evaporative losses in different soil crust types, including physical crusts, BSCs in different developmental stages, and in soils underlying the different BSC types. Specifically, our goals were to 1) compare evaporative losses of physically or biologically-crusted soils to soils where these crusts were scraped away and 2) examine if the crust type and the developmental stage of the BSC influenced evaporation. This work will contribute to a better understanding of how both physical crusts and BSCs affect evaporative loss, and thus soil moisture, in semiarid areas.

MATERIAL AND METHODS

Evaporation measurements were conducted in four representative crust types at El Cautivo experimental site (Tabernas Desert) (Fig. 1a): 1) a physical soil crust (P) formed by raindrop impact, 2) an early-successional BSC that presents an incipient colonization by cyanobacteria (IC), 3) a cyanobacteria-dominated

BSC (C), where cyanobacteria coverage represents around 80% and a high proportion of pioneer lichens (*Collema spp*) are present, and 4) a lichen-dominated BSC (L) mainly covered by *Squamarina lentigera* (80%). We measured evaporation using microlysimeters containing these crust types.

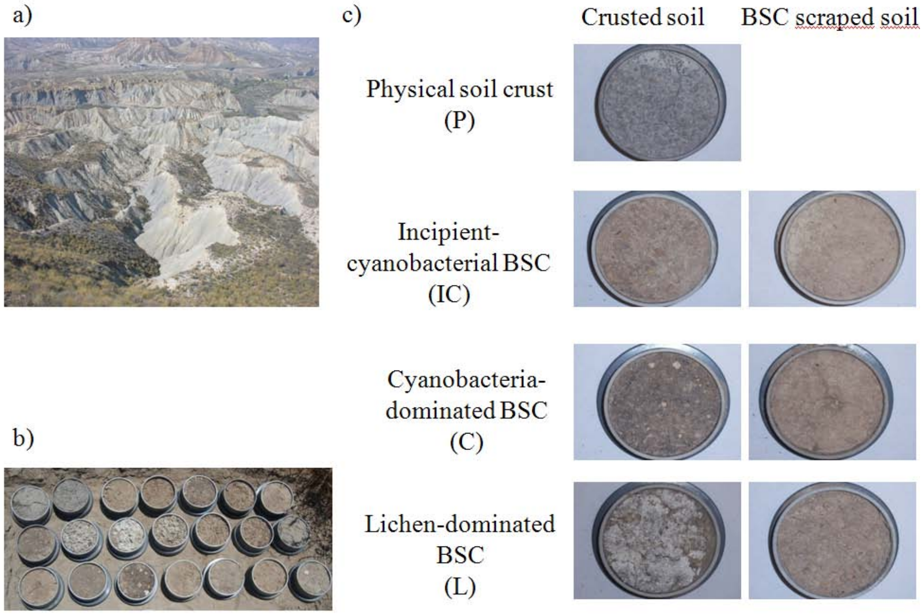

Fig. 1. a) El Cautivo experimental site (Tabernas Desert, SE Spain), b) microlysimeters placed in the field and c) micro-lysimeters containing the different crust types and scraped soils.

Determination of some properties of the crust and the underneath soil

Three samples of each crust type (0-0.005 m depth; surface layer) and the soil underneath (0-0.05 m depth) were collected in an area adjacent to the microlysimeters for analysis of their properties. Exopolysaccharides from the crust were extracted with ethanol, hydrolyzed to glucose, and analysed using a Synergy HT Multi-Detection Microplate Reader (BioTek Instruments, Inc., Vermont, USA) at 480, 486 and 490 nm (Dubois et al., 1956). Different glucose concentrations were plotted against absorbance to obtain a standard curve of glucose solutions and results were expressed as micrograms of glucose per gram of dried crust sample at the 480nm wavelength. In addition, we measured other factors in the underlying soils that influence soil water-holding capacity (WHC), including soil particle-size distribution (using the Robinson's pipette method; Gee and Bauder, 1986); total organic carbon content (OC) by oxidation with dichromate (Walkley and Black, 1947); and WHC at −33 and −1500 kPa with the Richard's pressure-membrane extractor.

Soil surface roughness was measured by obtaining the surface area of the soils using a Terrestrial Laser Scanner Leica ScanStation 2 (Leica Geosystems AG, Heerbrugg, Switzerland). The instrument was mounted on a tripod perpendicularly to the surface of the microlysimeters and the height points of the surface were registered every 1 mm. From these points, the actual area of each microlysimeter was determined using the software SAGA 2.0.5 (Free Open Source Software, Hamburg, Germany). A tortuosity index was then calculated by dividing the actual and the projected area of the microlysimeter (0.00785 m^2). Thus, this index is a measure of the surface roughness of the soil surface contained within each microlysimeter, and a higher index value indicates a higher soil surface roughness. We also measured the effect BSCs had on soil temperature in the field. Temperature probes (ECT soil temperature sensors, Decagon Devices, Inc., Pullman, Washington) were placed 0.02 m under the crusts in the field immediately following a rain storm that occurred one week after the evaporation experiment was performed.

Evaporation measurements

Evaporation measurements were conducted in late spring in 0.05 m-radius and 0.05 m-height polyvinyl chloride (PVC) microlysimeters containing the different crust types. The design and installation of the microlysimeters was made following the methodology proposed by Daamen et al. (1993). Samples of the crust types were selected at a piedmont very close to each other to ensure that topographic and ambient conditions from where they were collected were similar. The microlysimeters were inserted into the crust types one month before the evaporation measurements were conducted to allow stabilization. For our experimental treatments, we also removed (by scraping) the surface crust (around 0.005 m thickness) from all but the physical crust type, thus creating three additional experimental units: 5) incipient cyanobacteria-scraped (IC-S), 6) cyanobacteria-scraped (C-S), and 7) lichen-scraped (L-S). We did not apply the scraping treatment to the physical crust as it is an abiotic crust with a minimal cover of living organisms. The crust removal was conducted just before starting the evaporation measurements. Three PVC collars were inserted per experimental unit (N = 21 collars).

Before their extraction from the soil (in order to conduct the evaporation measurements), the microlysimeters and the surrounding soil were saturated to at least 0.1 m depth. The microlysimeters were then carefully removed from the soil and their bases sealed to a PVC sheet that perfectly fitted the microlysimeters (Fig. 1c). The scalping treatment was applied once the microlysimeters were extracted from the soil and sealed. All microlysimeters were then immediately placed in the field with their top part close to the ground surface (Fig. 1b) and evaporation measurements started at about 8:00 local time. The same methodology was employed in previous works in our study areas (Domingo et al., 1999; Villagarcía et al., 2010). Evaporation measurements were taken from the time of saturation to when soils were dry. They were manually weighed using a calibrated balance with a precision of 0.1 g. The average weight of the microlysimeters was 810 ± 75 g. For the first two days, the lysimeters were weighed every two and half hours from sunrise to sunset to examine daily curves of evaporation. To establish the curve from saturation to dry soil, they were weighed once in the morning (at the same first hour as the previous days) until the weight loss was less than 3 g day^{-1}(several days). Once the field experiment was finished, the microlysimeters were taken to the laboratory and soil samples were dried in an oven at 105ºC for 48h. Gravimetric water content of each sample was defined as the difference between the weight of the microlysimeter under saturation conditions (initial weight after wetting and extracting the microlysimeter from the soil) and its dry weight. Evaporation results were expressed as the ratio between water loss (mm) and the initial water content of the microlysimeter (mm), hereafter defined as the “evaporation ratio”.

Data analysis

Significant differences were tested by using a one-way ANOVA and the LSD´s post-hoc test. Significance was established at $P<0.05$. The dependent variables tested were 1) the physico-chemical characteristics analysed, including the crust exopolysaccharide content and soil texture, OC and WHC of the underlying soils; 2) the tortuosity index; 3) gravimetric water content of the microlysimeters under saturation conditions; and 4) variables derived from the evaporation measurements, including a) evaporation at different times of the day during the first two days, b) evaporation from sunrise to sunset during the first two days, and c) evaporation between days across the drying curve (saturation to dry soils). STATISTICA 8.0 (StatSoft, Inc., Tulsa, Oklahoma, USA) was used to analyse the data.

RESULTS

Crust and soil properties

As can be seen in Table 1, there were significant differences in the physico-chemical characteristics of the crusts and the underlying soils. Exopolysaccharide content was significantly higher in lichen than cyanobacterial BSCs and significantly higher in these two than physical crust and incipient-cyanobacterial BSCs. Soil texture was similar under the different crust types, with more than 65% of soil fines and ~30% sand. OC was higher in the soil under lichen than cyanobacterial BSCs and higher under both of these crusts than under physical crust and incipient-cyanobacterial BSCs. Soils under lichen and cyanobacterial BSCs also had higher water holding capacity than soils under physical crusts and incipient-cyanobacterial BSCs. Thus, the available water for plants in the soil, calculated as the difference between gravimetric water content at field capacity (-33 kPa) and at the wilting point (-1500 kPa), was significantly higher under lichen and cyanobacterial BSCs than under physical crusts and incipient-cyanobacterial BSCs.

Table 1. Mean and standard deviation of exopolysaccharide content in the different crust types, and soil texture, total organic carbon (OC) and available water for plants (difference between gravimetric water content at field capacity and at the wilting point) in the top 0.05 m of soil below the different crust types: physical (P), incipient-cyanobacterial (IC), cyanobacteria-dominated (C) and lichen-dominated (L) crusts. Different letters indicate significant differences within a column.

	Crust	Soil below the crust (0-0.05 m depth)			
	Exopolysaccharide content (ug glucose g soil^{-1})	Sand (%)	Silt + clay (%)	OC (%)	Available water (kg kg^{-1})
P	^{a}35.0 ± 17.9	^{a}34.9 ± 5.6	^{a}65.1 ± 5.6	^{a}0.49 ± 0.09	^{a}11.55 ± 1.74
IC	^{a}54.2 ± 18.4	^{a}32.5 ± 2.1	^{a}67.5 ± 2.1	^{a}0.54 ± 0.14	^{a}14.36 ± 3.24
C	^{b}533.6 ± 155.9	^{a}30.3 ± 7.8	^{a}69.7 ± 7.8	^{b}0.79 ± 0.02	^{b}18.78 ± 3.44
L	^{c}1419.9 ± 56.2	^{a}27.4 ± 3.2	^{a}72.6 ± 3.2	^{c}1.16 ± 0.11	^{b}17.36 ± 1.80

Table 2 shows the tortuosity index for the different crust types before and after crust removal, and gravimetric water content in the crust types and scraped soils under saturation conditions. The lichen crusts showed significantly higher tortuosity/roughness than the physical and incipient-cyanobacterial crusts. When comparing the crusted and its respective scraped soil type, only the lichen-scraped soils showed marginally significant lower roughness than the lichen-crusted soils (P=0.08). There were no significant differences in roughness among the scraped soils (P=0.31). Water content under saturation conditions, although not significantly different, tended to be somewhat higher in the lichen and cyanobacterial BSCs than in physical crusts and incipient-cyanobacterial BSCs. When comparing the scraped soils, incipient cyanobacteria-scraped samples had significantly lower water content than the cyanobacteria-scraped and lichen-scraped samples. No significant differences were found between the crusted and its respective scraped soil.

Table 2. Mean and standard deviation of the tortuosity index (ratio between the actual area of the soil surface and the projected area of the microlysimeter) and gravimetric water content under saturation conditions (kg kg^{-1}), for the types of crusted and scraped soils. Different letters indicate significant differences within a column. P: physical crusts; IC: incipient-cyanobacterial crusts; C: cyanobacteria-dominated crusts, and L: lichen-dominated crusts.

	Tortuosity index m^2 m^{-2}		Gravimetric water content kg kg^{-1}	
	Crusted soil	Scraped soil	Crusted soil	Scraped soil
P	^{a}1.13 ± 0.05		^{a} 0.20 ± 0.01	
IC	^{a}1.11 ± 0.02	^{a}1.15 ± 0.02	^{a} 0.19 ± 0.03	^{a} 0.17 ± 0.05
C	^{ab}1.23 ± 0.04	^{a}1.21 ± 0.05	^{a} 0.23 ± 0.04	^{b} 0.24 ± 0.01
L	^{b}1.33 ± 0.13	^{a}1.14 ± 0.04	^{a} 0.22 ± 0.02	^{b} 0.23 ± 0.01

Soil temperatures under the different crust types

Fig. 2 shows soil temperature in the wet soil under the BSCs. During the night, temperatures were slightly lower under the incipient-cyanobacterial BSC than under the cyanobacterial and lichen BSCs (1ºC difference). Once solar radiation began to heat the soil surface, soil temperatures increased more rapidly in the incipient-cyanobacterial and, especially, in the cyanobacterial BSC, compared to the lichen BSC. Between around 12:00 and 19:00 local time, the difference between the minimum temperature (lichen crust) and the maximum temperature (cyanobacterial crust) observed exceeded 2ºC, reaching a maximum peak around 13:00 local time where the difference in temperature between both BSCs ranged from 4.8 to 5.8 ºC.

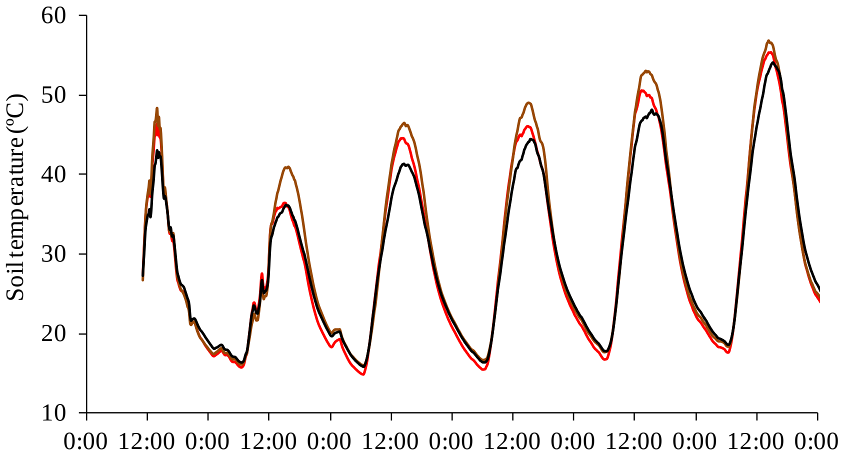

Fig. 2. Soil temperature at 0.02 m depth under the incipient-cyanobacterial (red line), the cyanobacterial (brown line) and the lichen-dominated (black line) BSCs after a rain in late spring.

Evaporation of crusted and uncrusted soils

Diurnal ambient conditions and gravimetric water content (kg kg^{-1}) of the microlysimeters during the days of the experiment are shown in Table 3. After wetting, mean evaporative loss in the experimental units (both unscraped and scraped) was 70.8 ± 13.6 g during the first day and 27.8 ± 10.0 g during the second day. For the rest of the days, evaporative loss was around 11.5 ± 2.7 g. After five days, the loss of weight of the microlysimeters was no longer significant (< 3 g day^{-1}; average dry weight of the samples was 438 ± 67 g).

Table 3. Mean and standard deviation of different ambient condition variables and gravimetric water content of the microlysimeters during each day of the experiment.

	Wind speed ms^{-1}	Air temperature ºC	Relative humidity %	Gravimetric water content kg kg^{-1}
Day 1	1.06 ± 0.46	30.72 ± 2.34	30.94 ± 6.04	0.21 ± 0.03
Day 2	1.13 ± 0.36	27.60 ± 2.36	47.88 ± 9.78	0.11 ± 0.02
Day 3	1.52 ± 0.67	30.53 ± 2.34	36.40 ± 9.42	0.06 ± 0.01
Day 4	1.39 ± 0.64	30.97 ± 2.15	30.94 ± 6.31	0.04 ± 0.01
Day 5	1.59 ± 0.50	28.81 ± 2.99	35.29 ± 14.86	0.01 ± 0.01

Fig. 3 shows the daily curve of evaporation during the first two days in the crusted and scraped soils. Daily evaporation followed the typical curve, with the maximum evaporation peak at midday. During the first day, when soil water content was high, there was no significant difference among any of the crust types or their underlying soil. During the second day, when soil moisture was moderately low, the more developed BSCs (C and L) had significantly higher evaporation than the physical crusts and incipient-cyanobacterial BSCs, especially during the time of higher solar radiation. The same response was found in the scraped soils, with lower evaporation throughout the day in the incipient cyanobacteria-scraped than in the cyanobacteria-scraped and lichen-scraped samples.

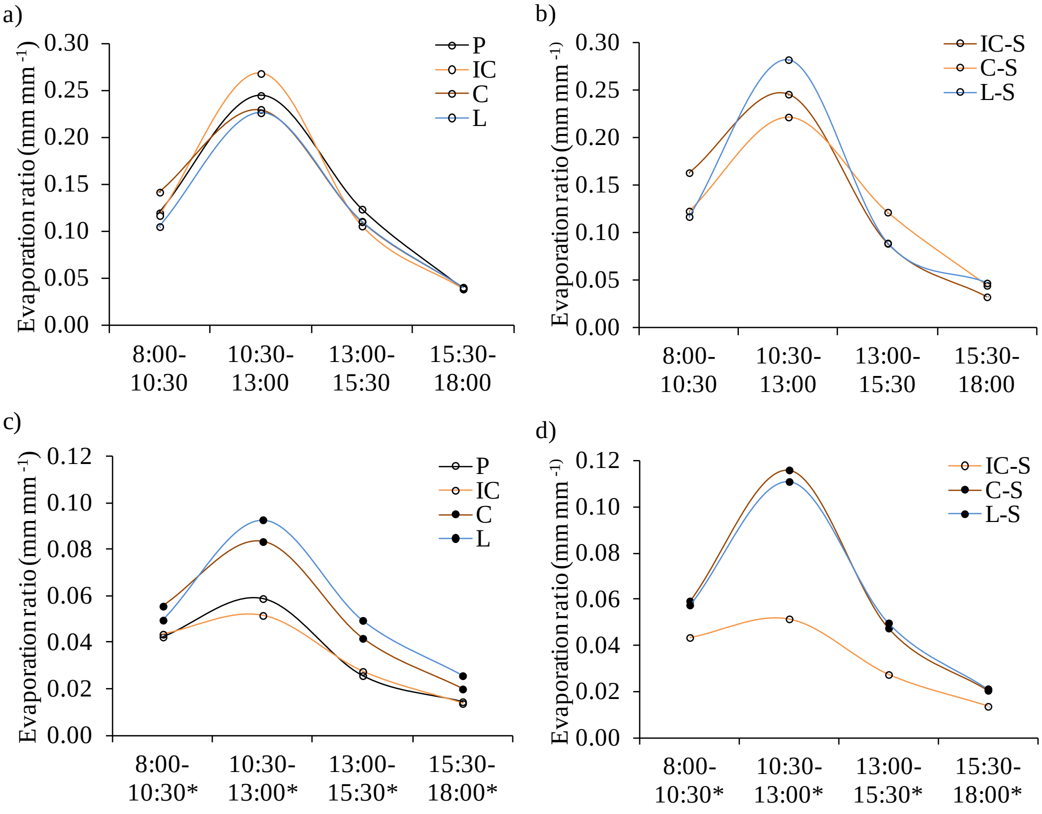

Fig. 3. Daily evaporation curve for Day 1 in the crusted (a) and scraped soils (b), and for Day 2 in the crusted (c) and scraped soils (d). Time intervals at which evaporation differed among soils are indicated with a "*" next to the time label. Filled-points indicate significant differences when compared to non-filled points at each time interval. P: physical crusts; IC: incipient-cyanobacterial crusts; C: cyanobacteria-dominated crusts, and L: lichen-dominated crusts.

Fig. 4 shows the evaporative loss in crusted and scraped soils from sunrise to sunset during the first two days, while Fig. 5 shows the complete evaporative cycle in the different crusted and scraped soils. The average water loss in the microlysimeters from saturation to dry soil was 121.5 ± 23.4 g (11.9 ± 2.1 mm). During the first day, all the microlysimeters lost approximately half of their water content. There were no significant differences in evaporation among the different crusted (*P*=0.69) and scraped (*P*=0.84) soils (Fig. 4). Between the crusted and its respective scraped soil, only the lichen BSC showed significantly lower evaporation than the underlying lichen-scraped soils (*P*=0.03).

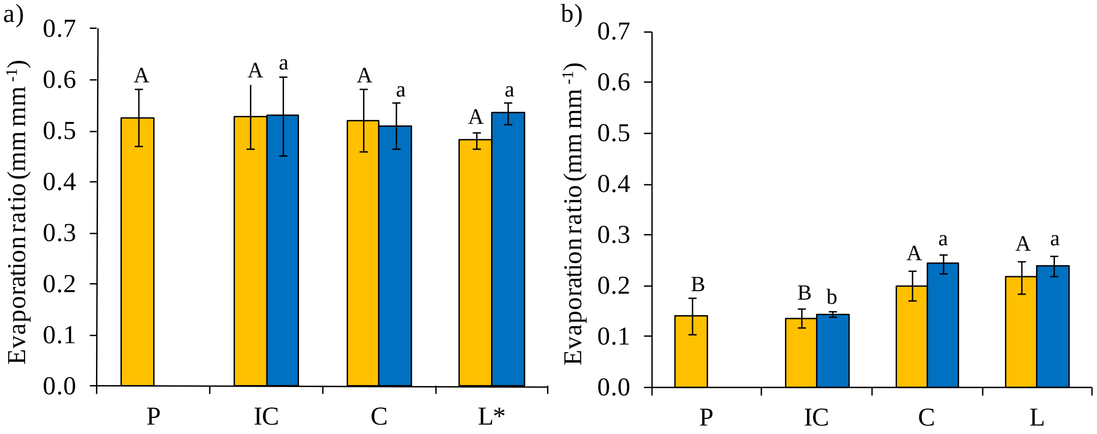

Fig. 4. Evaporative loss from sunrise to sunset in the crusted and scraped soils during a) the first day (gravimetric water content [kg kg^{-1}] was 0.21 ± 0.03), and b) the second day (gravimetric water content [kg kg^{-1}] was 0.11 ± 0.02) after soil saturation. Significant differences in evaporation among the crust types (yellow bars) are indicated by different capitalized letters. Significant differences in evaporation among the scraped soils (blue bars) are indicated by different small letters. Significant differences between the crusted and its respective scraped soil are indicated with a "*" next to the symbol of the crust type. P: physical crusts; IC: incipient-cyanobacterial crusts; C: cyanobacteria-dominated crusts, and L: lichen-dominated crusts.

During the second day, and thus at a lower soil moisture, the microlysimeters lost between 14 and 22% of their initial water content. On this day, evaporation differed significantly, but only slightly, among the crust types (*P*=0.02), with physical crusts and incipient-cyanobacteria BSCs showing somewhat lower evaporation than cyanobacterial and lichen BSCs, coinciding with the response observed in the daily curve of the crusts on this day (Fig. 3). Evaporation was also higher in cyanobacteria-scraped and lichen-scraped than incipient cyanobacteria-scraped soils (*P*<0.001). When considering a given crust type, evaporation tended to be slightly higher in the scraped than the crusted soil, but differences were not significant. After approximately three days, there was an inflection point, after which the decrease in evaporation in the crusted and scraped soils was constant (Fig. 5).

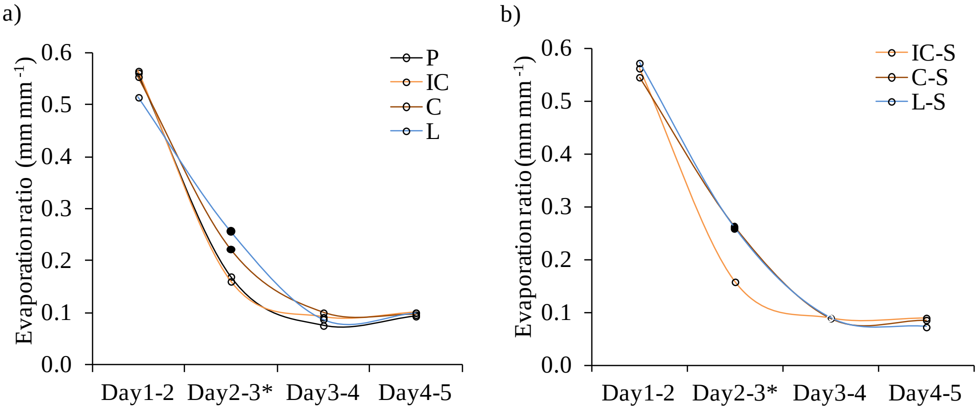

Fig. 5. Drying curve from saturation to dry soil of the crusted (a) and scraped soils (b), expressed as the ratio between the difference in weight of the micro-lysimeter between days (measured at the same time of the day) and the initial water content of the micro-lysimeter. Time intervals between days at which evaporation differed among soils are indicated with a "*" next to the day label. Filled-points indicate significant differences respect non-filled points at each time interval. P: physical crusts; IC: incipient-cyanobacterial crusts; C: cyanobacteria-dominated crusts, and L: lichen-dominated crusts.

As a result of the differences observed in evaporation among crust types during the second day, the only significantly different water losses between days among crust types occurred between the second and the third day. Between these days, the cyanobacterial and lichen BSCs and their underlying soils (C-S and L-S) showed significantly higher evaporation than the physical crusts and incipient-cyanobacteria-crusted and scraped soils (crusted soils, *P*=0.04; uncrusted soils, *P*<0.001). When comparing one crust type with its underlying soil, evaporation only differed between lichen-crusted and scraped soils between the first and the second day (*P*=0.02), where the lichen-scraped soils showed higher evaporation than the lichen-crusted soils, as also shown in Fig. 4.

DISCUSSION

Previous reviews and studies in the literature have speculated on how BSCs might affect evaporation, although few studies have actually measured this effect. It is been suggested that BSCs can reduce evaporation by 1) capping the soil surface and clogging soil pores due to swelling of exopolysaccharides in the BSCs and the presence of organisms at the surface (Campbell, 1979; Brotherson and Rushforth, 1983; Kidron et al., 1999; Belnap et al., 2005; Fischer et al., 2010) and 2) reduction of soil surface cracks, limiting pathways for water vapour to escape (Verrecchia et al., 1995). In contrast, BSCs may enhance evaporation by 1) retention of water at the soil surface by crustal organisms, 2) creating greater surface roughness that increases the surface area for potential evaporation (Belnap et al., 2005) and 3) darkening the soil surface and increasing soil temperatures compared to adjacent uncrusted soils (Harper and Marble, 1988) or light-coloured crusts (Cantón et al., 2004b). Evaporation can also vary depending on crust morphology or water uptake and storage by thalli and rhizines of some moss and lichen species (Larson and Kershaw, 1976; Larson, 1981). However, it is been also suggested that water loss and gain in BSCs is a passive process, as they do not possess mechanisms to control the water balance (Blum, 1973).

We expected higher evaporation in the more developed crusts, given their higher initial water content and higher roughness (Table 2) which would provide higher surface area for evaporation. However, our results show little difference in evaporation rates between the different crust types and underlying soils. On the first day, when up to 55% of the water from saturated soils was lost, there was no significant difference among our experimental units, with the exception of lichen-crusted versus lichen-scraped soils (Fig. 4). It was only during the second day, when soils had moderately low soil moisture (~11%, Table 3), that we observed a higher evaporation rate in well-developed crusts (C and L) compared to poorly-developed crusts (P and IC), but the absolute differences were low. The removal of the crust did not result in any significant changes in evaporation. Under very low soil moisture conditions (after Day 2, <6% soil moisture, Table 3), evaporation was again similar in the crusted and scalped soils.

Soil surface roughness appeared to have no effect on evaporation rates (Table 2). Rougher crusts had similar evaporation rates as smoother crusts on Day 1 (Fig. 4), and on Day 2, rougher crusts (C and L) showed higher evaporation than smoother crusts (P and IC), but evaporation rates were not significantly changed when these crusts were removed and the surfaces made smoother.

Despite our expectations, higher temperatures were also not consistently associated with evaporation. Crusts that darken the soil surface could increase evaporation by increasing soil surface temperatures (Harper and Marble, 1988). However, despite temperatures being the lowest under our light-coloured lichen BSCs and highest under our dark-coloured cyanobacterial BSCs during the hottest hours of the day (Fig. 2), we observed no difference in evaporation at high and very low soil moisture between these two crust types. At moderately low moisture, both the lichen and cyanobacterial BSCs showed similar evaporation and higher evaporation than the physical crusts and incipient-cyanobacterial BSCs (see daily curves in Fig. 3). George et al. (2003) also reported no correlation between evaporation and soil temperature, with cyanobacterial crusts taking longer to dry than both lighter-coloured lichen dominated crusts and bare soils, regardless of the darker cyanobacterial crusts having the highest temperature. In contrast to our results, Cantón et al. (2004b) found higher soil moisture under white-coloured lichen crusts than under vegetation and marl surfaces (comparable to our physical crusts) in summer and attributed this to reduced evaporation caused by the white colour of the lichens and the presence of calcium-oxalate crystals in the lichen cortex.

Although there were some differences in evaporation among the types of soil crusts on Day 2 (less-developed P and IC crusts had lower evaporation than the better-developed C or L crusts), evaporation did not significantly change when the BSCs were removed. This implies that the differences in evaporation among crusts types during the second day were not due to the crust type itself, but to differences in the properties of the underlying soil. Thus, the presence of BSCs might not have a direct influence on evaporation, but rather an indirect effect by modifying the characteristics of underlying soils. Xiao et al. (2010) reported a similar result, finding evaporation rates in moss-crusted and uncrusted soils depended on underlying soil texture, not the presence of the moss.

There are many ways the presence of BSC organisms can affect underlying soils. Likely most important is their ability to improve soil structure and porosity. In this study, the exopolysaccharides content of well-developed cyanobacterial and lichen BSCs was much higher than in physical crusts (represented by marl surfaces, consisting of regolith fragments which lack any kind of soil structure) or incipient-cyanobacterial BSCs (with low biomass of crust organisms) (Table 1). Exopolysaccharides bind soil particles together (Baily et al., 1973; Schulten, 1985; Bertocchi et al., 1990), increasing the formation and stability of aggregates and thus soil porosity (Belnap, 2006; Miralles-Mellado et al., 2011). The abundance of burrowing micro-arthropods also increases with the developmental stage of BSCs (Darby et al., 2007), and this may be partially explained by the higher availability of carbon-based polysaccharides on which they feed (Mager, 2010). More soil aggregates and burrowing microfauna both increase the size and number of micro- and macropores in the soil, through which water can be more easily lost, both via infiltration and evaporation (Belnap, 2003). Moreover, increased organic matter that is also associated with greater crust development, increases the water holding capacity of soils (this study, Tongway and Ludwig, 1990), prolonging the time water can be kept on or at the soil surface, an thus contributing to a greater evaporation rate (Gao et al., 2010). Gravimetric water content under saturation conditions was higher in the lichen-scraped and cyanobacteria-scraped soils than in the incipient cyanobacteria-scraped soils (Table 2). This higher initial water content may partially explain the greater evaporative losses on Day 2. However, this difference in the evaporation rate was small and, for the complete evaporative cycle, not significantly different among the crust types or underlying soils. Two possible reasons could explain this result: 1) the influence of the crust on soil characteristics (surface roughness, temperature, porosity, etc) was not sufficient to significantly change evaporative losses or 2) the positive and negative effects of soil characteristics on evaporation counteract each other, resulting in no overall effect. This could be one or more variables offsetting each other. In the first case, soil OC and crust polysaccharides may lead to greater evaporative losses due to holding moisture at the soil surface but decrease evaporation by clogging soil pores. In the latter case, the clogging of soil pores by polysaccharides could be offset by higher surface roughness that may provide greater surface area for evaporation.

CONCLUSIONS

In this study, we examined the evaporation from different crust types and their underlying soils under specific ambient conditions. For the complete evaporative cycle, water loss in the different crusts and scraped soils tested was similar. Therefore, our results suggest that the types of BSCs used in this experiment did not greatly modify evaporation relative to physical crusts and scraped soils, although some differences were seen in soil water content at saturation. These findings have important implications for the modelling of evaporative loss in semiarid areas with similar BSCs to those in this study, as the open spaces between plants in these areas could be generally considered equivalent to bare soil and errors in the estimation of evaporation due to loss of the BSCs would be negligible. However, this is limited to modelling of soil evaporation. BSCs exert an important influence on other hydrological processes such as infiltration-runoff and soil water content. Previous work in our study areas has shown that infiltration generally increases with increased BSC development (Chamizo et al., 2012b) and, in this study, it is also reported that water content at saturation and available water for plants were greater in biological than in physical crusts and greater in well- than in poorly-developed BSCs. Thus, BSCs are likely to have a significant, and probably positive, effect on the total water balance. Nevertheless, there are limitations to our approach that need further research. For instance, most rain events are small in arid areas, and thus soils are seldom saturated, as they were in this study. In addition, it would be instructive to examine the effect of different crust types on evaporation along a gradient of varying ambient conditions, in different seasons and on different soil textures, as all these factors may influence evaporation. Given the likelihood that future climate will change the species composition of BSCs in this and other areas, it is also important these studies be extended to the new and novel BSC communities that may emerge.

CHAPTER V

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

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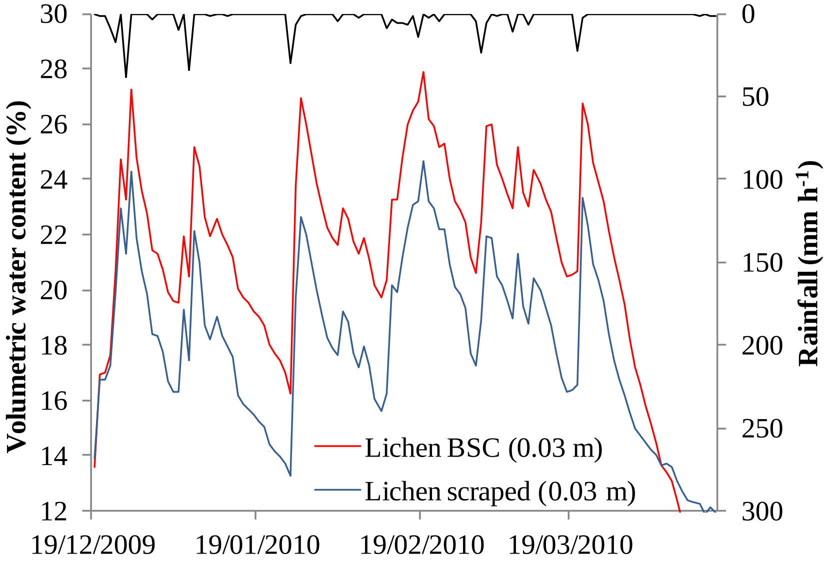

ABSTRACT

The interplant soil surfaces in most arid and semiarid ecosystems are covered by biological soil crusts (BSCs). These organisms 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 periods, removal of BSCs led to decreased soil moisture, especially in the upper layer (0.03 m), compared to soils covered by BSCs. However, no difference was found in soil moisture under either crusted or scalped soils during dry soil periods. Soil water loss was also generally faster in soils with no BSCs than in soils covered by them. The type of BSC influenced soil moisture differently depending on soil water content. During wet periods, soil water loss was faster and soil moisture lower under cyanobacterial than under lichen BSCs. On the contrary, during long periods of soil drying, lichen-crusted soils lost water faster and showed lower moisture than under cyanobacteria crusts. Decrease in soil moisture was more noticeable after removal of lichens than cyanobacterial BSCs, and more so in fine than in coarse-textured soils. Our results show the major role of the presence of BSCs, as well as the type, in soil water availability in semiarid ecosystems.

Keywords: cyanobacteria, lichen, scalped soil, soil moisture, soil water loss.

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 maximized 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 comprised of 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., 2003b), thereby affecting soil water availability (Cantón et al., 2004b), and consequently, essential ecological processes such as C and N assimilation, mineralization 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 (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 reduces erosion compared to physical crusts (Chamizo et al., 2012b). Despite their recognized 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., 2004b) 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., 2012c) 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, 2003a; Cantón et al., 2004b). 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., 2004b). 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., 2004b). 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, 2003a) 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.

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. We hypothesised that soil moisture would be higher in soils covered by BSCs than in the same soils where the BSC had been removed, 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., 2012c). 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. 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; iv) whether the influence of BSCs on soil moisture varies with soil texture.

MATERIAL AND METHODS

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 an important cover of pioneer lichens (*Collema spp, Fulgensia spp, Placynthium nigrum, Psora decipiens*, *Endocarpon pusillum*, *Toninia sedifolia*), and light-coloured lichen-dominated BSCs (Fig. 1b), predominantly composed of *Squamarina lentigera and Diploschistes diacapsis*. 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 x 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). A total of 48 moisture sensors were installed (3 probes x 2 depths x 2 treatments x 2 crust types x 2 study sites). All plots were located on flat ground to minimize 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 horizontally with the flat side of the prongs perpendicular to the surface to minimize any effect on vertical water fluxes (Fig. 1d). Installation was two 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, and therefore, calibration of the sensors for a particular soil type is unnecessary. 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 (cyanobacteria-crusted, cyanobacteria-scalped, lichen-crusted and lichen-scalped soil) 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-scraped soil) using ECT temperature probes (Decagon Devices, Inc., Pullman, Washington).

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

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 to September 2010) was analysed using generalized 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 generalized linear models (which handle non-normal data) (Bolker et al., 2008). We used GLMMs to analyse the effect of our fixed predictor factors (crust type, disturbance treatment and depth) on soil moisture, including the time (in days) and the block (each pair of undisturbed BSC-crusted plot and its adjacent BSC-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.

RESULTS AND DISCUSSION

Factors influencing soil moisture

The GLMM results for each study site are shown in Table 1. The P-values based on the posterior distribution (pMCMC) showed significant interaction of all pairs of factors for soil moisture in fine-textured soils (El Cautivo). In coarse 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 predictor factors affecting soil moisture are shown in Fig. 2. Soil moisture at 0.03 m behaved the same in fine and coarse-textured soils, that is, it was similar under cyanobacterial and lichen BSCs, and higher under them than in the soils where they 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 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 soils, moisture at 0.10 m was higher in the soils where the BSCs had been removed than in BSC-crusted soils. In contrast, in coarse soils, moisture at 0.10 m was similar under both BSC-crusted and scalped soils.

Table 1. Factors affecting soil moisture at each study site according to GLMM. The second and third columns show the model estimates and the mean estimates across Markov chain Monte Carlo (MCMC) sampling. HPD95 lower and HPD95 upper are the respective 95% lower and upper highest posterior density (HPD) confidence intervals for the fixed effects. The final two columns show P-values based on the posterior distribution (pMCMC) and on the t-distribution, respectively.

El Cautivo (fine-textured soils)

Fixed factors	Estimate	MCMCmean	HPD95lower	HPD95upper	pMCMC	Pr(>|t|)
(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 factors	MCMCmean	HPD95lower	HPD95upper
Day (Intercept)	0.0278	0.0270	0.0284
Block (Intercept)	0.0110	0.0042	0.0215

Las Amoladeras (coarse-textured soils)

Fixed factors	Estimate	MCMCmean	HPD95lower	HPD95upper	pMCMC	Pr(>|t|)
(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 factors	MCMCmean	HPD95lower	HPD95upper
Day (Intercept)	0.0326	0.0318	0.0332
Block (Intercept)	0.0112	0.0046	0.0213

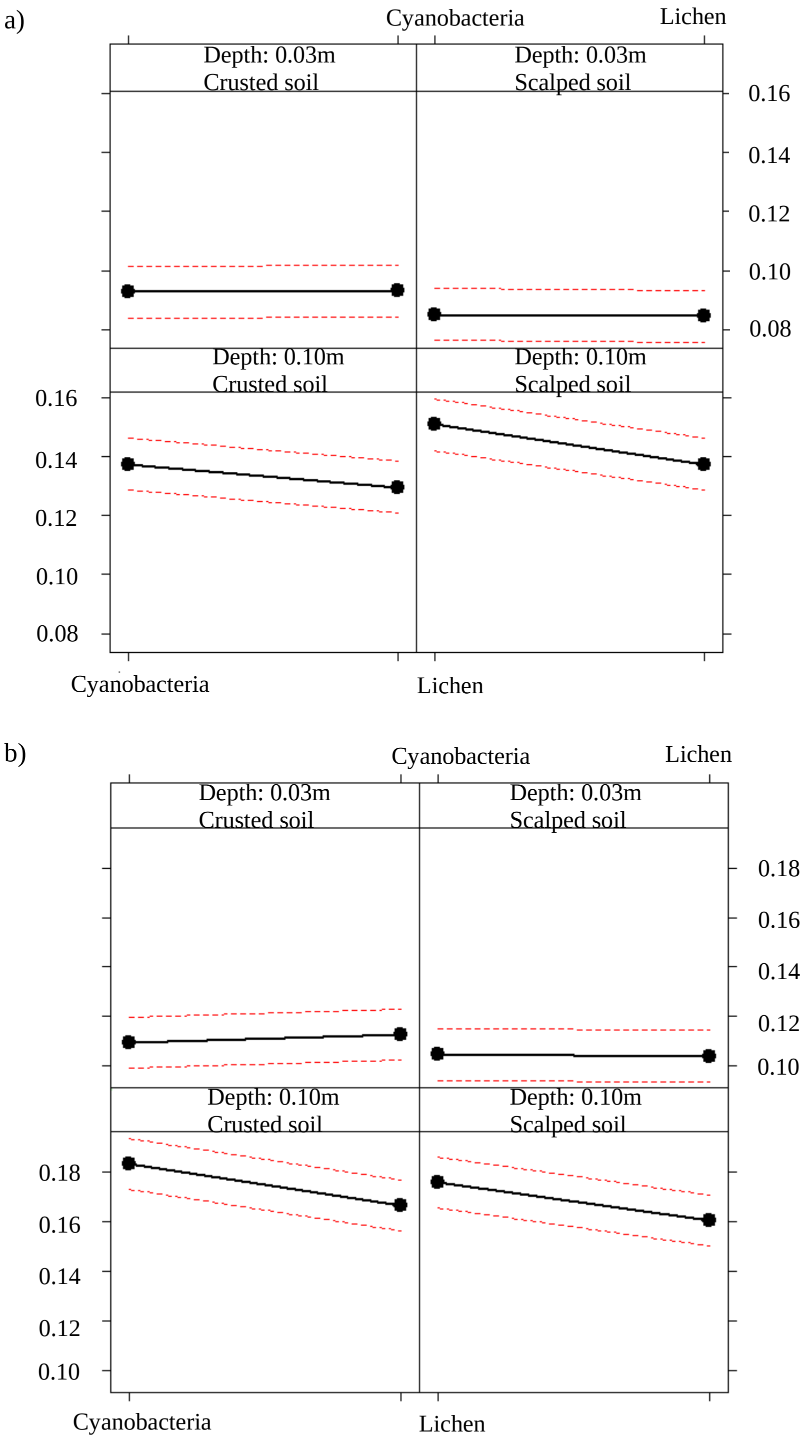

Fig. 2. Partial effects of the significant factors in the GLMM affecting soil moisture in fine (a) and coarse-textured soils (b). The factors were: BSC type (cyanobacterial or lichen BSC), indicated by the black points; disturbance treatment (BSC-crusted or scalped soil, on the left and right squares, 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-percent pointwise confidence interval is drawn around the estimated effect.

Influence of BSC removal

BSC removal had a different effect on soil moisture depending on depth and soil water content. During wet periods (soil water content over 15%), removal of the BSCs led to a decrease in soil moisture at 0.03 m compared to BSC-crusted soils (Figs. 3a and 3b). BSCs have been reported to increase soil water retention more significantly in coarse than in fine soils (Chamizo et al., 2012c). We therefore expected BSCs to influence soil moisture content more in the former than in the latter. However, we found that in fact, removal of BSCs caused a greater decrease in soil moisture in fine (Fig. 3a) than in coarse soils (Fig. 3b). Warren (2003a) suggested that the influence of BSCs in enhancing pore formation, and thereby infiltration, with respect to the same physically crusted soil was more important in fine soils. This is because they are characterised by lower porosity and lower infiltration rates than coarse soils, in which porosity is larger and infiltration is faster. This could be the reason for the greater impact of BSC removal on soil moisture in fine than in coarse soils. Only the removal of cyanobacterial BSCs appeared to have a more significant effect in coarse-textured soils, which could be attributed to their colonization by mosses during the rainy season. On the other hand, it has been demonstrated that BSCs are able to change the physicochemical properties of the underlying soil (Belnap et al., 2003c), and that this effect is stronger immediately beneath the crust than deeper in the soil (Chamizo et al., 2012c). This explains the stronger impact of BSC removal on soil moisture content at 0.03 than at 0.10 m. At 0.10 m, BSC-crusted and scalped soils showed similar moisture during wet periods in both fine (Fig. 3c) and coarse soils (Fig. 3d), except for the cyanobacteria-crusted coarse soils, in which moisture was higher at 0.10 m than in scalped soils, also probably attributable to the presence of abundant moss in the undisturbed cyanobacterial BSCs.

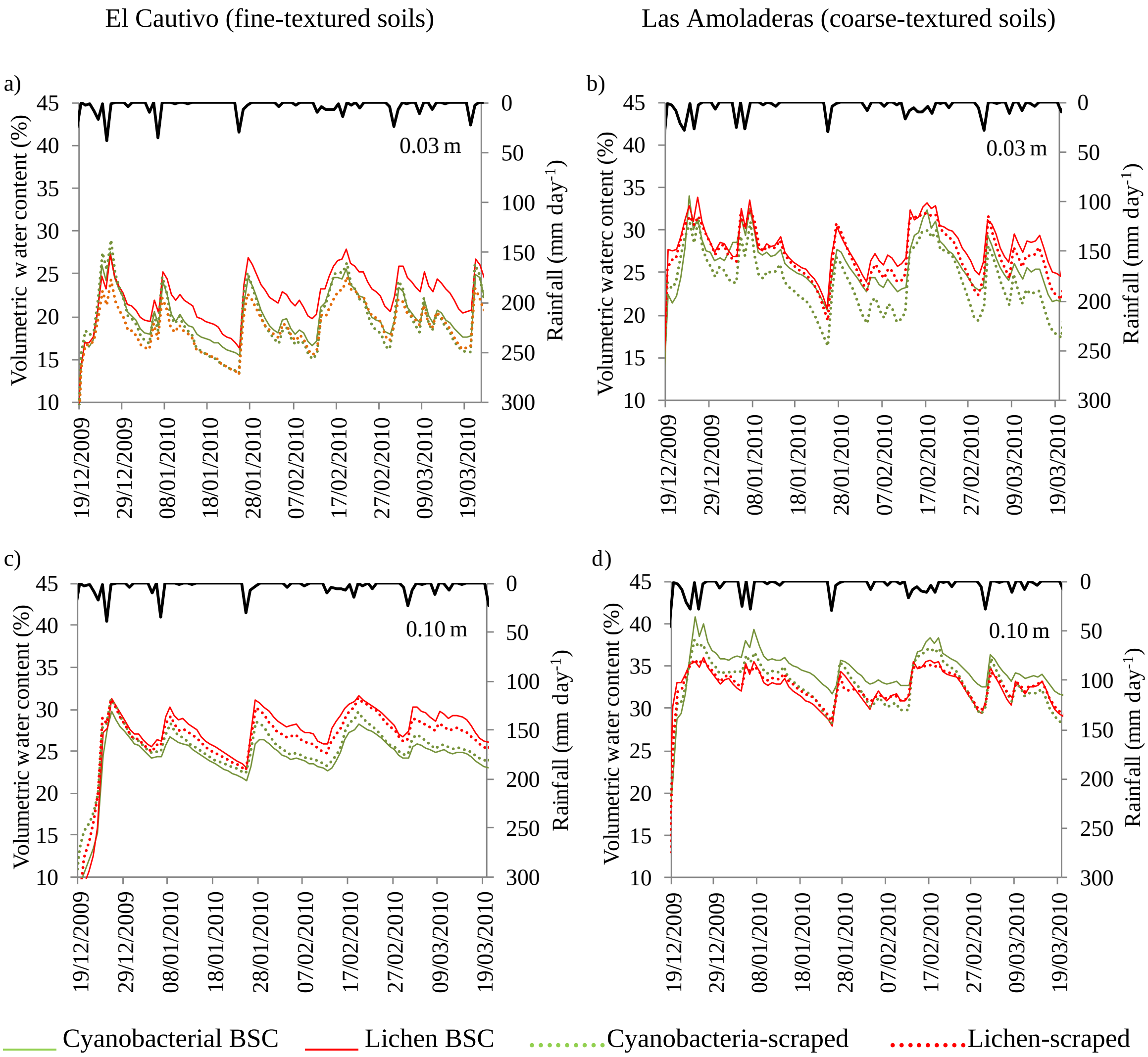

Fig. 3. Soil moisture in the types of BSC-crusted and scalped soils (average of the three plots per type of surface) at 0.03 m in fine (a) and coarse-textured (b) soils, and at 0.10 m in fine (c) and coarse-textured (d) soils, during wet periods.

Several articles have reported more 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) also reported that with high water content, moisture in the upper 0.10 m of soil was higher in soils with BSCs than in those without BSCs. Cyanobacteria filaments and anchoring structures of lichens bind soil particles 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 conservation of soil moisture (Verrecchia et al., 1995). Contrary to this positive effect on soil moisture, other studies (Harper and Marble, 1988; Belnap, 2006) have suggested less soil moisture due to darkening of the soil by some types of BSCs and the consequent increase in soil temperature and thus evaporation.

Fig. 4 shows the daily soil temperature in fine and coarse soils under the cyanobacterial BSC, lichen BSC and BSC-scalped soil. In fine soils (Fig. 4a), almost no difference in temperature was observed under the cyanobacterial BSC, lichen BSC or scalped soil during the study period. In coarse soils (Fig. 4b), soil temperature was slightly higher under lichens, in spite of their light colour, than under the cyanobacterial BSC or the BSC-scalped soil. Mean temperatures (ºC) in the coarse soils under lichens, cyanobacteria and scalped soils during winter were 13.6 ± 2.2, 11.4 ± 2.3 and 11.6 ± 2.2, respectively, and 35.4 ± 2.7, 34.9 ± 2.8 and 33.6 ± 2.4 during summer, respectively. Thus the lower surface moisture in the BSC-scalped soils than in crusted soils does not appear to be related to soil temperature.

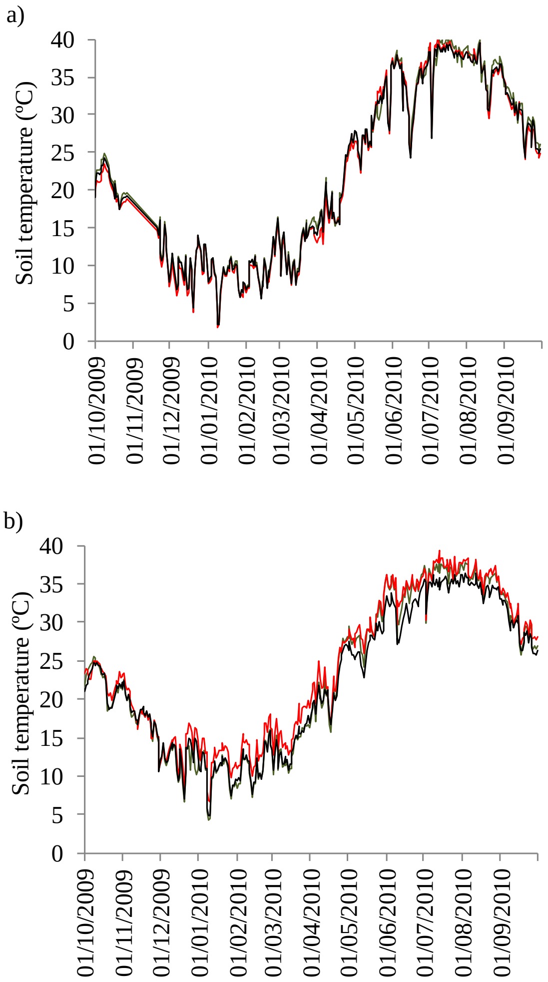

Fig. 4. Soil temperature at 0.02 m depth under the cyanobacterial-BSC (green), lichen-BSC (red) and BSC-scalped soil (black) (one plot of each type of surface cover), in fine-textured soils (El Cautivo) (a) and coarse-textured soils (Las Amoladeras) (b).

Fig. 5 shows soil water loss in the crusted 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 BSC-scalped than in crusted soils, in both fine (Fig. 5a) and coarse soils (Fig. 5b), but these differences were mainly at 0.03 m. At 0.10 m, both crusted and scalped soils showed similar evaporative losses. These soil moisture loss patterns in crusted and scalped soils were usually observed after rain throughout the year.

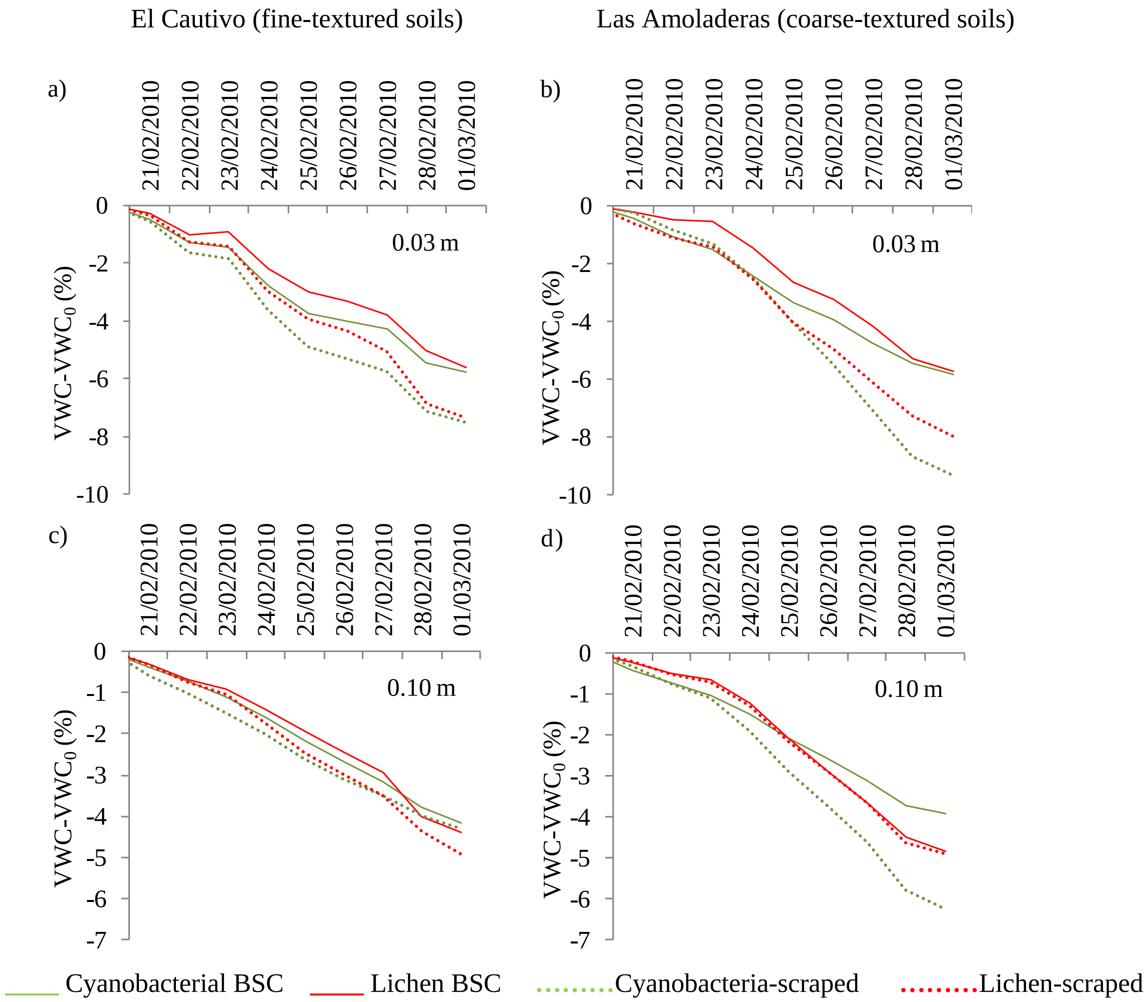

Fig. 5. Soil water loss, after several rains in winter, in the types of crusted and scalped soils (average of the three plots per type of surface) at 0.03 m in fine (a) and coarse-textured (b) soils, and at 0.10 m in fine (c) and coarse-textured (d) soils.

During dry periods (soil water content under 15%), removal of BSCs did not lead to any significant change in soil moisture at 0.03 m compared to either fine or coarse BSC-crusted soils (Fig. 6). This is consistent with previous results on evaporative losses in BSC-crusted and scalped fine-textured soils where evaporation was lower in lichen-crusted than scalped soils under saturation conditions, but showed no difference with moderate or low water content

(Chamizo et al., 2012a). Thus when soil is wet, swelling of cyanobacterial sheaths and subsequent blocking of soil pores (Verrecchia et al., 1995; Kidron et al., 1999) might enhance soil moisture in BSC-crusted soils, whereas under dry soil, the pore-clogging effect of BSCs would disappear, and soil moisture would be similar in crusted and scalped soils. In agreement with these findings, Booth (1941) found higher soil moisture in the upper 0.025 m soil layer under BSCs than under physical crusts after a short rain, but similar moisture under both when soil was dry.

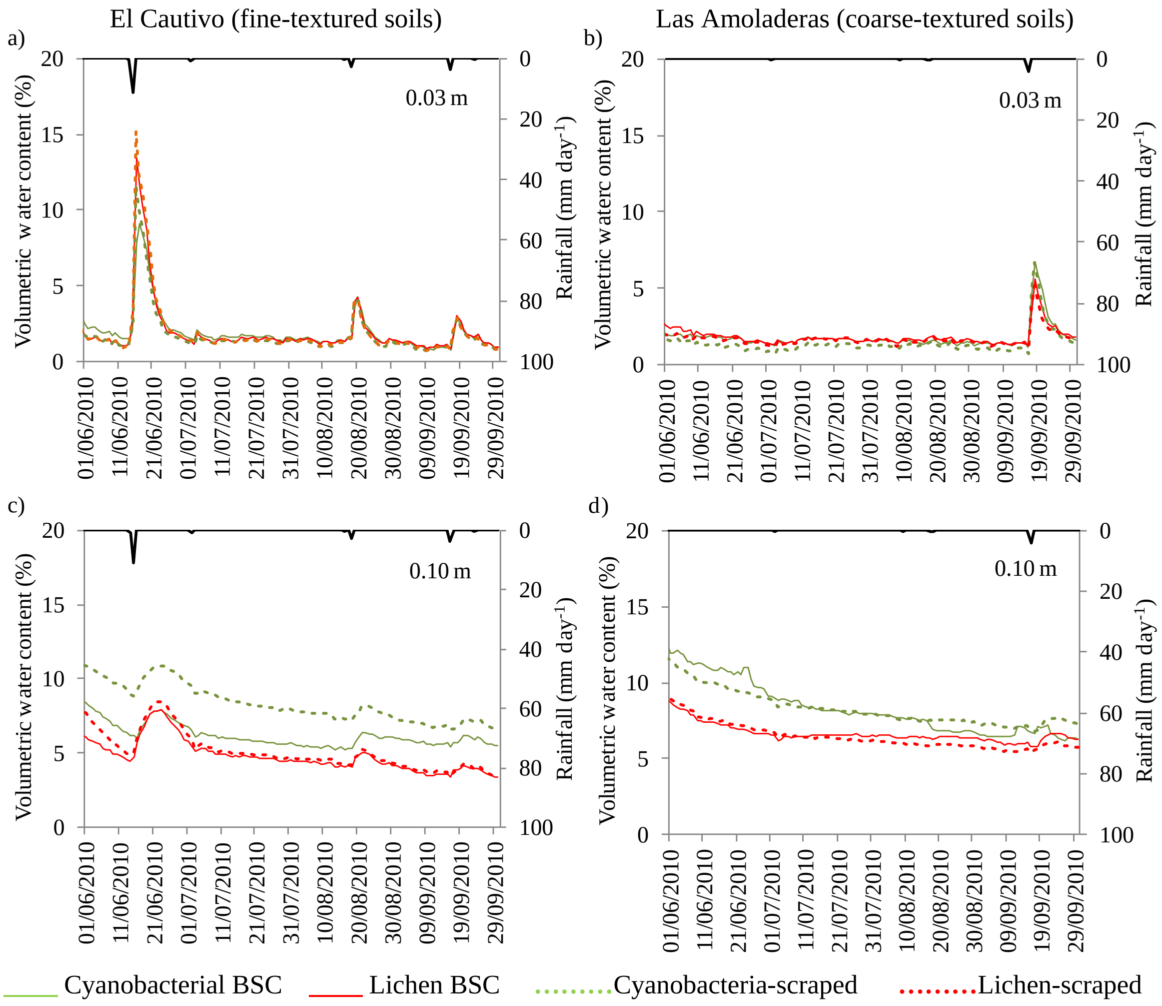

Fig. 6. Soil moisture in the types of BSC-crusted and scalped soils (average of the three plots per type of surface) at 0.03 m in fine (a) and coarse-textured (b) soils, and at 0.10 m in fine (c) and coarse-textured (d) soils, during dry periods.

Unexpectedly, we found that during dry soil periods, soil moisture at 0.10 m was higher in scalped lichen and cyanobacteria-crusted soils than in the respective BSC-crusted fine soils (Fig. 6c). This result could be attributed to denser growth of annual plants, especially during spring, in some of the scalped plots than in the adjacent BSC-crusted plots. Frequent rainfall during the study year favoured the proliferation of annual plants. Less growth of annuals in the plots with BSCs might be associated with an inhibiting effect of BSCs on seedling emergence, as supported by previous studies that have shown that BSCs impede seedling emergence of some species of vascular plants (Escudero et al., 2007). Nevertheless, it has also been suggested that this effect on seedling germination may be species dependent (Belnap and Lange, 2001). Two opposite effects of annuals on soil moisture could be noted during winter and early spring: i) on one hand, annual roots would increase soil moisture by increasing soil organic matter content and creating channels for water infiltration (Evans et al., 1981), but ii) on other hand, they would decrease soil moisture by consuming water during growth. However, in late spring, when their activity ceases, consumption of water would be minimal and increased organic matter promoted by annual roots would contribute to maintaining soil moisture. This could explain higher soil moisture in scalped than in adjacent crusted soils during dry soil periods (Fig. 7a). Crusted soils and adjacent scalped soils with similar or no annual cover showed similar soil moisture content at 0.10 m under these dry soil conditions (Fig. 7b).

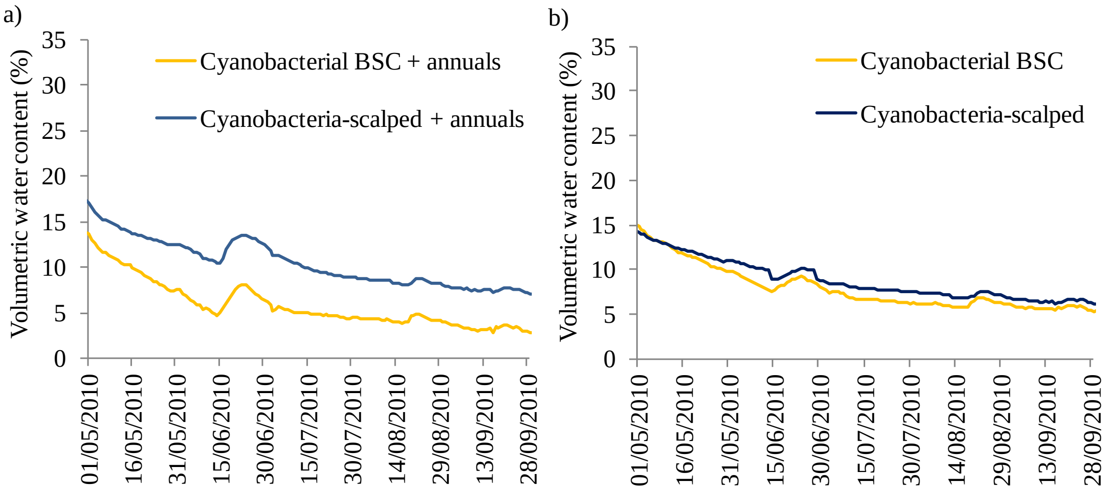

Fig. 7. Soil moisture at 0.10 m during dry periods, in cyanobacteria-crusted and adjacent scalped plots, with considerable (a) and scarce cover of annuals (b), in fine-textured soils.

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). Evapotranspiration, on the other hand, represents the most important process affecting loss of soil moisture. BSCs, through their influence on both the reduction of soil moisture losses from evaporation and the conservation of soil moisture, especially during periods of high soil moisture content, have a significant role in soil water availability in drylands.

When it rains, water input into dry soil triggers a series of biogeochemical and biological processes. The ecological processes activated after a soil moisture pulse event 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 can be expected to play 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 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, affects nutrient cycling and thereby, plant productivity. Loss of BSCs due to disturbances provoked by trampling or grazing in semiarid areas is expected to decrease soil moisture in the upper layers. Disturbance of BSCs would also favour compaction of soil (Chamizo et al., 2012b), 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, in general functioning of ecosystem processes might be predicted if BSCs are disturbed.

Nevertheless, the negative impact of BSC removal on soil moisture was less than we had expected. We attributed this to the fact that we compared soils colonised by BSCs with soils where they had been removed, but only after their long-term colonisation. The presence of BSCs could already have greatly modified the physicochemical properties of the underlying soils, thereby ameliorating the impact of their removal on soil moisture. Stronger differences might be expected in a comparison of soils covered by BSCs and typically bare or uncrusted soils. Previous work in the El Cautivo site has shown significantly higher moisture regimes in soils covered by lichens than in soils covered by physical crusts (Cantón et al., 2004b). Even during summer, lichen surfaces maintained higher moisture than surfaces covered by vegetation or physical crusts (Cantón et al., 2004b). This higher moisture in soils covered by well-developed BSCs is crucial for water-use efficiency and maintenance of higher vegetation, especially during the periods of greatest water deficit.

Influence of BSC type

The type of BSC influenced soil moisture differently depending on soil water content. During wet periods, soil moisture was higher under lichen than under cyanobacterial BSCs at 0.03 m, in both fine (Fig. 3a) and coarse soils (Fig. 3b), although the difference was not as strong in coarse soils. At 0.10 m, moisture in wet soil was higher under lichen than under cyanobacterial BSCs in fine soils. However, coarse cyanobacteria-crusted soils showed higher moisture at 0.10 m than coarse lichen-crusted soils (Fig. 3d). This is attributed to the appearance of moss during the rainy season, which was more abundant in the cyanobacterial than in the lichen plots. As described by previous research in Las Amoladeras, the growth of moss is quite frequent in this area, especially in years of favourable rain (Chamizo et al., 2012b). While moisture at 0.03 m was similar under lichens and mosses due to soil saturation in the top layer underneath both BSCs (Fig. 3b), the ability of moss to absorb large amounts of water (Maestre et al., 2002) and thus increase infiltration (Eldridge et al., 2010; Chamizo et al., 2012b), caused moisture to be higher in deeper soil (0.10m) underneath mosses than under lichen (Fig. 3d).

In general, our results confirm the hypothesis of higher moisture content under lichen than under cyanobacterial BSCs. BSCs increase soil water-holding capacity and organic matter, and this increases with BSC developmental stage (Belnap, 2006; Housman et al., 2006; Chamizo et al., 2012c). More organic matter contributes to the formation of more soil aggregates, which enhances the proportion of pores and thereby infiltration (Warren, 2003a; Ludwig et al., 2005). Several studies have documented the increase in the volume of larger pores promoted by 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, rougher lichen BSCs accompanied by the better soil properties underneath them, contribute to increasing infiltration more than 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., 2003c). Thus we found greater moisture under more developed lichen BSCs than in soils covered by less developed cyanobacterial BSCs. As a consequence, decrease in soil moisture was more noticeable after removal of lichens than cyanobacterial BSCs (Fig. 3).

Under these wet soil conditions, soil water loss was faster in cyanobacteria than in lichen-crusted soils at 0.03 m (Figs. 5a and 5b), but similar in both at 0.10 m (Figs. 5c and 5d), in fine and coarse soils. Two reasons could explain these slower water losses underneath lichen than under cyanobacteria crusts: i) greater exopolysaccharide content in lichen than cyanobacterial BSCs (Chamizo et al., 2012a) and swelling of these compounds upon wetting, blocking soil pores, thereby limiting evaporation; ii) synthesis of hydrophobic compounds by lichen species could reduce evaporative losses, as the presence of hydrophobic soil layers has been reported to decrease evaporation by interrupting capillarity flow through soil (Shokri et al., 2008).

When soil conditions were dry, no difference was found in soil moisture underneath cyanobacterial or lichen BSCs at 0.03 m, in either fine (Fig. 6a) or coarse soils (Fig. 6b). However, some differences were found between BSCs at 0.10 m, where cyanobacteria-crusted soils showed higher moisture than under lichen crusts in both types of soils (Fig. 6c and 6d). In addition, contrary to the pattern observed under wet soil conditions, soil water loss during long drying periods was faster under lichen than under cyanobacterial BSCs at both 0.03 m and 0.10 m, in both fine (Fig. 8a) and coarse soils (Fig. 8b). Lichen-crusted soils have larger meso and macroporosity (Cantón et al., 2003; Malam Issa et al., 2009; Miralles-Mellado et al., 2011) that might increase the evaporative loss of water during soil drying and contribute to reduced soil moisture. Cantón et al. (2004b) also found at this site that, despite lichens having high initial soil moisture, they dried out at a rate similar to soils covered by vegetation or physical crusts, probably because of the high macroporosity (up to 37%) underneath the lichens (Cantón et al., 2003; Miralles-Mellado et al., 2011). Similarly, George et al. (2003) reported that soil profiles covered by lichens dried out faster than cyanobacteria-crusted 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.

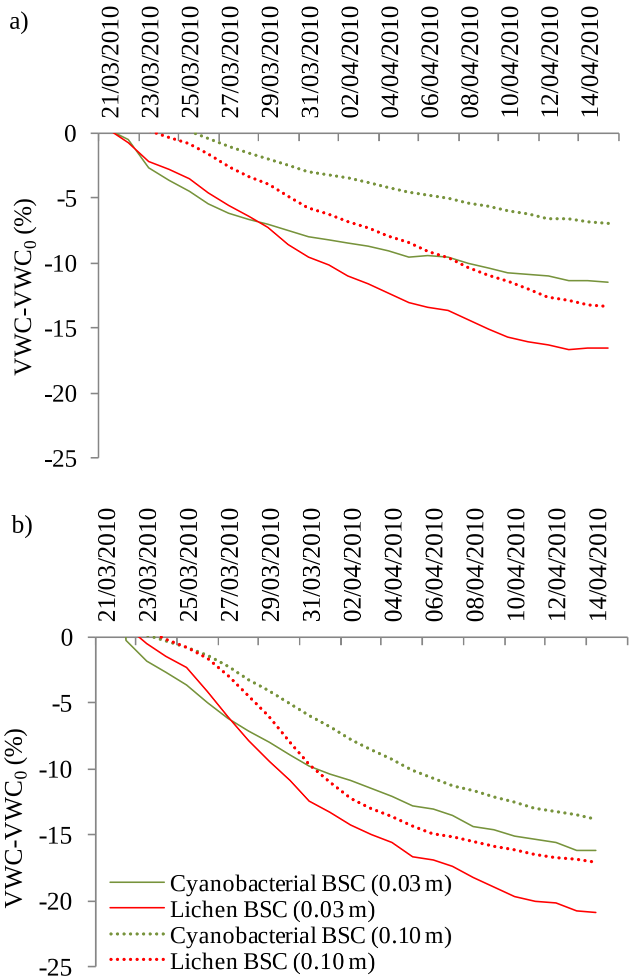

Fig. 8. Soil water loss at 0.03 and 0.10 m, during a long drying period in spring, in the types of crusted soils (average of the three plots per type of surface) in fine (a) and coarse-textured (b) soils.

Thus lichen BSCs seem to affect soil moisture in two different ways: i) during rain, they increased infiltration resulting in more soil moisture than underneath cyanobacterial BSCs (Fig. 3). In addition, in the wet soil, more effective pore clogging by lichen BSCs due to their higher exopolysaccharide content and absorption of water by thalli, and probable synthesis of hydrophobic compounds during periods of biological activity could be responsible for lower water losses in soils covered by lichens compared to those covered by cyanobacterial BSCs (Fig. 5). ii) Under moderate or low soil water content, after the exopolysaccharide and hydrophobic compounds decompose, the larger porosity in lichen-crusted soils (Miralles-Mellado et al., 2011) results in more rapid evaporative loss of soil water (Figs. 8a and 8b), leading to less soil moisture in soils covered by lichens than by cyanobacterial BSCs (Figs. 6c and 6d).

Influence of soil texture

Fine soils have a higher water retention capacity (mean water holding capacity at -33 kPa in our fine soils was 26.7% ± 3.3) than coarse soils (mean water holding capacity at -33 kPa in our coarse soils was 15.7% ± 1.8), and we therefore expected higher moisture in the former than in the latter. Contrary to expected, coarse soils showed higher moisture peaks during rain and higher moisture content throughout the year than fine-textured soils (Fig. 3). During periods when soil was wet, soil water loss was slightly faster in fine than in coarse soils, especially at 0.03 m (Fig. 5). This higher moisture content in coarse soils can be associated with its better conditions. The site with fine soil is a badlands characterised by steep slopes, poorly-developed soils, with low organic matter, and poor soil aggregation (Chamizo et al., 2012c) and soil structure, which favour high runoff coefficients (Chamizo et al., 2012b). The site with coarse soil has low slope angles, and soil has higher organic matter and infiltration as well as a petrocalcic horizon limiting water losses from deep infiltration. This site is also close (around 2 km) to the Mediterranean Sea coast and undergoes less hydric stress due to lower vapour pressure deficit (mean annual VPD at 12 p.m. in the site with coarse soils was 1.3 ± 0.8 kPa, whereas it was 1.9 ± 1.2 kPa in the site with fine soils) and consequent evaporation. Thus, negligible water loss from drainage and the source of highest soil water losses being evaporation cause 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 soils (Noy-Meir, 1973). Nevertheless, we found that during long drying periods (Fig. 8), soil water loss tended to be somewhat faster in coarse than in fine soils, which might indicate that, as soils dry out, fine soils are more efficient in retaining water than coarse soils.

CONCLUSIONS

Removal of BSCs decreased soil moisture content, especially in the uppermost layer of the soil, during wet soil periods. During dry periods, both BSC-crusted and scalped soils showed similar moisture content. 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 emphasize 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 than less-developed BSCs (cyanobacterial BSCs) in periods of higher water content. During dry periods, greater porosity in soils covered by well-developed BSCs leads to higher evaporative losses and decreased soil moisture than in soils covered by less-developed BSCs. Therefore, not only the presence of BSCs, but also the type of BSC covering the interplant spaces plays a significant role in water fluxes and soil water content in drylands.

CHAPTER VI

Discriminating soil crust type, development stage and degree of disturbance in semiarid environments from their spectral characteristics

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ABSTRACT

Biological soil crusts (BSCs) are increasingly recognized as common features in arid and semiarid ecosystems and play an important role in the hydrological and ecological functioning of these ecosystems. However, BSCs are very vulnerable to, in particular, human disturbance. This results in a complex spatial pattern of BSCs in various stages of development. Such patterns, to a large extent, determine runoff and erosion processes in arid and semiarid ecosystems. In recent years, visible and near infrared (Vis-NIR) diffuse reflectance spectroscopy has been used for large-scale mapping of the distribution of BSCs. Our goals were (i) to demonstrate the efficiency of Vis-NIR spectroscopy to discriminate vegetation, physical soil crusts, various developmental stages of BSCs, and various types of disturbance on BSCs and (ii) to develop a classification system for these types of ground cover based on Vis-NIR spectroscopy. Spectral measurements were taken of vegetation, physical crusts, and various types of BSCs prior to, and following, trampling or removal with a scraper in two semiarid areas in SE Spain. The main spectral differences were: (i) absorption by water at about 1450 nm, more intense in spectra of vegetation than in that of physical crusts or BSCs, (ii) absorption features at about 500 and 680 nm for the BSCs, which were absent or very weak for physical crusts, (iii) a shallower slope between about 750 and 980 nm for physical crusts and early-successional BSCs than for later-successional BSCs and (iv) a steeper slope between about 680 and 750 nm for the most developed BSCs. A partial least squares regression-linear discriminant analysis of the spectral data resulted in a reliable classification (Kappa coefficients over 0.90) of the various types of ground cover and types of BSC disturbance. The distinctive spectral features of vegetation, physical crusts and the various developmental stages of BSCs were used to develop a classification system. This will be a promising tool for mapping BSCs with hyperspectral remote sensing.

Keywords: biological soil crust, physical soil crust, disturbance, reflectance, spectroscopy quantitative analyses, classification system.

INTRODUCTION

Abiotic or physical soil crusts are compacted surface layers ranging from several millimetres to several centimetres in thickness and frequently found in arid and semiarid regions. Under adequate conditions of climate and soil stability, bare soils and physical crusts are colonised by micro-organisms gradually forming biological soil crusts (BSCs), which are an association of soil particles with cyanobacteria, algae, microfungi, lichens and bryophytes. Within the succession of BSCs in arid and semiarid regions, cyanobacteria are the first colonisers. Polysaccharides exuded by cyanobacteria bind soil particles together (Verrecchia et al., 1995), stabilizing the soil surface and permitting later colonization by lichens and mosses (Belnap, 2006).

BSCs are widespread in arid and semiarid ecosystems and play an important role in the hydrological and ecological functioning of these ecosystems. They alter many soil surface characteristics affecting surface runoff and thereby, the distribution and colonization of vascular plants (Belnap, 2006). They also increase soil stability and reduce wind and water erosion by protecting the soil against raindrop impact and the erosive force of wind (Maestre et al., 2011). However, some studies indicate that BSCs lead to increased runoff (Zhan and Miller, 1996). The effect of this additional runoff on erosion should be evaluated on larger spatial scales to assess the combined impact of these effects and the potential for water harvesting from crusted areas to nourish adjacent vegetated areas (Cantón et al., 2011). A tool able to estimate the spatial distribution of BSCs at hillslope and catchment scale would be required for establishing such effects. Furthermore, BSCs have been demonstrated to be very vulnerable to disturbances such as tracked-vehicle traffic, grazing and trampling by livestock, especially in soils with limited aggregate stability. The loss or disturbance of BSCs is one of the factors leading to accelerated soil erosion and other forms of land degradation (Belnap, 1995). The protection offered by BSCs prevents soil and nutrient loss, which can rapidly be exacerbated following disturbance to a crust. Therefore, it is important to identify the distribution of BSCs and monitor their spatial and temporal changes (Chen et al., 2005).

In recent years, proximal and remote sensors measuring the visible and near infrared (Vis-NIR; 350–2500 nm) reflectance of soils have been exploited for detecting, mapping and monitoring BSCs. Some attempts at mapping crusts from field and remote sensing data have been made to include soil crusting as an input parameter in runoff and erosion models. However, these have been mainly restricted to physical crusts (Cerdan, 2001; King et al., 2005). Biological crust-covered surfaces, as input parameters in runoff and erosion models, have, so far, only been mapped from morphological descriptions in the field for small areas (Cantón et al., 2002). The potential of spectroscopy for mapping soil crusts has been reported in a few publications. Ben-Dor et al. (2004) showed that physical crusts can be spectrally modelled. The spectral characteristics of BSCs have been analysed by several authors (Karnieli et al., 1999; Chen et al., 2005; Weber et al., 2008) and several indices such as simple combinations of spectral bands, have been tested for mapping BSCs from hyperspectral images. Karnieli (1997) developed an index to separate cyanobacteria-dominated BSCs from bare sand. Chen et al. (2005) developed an index to differentiate lichen-dominated BSCs from bare soil and plants. Weber et al. (2008) developed an index to distinguish BSCs (mainly dominated by cyanobacteria) from surfaces devoid of BSCs. However, a universal method to distinguish between BSCs and other types of cover has not yet been developed (Karnieli et al., 2003), nor has an index applicable to different ecosystems been proposed. Moreover, a methodology to distinguish different types of BSCs, ranging from early-successional BSCs such as cyanobacterial crusts to well-developed BSCs, such as lichen and moss crusts, has not yet been proposed. Few papers have analysed the changes in spectral characteristics when BSCs are disturbed by the common activities of livestock grazing and recreational use (resulting in trampling and/or scraping). As far as we know, only the work by Ustin et al. (2009) deals with this topic, demonstrating the potential for spectral detection of BSCs following experimentally controlled increases in summer precipitation, dry nitrogen deposition and mechanical disturbance by walking.

The objective of the present paper was twofold: (i) to demonstrate the efficiency of quantitative Vis-NIR spectral analysis to discriminate vegetation, physical crusts and various developmental stages of BSCs, and various types of disturbance to BSCs and (ii) to develop a classification system for vegetation, physical crusts and the various developmental stages of BSCs, applicable in a variety of semiarid ecosystems.

MATERIALS AND METHODS

Spectral measurements

Spectral measurements were conducted in plots (described below) covered by the main crust types identified at each study site. In El Cautivo, they were: (i) physical crusts (P), which form over the mudstone regolith and cover all bare soil in this area, (ii) BSCs with incipient colonization by cyanobacteria (IC), (iv) dark BSCs mainly dominated by cyanobacterial species (C) which, along with frequent small, dark lichens including *Collema spp* cover about 80–90% of the soil surface, while a physical crust (7–10%) and light-coloured lichens (2–12%) cover the rest and (iv) light-coloured lichen-dominated BSCs (L), consisting mainly of *Squamarina lentigera* and *Diploschistes diacapsis (*about 70–90%), with some cyanobacteria (10–20%) and physical crust (3–10%). These three types of BSCs represent a transition from poorly- to well-developed BSCs (Lázaro et al., 2008). In Las Amoladeras, the main crust types were: (i) cyanobacteria-dominated BSCs (C), cyanobacteria covering approximately 60–85% with some patches of physical crust (10–20%) and moss (2–20%), (ii) mixed lichen-moss BSCs (Lm), where lichen cover (mainly *Squamarina lentigera* and *Diploschistes diacapsis*) represented about 50–65%, and moss 30–40% and (iii) moss-dominated BSCs, where moss represented some 55–60% and the rest was covered by cyanobacteria (30%) and physical crust (2-10%). Crust spectral response was examined in either an intact (or undisturbed) state and then, six months after disturbance, by foot trampling (800 steps distributed homogeneously on the plot) or removal with a scraper (hereafter scraping). Note that scraping entirely removed the crust, whereas trampling disrupted the crust, but left the fragments in the plot. The six-month interval was to allow for stabilization and reorganisation of soil surface particles after a couple of rainfall events so that the soil surface conditions were comparable among plots. Only the undisturbed physical crusts were analysed as these form quickly after rainfall (within a few minutes following cessation of the disruption; Ben-Dor et al., 2003). Furthermore, the changes in the surface conditions of such crusts after trampling or scraping are hardly visible.

Spectra were acquired using a GER 2600 portable spectroradiometer (Spectra Vista Corporation, Poughkeepsie, New York, USA) with an optical resolution of 0.5 nm between 350 and 1000 nm and a resolution of 11.5 nm between 1000 and 2500 nm. Spectral measurements were made between 12:00 and 16:00 local time during a five-day period in February 2008, under clear sky conditions following a rain-free period of two weeks. *In situ* soil-moisture sensors indicated water contents of approximately 7% in El Cautivo and 13% in Las Amoladeras at a depth of 0.04 m. Surface reflectance measurements were taken with a fibre-optic tube (23º field of view, FOV), at a height of about 0.6 m from the soil surface (ground IFOV approximately 0.20 m^2) on plots (2 x 2 m) representing individual crust types subjected to replicates of the various treatments. About ten to fifteen replicate measurements were collected within each plot. Because the area of soil surface covered by physical crusts in Las Amoladeras was scarce, only a few reflectance spectra were acquired from this surface. The reflectance spectra of various plant species were also acquired at both sites. Each spectral measurement consisted of the computerized average of five individual spectra. Before measuring each plot, a white reference was obtained using a Spectralon$^{(r)}$ panel to compute the reflectance factor. Data were acquired with GER 2600 Data Collection Software on a laptop connected to the spectroradiometer.

Data pretreatment

Since measurements were taken under field conditions, the spectral ranges between 350 and 400 nm and between 1752 and 2514 nm were affected by strong noise and were not considered further. Furthermore, the spectrum was divided into two parts, each with different spectral resolutions (400–1000 nm and 1000–1752 nm), and a cubic polynomial smoothing filter with a 17 bands-window size was applied to each part (Savitzky and Golay, 1964).

Statistical analysis

Spectral datasets are usually (near) multi-colinear because they often consist of a large number of highly correlated variables (the reflectance at every wavelength across the spectrum) and a small number of samples (Næs and Mevik, 2001). To tackle this problem, principal component analysis (PCA) and partial least squares regression (PLSR) can be used to compress the spectral information onto a smaller number of non colinear variables termed principal components (PCs). The model structure of PCA and PLSR is (Næs et al., 2002, Equation 1):

$$X = TP' + E \qquad (1)$$

$$y = Tq + f \qquad (2)$$

where X is the matrix of predictor (column-centred) variables, y is the vector of response, T is the score matrix representing the new PCs, matrix P and vector q are the loadings (weights) of the original variables on each PC, and matrix E and vector f are the residuals in X and y, respectively. These PCs are linear combinations of the original variables and the loadings that are orthogonal to each other. In PCA, the scores are calculated such that the first PC accounts for the largest variation in the data and has the maximum variance of the scores, and the following PCs explain as much of the remaining variation as possible. While PCA is an unsupervised method and only the spectral data are considered, PLSR exploits both predictor variables and the response to extract PCs that are maximizing the covariance between the scores and the response. Here we used PCA and PLSR in combination with linear discriminant analysis (LDA) on Vis-NIR spectral data to assess the extent to which it is possible to discriminate and predict both ground cover classes (vegetation, physical crusts and different developmental stages of BSCs) and the nature of disturbance (trampling, scraping) we imposed upon the BSCs. Half of the spectra were randomly selected to create a training set and the rest were used as a test set. A PCA was run on the training set and the first two PCs explaining approximately 90% of the spectral variation were retained. Similarly, a PLSR was fitted to the training set using dummy variables representing the ground cover classes to predict. The optimal number of components (with a maximum of 10 components) was determined using leave-one-out cross-validation (Wehrens and Mevik, 2007). Then, a LDA was applied separately on the PC scores obtained by PCA or PLSR and the classification efficiency of both approaches (PCA-LDA and PLSR-LDA) were compared with the test set. A confusion matrix was created by counting the number of well and wrongly classified classes in the test set and the performance of the classification was assessed by calculating the Cohen’s Kappa coefficient. This procedure was applied to spectral data obtained from each study site individually and then for the two study sites together. Similarly, the same approach was applied to a sub-set of the data for undisturbed crusts and those that had been disturbed.

Based on the outcome of these analyses, several variables were defined from the raw spectral data for the vegetation, physical crusts and undisturbed BSCs. Their appropriateness for classification and mapping of various BSCs as well as their ability to distinguish between BSCs, physical crusts and vegetation was tested. The variables tested were the albedo or average reflectance (for the entire spectral region and for specific spectral regions), calculated as the square root of the sum of the squares of reflectance at every wavelength; slopes were calculated as the difference in reflectance between two selected wavelengths divided by the spectral gap between these wavelengths. The spectral absorptions at specific wavelengths were computed by application of the continuum removal (CR) technique (Clark and Roush, 1984), which allows normalizing reflectance spectra and comparing individual absorption features from a common baseline. First, the convex hull of the spectrum was computed and the set of points on the hull (the local maxima) were connected by a straight line. The continuum removal (CR) values were then computed by dividing the reflectance by the interpolated line. The two end points are on the hull and their value was therefore equal to 1.0.

Values less than 1.0 indicated the presence of absorption features. The continuum removal was computed using ENVI 4.5 (ITT VIS, Boulder, USA).

All statistical analyses were carried out using R software version 2.12.2 (R Development Core Team, 2010) and in particular, the PLS package of Wehrens and Mevick (2007) for PLSR, Ade4 package of Chessel et al. (2004) for PCA and MASS package of Venables and Ripley (2002) for LDA.

RESULTS AND DISCUSSION

Reflectance of undisturbed crust types and vegetation

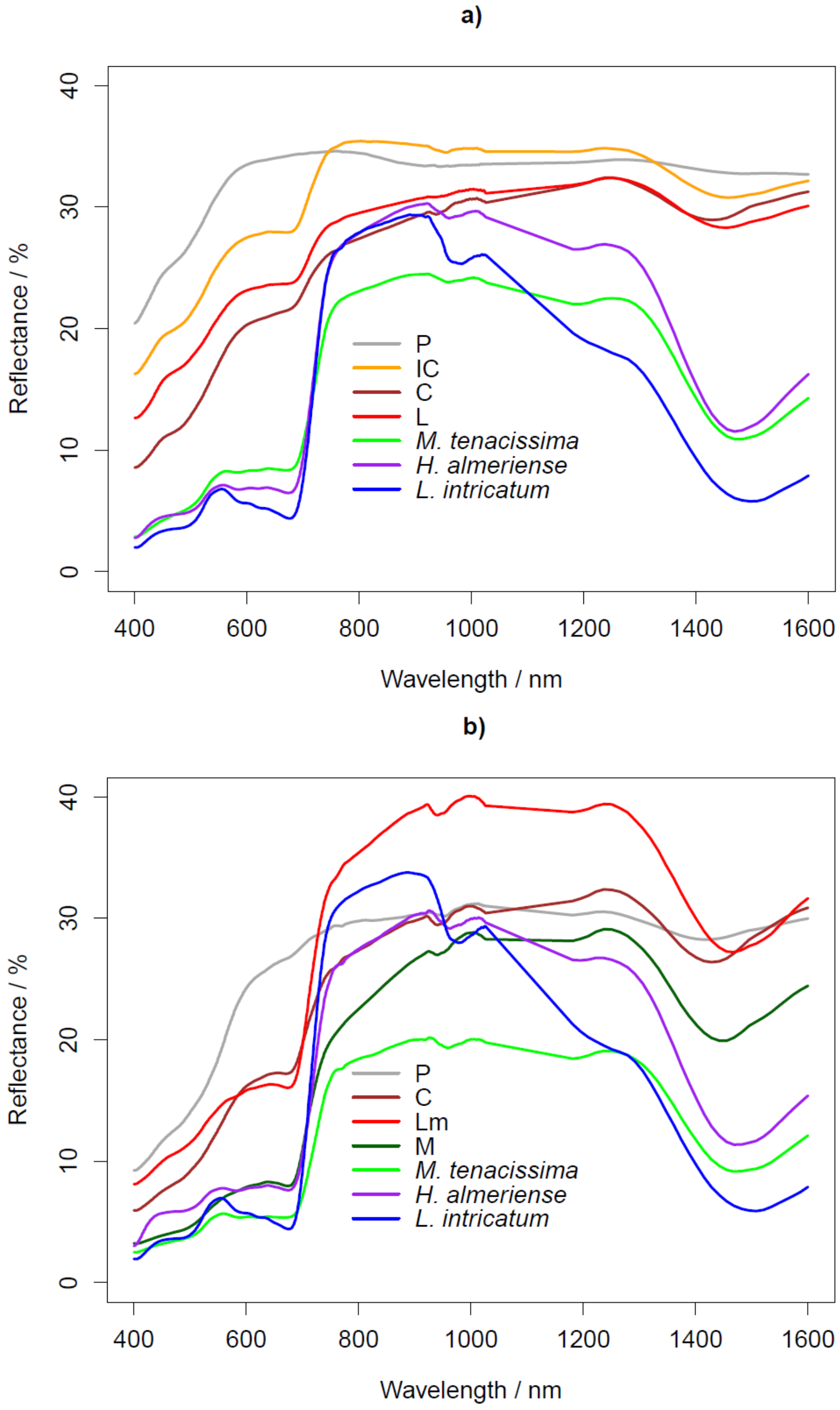
The number of measurements, mean reflectance and standard deviation for the various types of ground cover at 550, 680 and 750 nm is shown in Table 1. The spectral variability was greater for the BSCs than for physical crusts or vegetation. Only M crusts showed small variability in their spectral signal and a reflectance in the Visible (Vis) bands that was very similar to that of vegetation. Vegetation showed a large variability in the NIR.

Table 1. Number of measurements per type of ground cover (vegetation and undisturbed crust types) and mean spectra and standard deviation at three important wavelengths.

Study area	Cover type	N	Mean reflectance ± standard deviation		
			550 nm	680 nm	750 nm
El Cautivo	Vegetation	27	5.2 ± 1.9	7.7 ± 3.5	22.8 ± 5.1
	Physical crust	40	27.1 ± 0.9	34.3 ± 1.3	34.6 ± 1.3
	Incipient-cyanobacterial crust	30	21.2 ± 2.3	28.0 ± 3.1	34.8 ± 3.2
	Cyanobacterial crust	50	12.9 ± 2.3	21.7 ± 4.0	26.3 ± 4.7
	Lichen crust	60	17.6 ± 4.2	23.8 ± 5.8	28.6 ± 6.5
Las Amoladeras	Vegetation	23	4.6 ± 1.6	6.1 ± 1.9	21.3 ± 7.6
	Physical crust	9	14.0 ± 1.6	26.9 ± 2.2	29.2 ± 2.3
	Cyanobacterial crust	45	9.2 ± 3.0	17.4 ± 6.2	25.7 ± 8.1
	Mixed lichen-moss crust	60	11.5±3.7	16.2±5.8	32.7±5.4
	Moss crust	45	4.6±1.2	8.1±1.6	19.9±1.9

The bare physical crusts showed the greatest reflectance across the spectrum (Fig. 1). The BSCs presented an absorption peak at about 680 nm (from chlorophyll *a*), which was absent or very weak in the physical crusts. Vegetation was characterised by a small reflectance in the Vis (from absorption by photosynthetic pigments) and a large reflectance in the NIR and a reflectance peak at 550 nm, which is absent in BSCs (Karnieli et al., 1999; Chen et al., 2005). The spectral shapes of BSCs were similar but differed in their albedo, which decreased in the order IC-L-C in El Cautivo, and Lm-C-M in Las Amoladeras. An increase in reflectance from 400 nm to about 600 nm was observed followed by an absorption feature at about 680 nm. Between approximately 680 and 750 nm, there was a marked increase in the reflectance of all BSCs. The reflectance of the cyanobacterial and lichen BSCs at El Cautivo, continued to increase up to around 1220 nm, whereas that of incipient-cyanobacterial BSCs slightly decreased from approximately 750 and 980 nm, and then slightly increased up to about 1220 nm (Fig. 1a). Beyond this wavelength, reflectance decreased until it reached a minimum at approximately 1450 nm, which was caused by absorption by water. The same features were observed in spectra obtained from BSCs at Las Amoladeras, but the slopes between approximately 680 and 750 nm and between approximately 750 and 980 nm were much steeper (probably because of the presence of moss; Fig. 1b). Weber et al. (2008) described the spectral curves of cyanobacteria-, lichen- and moss-dominated BSCs in a semiarid area and also found poor reflectance at about 400 nm, which gradually increased to 600 nm, fell to a local minimum at about 680 nm and showed a strong acclivity between 700 and 830 nm. The bulb-shaped feature at about 1000 nm was probably an artefact at the splice between the two sensors.

Fig. 1. Mean reflectance spectra of different species of vegetation (*Macrochloa tenacissima*, *Helianthemum almeriense* and *Lycium intricatum)* and the types of soil crusts (P: physical crust; IC: incipient-cyanobacterial BSC; C: cyanobacteria-dominated BSC; L: lichen-dominated BSC; Lm: mixed lichen-moss BSC; M: moss-dominated BSC), at El Cautivo (a) and Las Amoladeras (b).

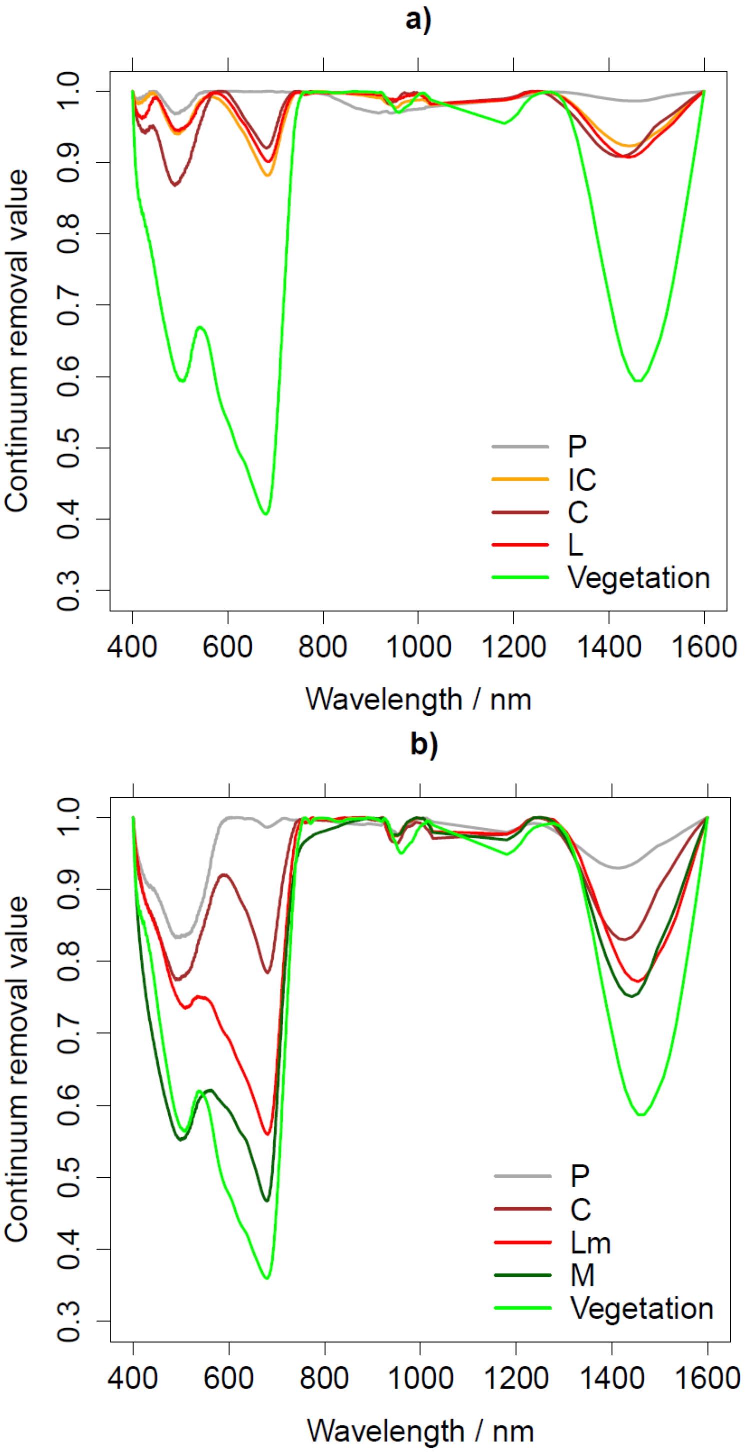


The absorption feature that appears in BSC spectra at approximately 680 nm has been described by several different authors (O'Neill, 1994; Karnieli and Sarafis, 1996; Karnieli et al., 2003). Cyanobacteria are the first colonisers in the succession of BSCs under arid or semiarid conditions, and later, if conditions permit, lichens and mosses colonise (Belnap, 2006). As the cyanobacterial biomass increases and later-successional species appear, the consequent increase in chlorophyll *a* and coloured pigments increases the colouration of the soil surface (Belnap et al., 2008). As crust darkens during development, the absorption features in the red wavelengths increase and reflectance decreases (Karnieli et al., 1999; Chen et al., 2005). Thus, the cyanobacterial BSCs showed less reflectance than the incipient-cyanobacterial BSCs (Fig. 1a). However, greater BSC development does not always imply a decrease in reflectance because it depends on BSC composition. Later-successional lichen species such as *Squamarina lentigera* and *Diploschistes diacapsis,* common on gypsiferous soils in semiarid areas of the Mediterranean region (Martínez et al., 2006), are light-coloured and therefore, show greater reflectance in the Vis than do cyanobacterial BSCs. Thus, lichen and lichen-moss crusts showed more reflectance than cyanobacterial BSCs (Fig. 1). The dark moss BSCs are later-successional BSCs, and showed the least reflectance (Fig. 1b).

Continuum removal values of undisturbed crust types and vegetation

Continuum-removed reflectance values showed absorption features at approximately 500, 680 and 1450 nm, which were more intense for vegetation than for BSCs and very weak or absent for physical crusts (Fig. 2). Absorption features in the Vis were more intense for the BSCs from Las Amoladeras than those from El Cautivo (Fig. 2), probably because of the greater pigment content of the crusts at Las Amoladeras, also accompanied by a greater organic carbon (OC) and total N content (on average 19 g kg^{-1} and 1.76 g kg^{-1}, respectively, in the C crust in Las Amoladeras, and 12 g kg^{-1} and 1.71 g kg^{-1}, respectively in El Cautivo, unpublished data).

Fig. 2. Mean spectra (continuum removed) of vegetation and the various crust types ((P: physical crust; IC: incipient-cyanobacterial BSC; C: cyanobacteria-dominated BSC; L: lichen-dominated BSC; Lm: mixed lichen-moss BSC; M: moss-dominated BSC), at El Cautivo (a) and Las Amoladeras (b).



In El Cautivo, the absorption at about 680 nm (from chlorophyll *a*) was similar among the BSCs (mean CR at about 680 nm was 0.88 ± 0.04 in IC crusts, 0.92 ± 0.01 in C and 0.90 ± 0.02 in L), whereas the absorption at approximately 500 nm was more pronounced in the cyanobacterial BSCs (mean CR 0.87 ± 0.01) than in the other BSCs (mean CR in the IC and L crusts was 0.94 ± 0.02) (Fig. 2a). This absorption feature at approximately 500 nm could be attributed to the presence of carotenoid pigments, which absorb light between 400 and 500 nm (Weber et al., 2008). One of the functions of carotenoids is to protect the photosynthetic system from excess UV radiation. Carotenoids are often formed in cyanobacteria in response to high light intensities, temperature and other stress factors (Reuter and Müller, 1993). While cyanobacteria could employ carotenoids, as well as other pigments and metabolites, as a protection against excess light, the main lichen mechanism for decreasing the influx of ultraviolet radiation is Ca oxalate crystals or calcite in the cortex of the mycobiont (Dietz et al., 2000). This might explain why the absorption by lichen BSCs at 500 nm was not as intense as by cyanobacterial BSCs, despite them being more developed. In Las Amoladeras (Fig.2b), CR values at about 500 and about 680 nm increased from physical crusts towards the most developed BSCs (thus P<C<Lm<M). This could be attributed to increased BSC development and moss cover. The absorption feature observed at about 680 nm for physical crusts was probably caused by very early colonization by cyanobacteria. This was difficult to detect visually.

Absorption by water at about 1450 nm was more intense in the spectra of vegetation than those of BSCs. Wang et al. (2009) have used this absorption feature as an estimation of plant water content. This absorption was more intense in spectra of BSCs at Las Amoladeras than in those at El Cautivo, since soil moisture was greater at Las Amoladeras at the time the spectra were collected. In general, Las Amoladeras undergoes less hydrological stress than El Cautivo because of its proximity (about1 km) to the Mediterranean Sea. Absorption by water was similar in extent in all BSC spectra at El Cautivo, whereas it was more intense in lichen-moss and moss spectra, than in cyanobacterial type BSCs at Las

Amoladeras. Verrecchia et al. (1995) suggested that BSCs contribute to the retention of soil moisture. This is supported by Cantón et al. (2004b) who found reduced soil moisture content under physical soil crust surfaces than under lichen covered soil in El Cautivo. Our findings suggest that the spectral features associated with water may assist discrimination of BSCs and physical crusts.

Effects of disturbance on the spectral characteristics of BSCs

As the presence of BSCs usually darkens the soil, trampling and scraping caused an increase in albedo. Trampling and scraping the BSC also flattened the soil surface, causing an increase in reflectance from a decrease in light scattering and shadow hiding effect (Matthias et al., 2000). The reflectance was greater when the BSC was scraped than when it was trampled (Fig. 3). This difference is explained by the fact that scraping entirely removed the BSC, whereas trampling caused a breakdown of the BSC but left the fragments on the plot, conferring increased roughness and darker colour to the soil and thus decreasing the albedo. Trampling had a stronger effect on reflectance in El Cautivo than in Las Amoladeras. The latter site suffers from frequent trampling by livestock and therefore the spectral response arising from further trampling is reduced. The spectral curves were especially similar for the undisturbed and trampled BSC in Las Amoladeras in the spectral region between approximately 700 and 1300 nm (Fig. 3b).

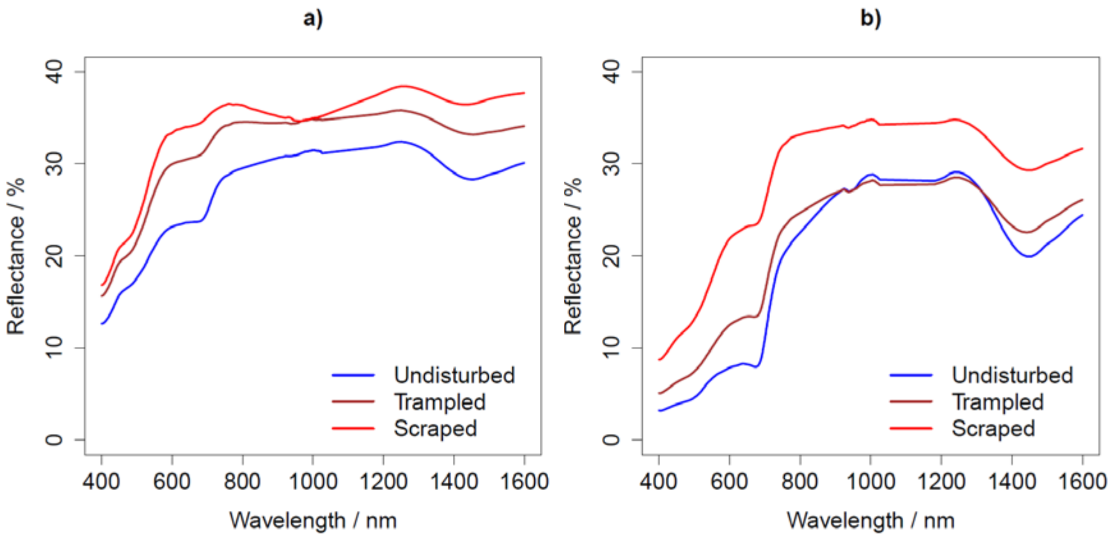


Fig. 3. Mean reflectance spectra of the lichen-BSC at El Cautivo (a) and the moss-dominated BSC at Las Amoladeras (b) before and after scraping or trampling.

Absorption by pigments at about 500 and about 680 nm and by water at about 1450 nm was strongest in the undisturbed crusts, somewhat weaker in the trampled crusts and weakest in the scraped crusts. Absorption by chlorophyll *a* in the scraped plots, probably results from early colonization of these soils by cyanobacteria during the six months elapsed between scraping and acquisition of spectra. The reflectance slope at wavelengths between approximately 750 and 980 nm in spectra from trampled and scraped plots and P and IC (undisturbed) crusts was generally small and decreasing or nearly zero, whereas it was increasing and steep in spectra for the well-developed BSCs. This suggests that this spectral slope steepens as later-successional species colonise and promote development of these crusts. This slope might therefore be used as an indicator of successional dynamics of BSCs. Zaady et al. (2007) demonstrated the possibility of using the normalized difference vegetation index (NDVI) as an indicator of successional trends of BSCs following disturbance, but suggested that its reliability during the wet season, when microphytes are active, would exceed that during the dry season. Ustin et al. (2009) reported that cover of BSCs was proportional to the CR values between 2.010–2.140 nm. They found the least absorption in plots with decreased BSC cover as a consequence of increased summer irrigation and trampling treatments, and the most intensive in spectra from control plots of undisturbed BSCs.

Discrimination of undisturbed and disturbed crusts

Spectral data processing using PLSR-LDA improved discrimination between vegetation and the different (undisturbed) crust types on the one hand, and the various crust disturbances on the other hand, compared to PCA-LDA, as assessed by values of the Kappa coefficient close to 1.0 (Kappa coefficients were greater than 0.90 in most cases, Table 2). A Kappa coefficient of 1.0 implies perfect agreement between the measured and predicted classes (types of ground cover), whereas values close to zero indicate poor agreement.

The PLSR-LDA applied to the training set showed a very good discrimination between vegetation and the various crust types for each site separately. The confusion matrix comparing the predicted and observed classes in the test set indicated that all types of ground cover were appropriately classified for each site (Kappa coefficient = 1.0, Table 2). As can be seen in Fig. 4, application of PLSR-LDA to the training set for both sites combined also grouped the same types of ground cover together. The physical crusts from Las Amoladeras appeared to be similar to the incipient-cyanobacterial BSCs from El Cautivo. This may arise from early colonization of these physical crusts by cyanobacteria (as supported by the small absorption feature at about 680 nm in the physical crusts at Las Amoladeras, Fig. 2b). The Kappa coefficient (0.96) obtained in the confusion matrix from comparison of the predicted and observed classes in the test site for both sites combined (Table 2) indicated a reliable classification.

Table 2. Kappa coefficients resulting from the confusion matrix after confronting the measured and predicted classes of the different ground covers (V: vegetation; P: physical crust; IC: incipient-cyanobacterial BSC; C: cyanobacteria-dominated BSC; L: lichen-dominated BSC; Lm: mixed lichen-moss BSC; M: moss-dominated BSC and crust disturbance conditions (considering all crust types together and each crust type separately). Kappa coefficients close to 1 indicate good agreement between the measured and predicted classes in the confusion matrix, whereas values close to 0 indicate poor agreement.

	El Cautivo					Las Amoladeras					Both sites
	Cover types	Crust treatments (undisturbed, trampling, scraping)				Cover types	Crust treatments (undisturbed, trampling, scraping)				Cover types
	(Vegetation, P, IC, C, L)	All crust types (P, IC,C,L)	IC	C	L	(Vegetation, P ,C, Lm, M)	All crust types (P,C,Lm,M)	C	Lm	M	(Vegetation,P, IC,C, L, Lm, M)
PCA-LDA	0.68	0.04	0.59	0.75	0.41	0.70	0.53	0.64	0.88	1	0.53
PLSR-LDA	1	0.64	0.97	1	0.91	1	0.88	0.97	1	1	0.96

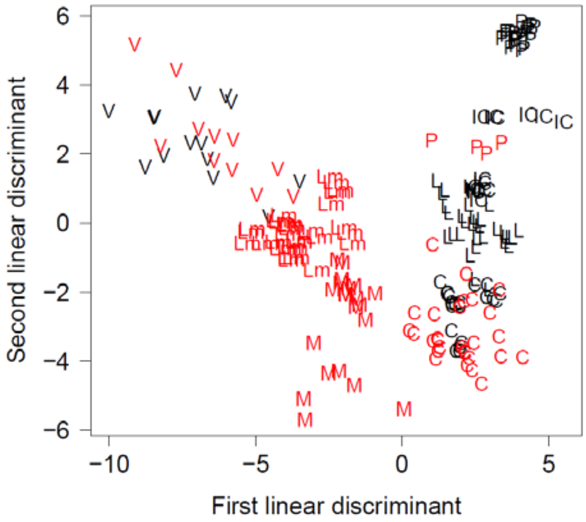


Fig. 4. Classification of vegetation (V) and the undisturbed crust types (see Fig. 1 for a legend to the crust types) arising from LDA of PC scores extracted by PLSR, for the two study sites combined, where black and red symbols indicate the corresponding surface types at El Cautivo and Las Amoladeras, respectively.

The loadings of the first two PLSR PCs as a function of wavelength indicated the relative contribution of the wavelengths in the constructed PCs for data from El Cautivo, Las Amoladeras and the two sites combined. In El Cautivo (data not shown), the first PC, explaining 86% of the variance, had the greatest loading values at approximately 680 1450 nm, corresponding with absorption by chlorophyll *a* and water, respectively. The second PC accounted for 8% of the variance and the largest loadings occurred at about 500 nm, and were probably related to absorptions by carotenoids. At Las Amoladeras (data not shown), the first PC accounted for 82% of the variance in reflectance, and large absolute loading values were found throughout the NIR, probably caused by differences in albedo in this region of the spectrum. The second PC accounted for 15% of the variance in reflectance, with the largest loading values in the region between approximately 680 and 1000 nm, probably because of absorption by chlorophyll *a* and differences in the slopes between 680–750 nm, 750–980 nm, and at wavelengths near 1450 nm because of absorption by water. The loadings of the first two PLSR PCs for both sites combined as a function of wavelength are shown in Fig. 5. The first PC accounted for 78% of the total variance in reflectance and the highest absolute loadings were found at about 680 and 1450 nm (similarly to the first PC at El Cautivo). The second PC accounted for 10% of the variance in reflectance, with the highest absolute loadings in the region between approximately 680 and 1000 nm and at about 1450 nm (in a similar way to the second PC at Las Amoladeras).

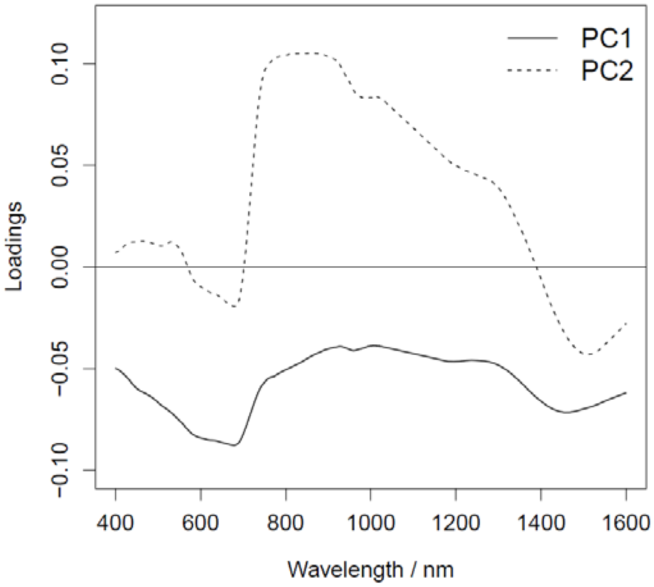


Fig. 5. Loadings of the first two PCs as a function of wavelength following application of PLSR to spectra of the various types of ground cover for the two study sites combined.

Application of PLSR-LDA to training sets including spectra from undisturbed and disturbed crusts for each site separately indicated reasonable resolution between undisturbed, trampled and scraped crusts at each site (Table 2). The classification of all crust types at El Cautivo indicated some overlap for those scraped and trampled (Fig. 6a). This overlap was reduced when data for an individual crust type were processed and scraping was clearly distinguishable from trampling (Fig. 6b). The loadings of the first PLSR PC, accounting for 92% of the total variance, showed large values throughout the spectrum, probably related to the albedo. The same procedure applied to spectral data from Las Amoladeras showed that the first PC accounted for 77% of the variance in reflectance, with the largest loadings at about 680 and about 1450 nm. The second component accounted for 21% of the variance, with the largest loadings in the region between approximately 750 and1300 nm (data not shown).

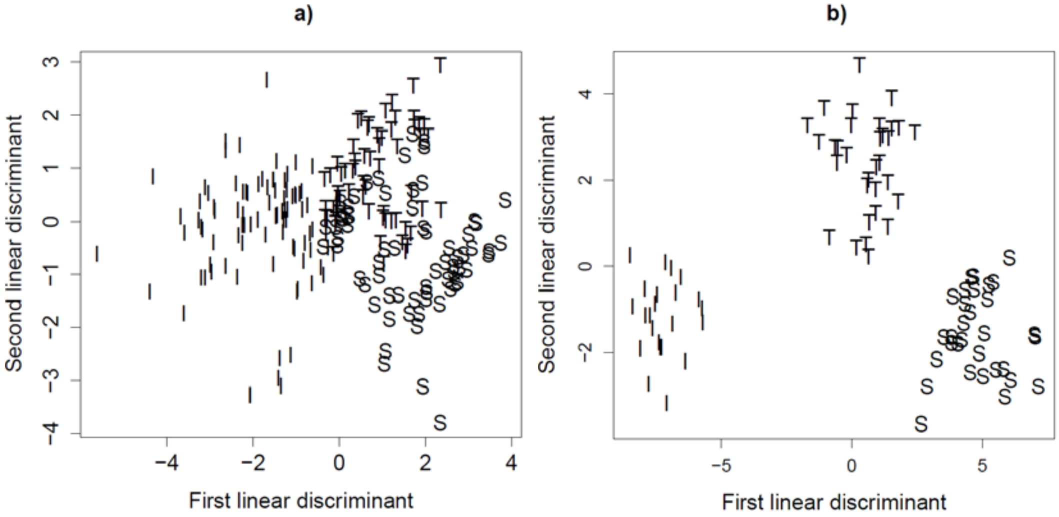


Fig. 6. Classification of crust disturbances (I: intact; T: trampled; S: scraped) at El Cautivo after applying PLSR–LDA, considering all the crust types (a) and only the cyanobacteria-dominated BSC (b).

Although there have been attempts to predict soil physical, chemical and biological properties using Vis-NIR reflectance spectroscopy (see review by Cécillon et al., 2009a), and PCA and PLSR of Vis-NIR spectra have been used to assess soil quality (Cécillon et al., 2009b), to our knowledge, these quantitative analyses have not been used to discriminate the developmental stages of soil crusts and disturbances to them as a prerequisite for a quantitative approach to mapping crust types in arid and semiarid areas.

A classification system to separate crust types

Some indices have been developed to distinguish BSCs from bare soil and plants (Karnieli, 1997; Chen et al., 2005; Weber et al., 2008). However, no index has yet been developed to discriminate different types of BSCs. From the outcome of a PLSR-LDA procedure on the spectral data, the CR value and slope variables appeared to be useful in distinguishing the spectra from these different types of ground cover as illustrated by box plots in the following ways (Fig.7):

(i) The CR value at about 1450nm (CR1450) can be used to differentiate vegetation from physical crusts and BSCs (Fig. 7a). As water content varies during the year, a more detailed analysis of the relationship between water content and this spectral feature is of interest.

(ii) The CR value at about 680 nm (CR680) (as well as that at CR1450 nm), can distinguish physical crusts from BSCs (Fig. 7b).

(iii) The slope between approximately 750 and 980 nm (Slp750-980) allows incipient-cyanobacterial BSCs to be distinguished from other BSCs (Fig. 7c).

(iv) The slope between approximately 680 and750 nm (Slp680-750) can be used to distinguish lichen-moss from cyanobacterial, lichen and, to a large extent, moss BSCs (Fig. 7d). Although the mean value for this variable was significantly greater in lichen-moss than in moss BSCs, the distributions overlap. This appears to be reasonable since both have a significant cover of moss which attenuates the underlying differences. Nevertheless, most of the samples of moss and lichen-moss BSCs were correctly classified with this slope.

(v) The CR value at about 500 nm (CR500) allows cyanobacterial, lichen and moss BSCs to be distinguished (Fig. 7e). Absorption by carotenoids followed the order M>C>L.

These observations provide a classification scheme distinguishing the various types of ground cover (Fig. 8), which applied to the complete data set provided a Kappa coefficient of 0.96, suggesting a reasonable degree of reliability.

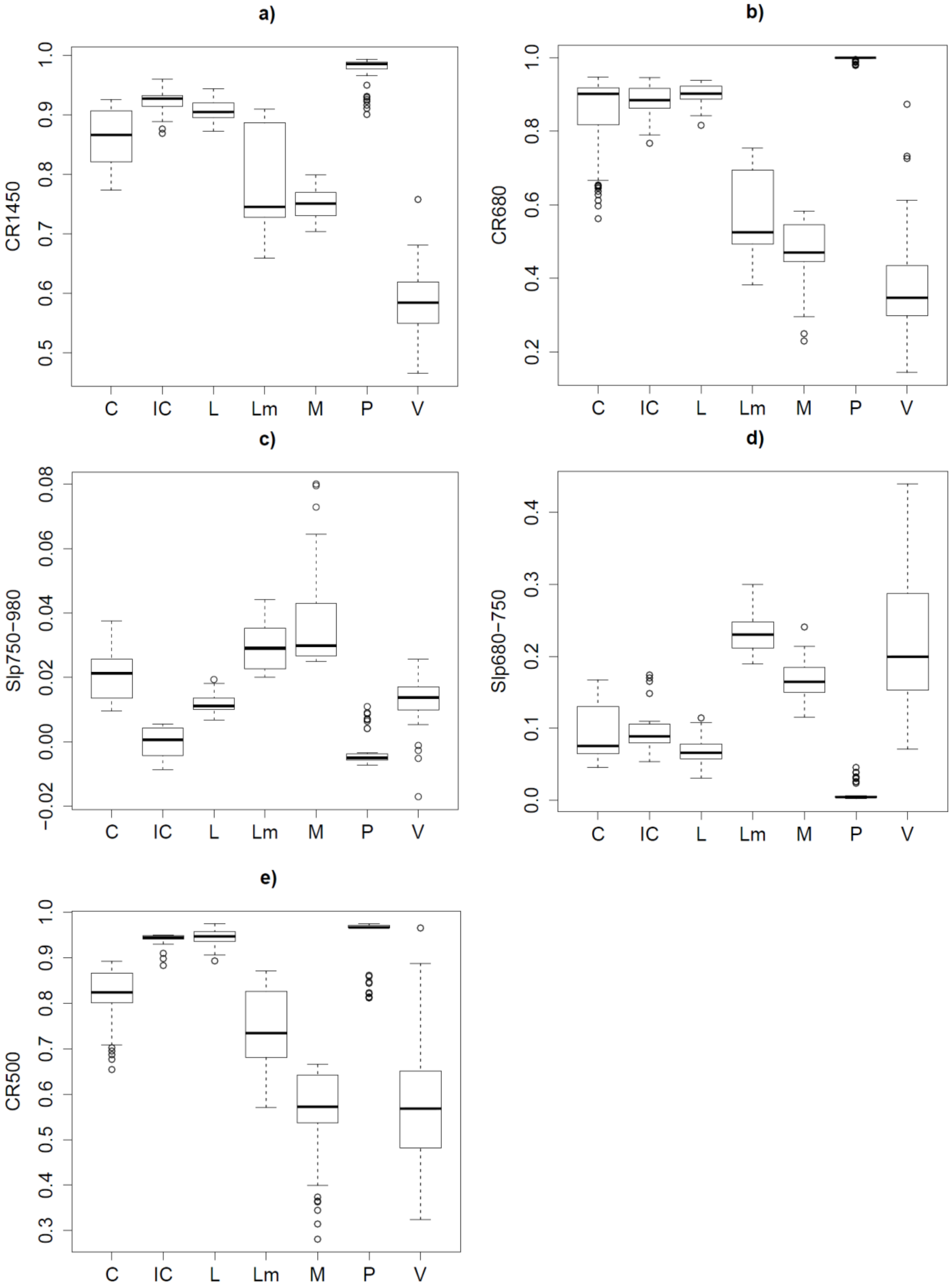


Fig. 7. Box plots of the variables: a) continuum removal (CR) value at ~1450 nm, b) CR value at ~680 nm, c) slope between 750 and 980 nm, d) slope between 680 and 750 nm, and e) CR value at ~500 nm. The cover types are: vegetation (V), and the types of soil crusts. (See Fig. 1 for a legend to the crust types).

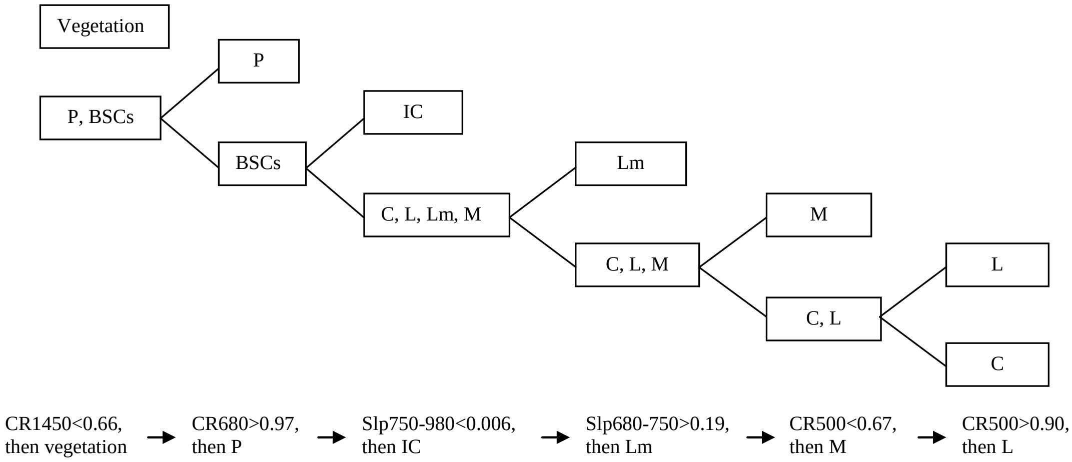


Fig. 8. Decision tree for the classification of vegetation and the types of soil crusts (See Fig. 1 for a legend to the crust types).

CONCLUSIONS

Quantitative analysis of the spectral characteristics of soil crusts demonstrates that some of these may be used to differentiate both cover type (vegetation, physical crusts and developmental stages of BSCs), and types of disturbance to BSCs. In general, as BSC development progresses, the crust darkens and its reflectance in the Vis decreases. However, late-successional lichen and lichen-moss BSCs were colonised by light-coloured lichen species, and consequently, these BSCs showed greater reflectance than less developed ones. Scraping BSCs increased their reflectance to a greater extent than trampling. Our data suggest that the negative or slightly flat slope between about 750 and 980 nm in spectra of physical crusts or incipient BSCs becomes positive and steeper as the crust was colonised by late-successional species. Changes in this feature over time may be an indicator of succession dynamics as BSCs develop and/or of various disturbances to their surfaces. This may allow both temporal and spatial mapping to assess soil aggradation and degradation in arid regions.

This study has demonstrated that reflectance spectroscopy provides a tool for objective measurement of soil crust development. In this respect, spectral sensing may constitute an alternative to visual assessment. The differences between the spectral features in vegetation, physical crusts and various types of BSCs provide the basis for a classification index based on absorption features at approximately 500, 680 and 1450 nm, and the slopes between approximately 680 and 750 nm and between approximately 750 and 980 nm. The application of the proposed index to multispectral or hyperspectral images with a suitable spectral and spatial resolution could be a powerful tool for mapping different types of BSCs in semiarid areas. The future challenge is to assess the efficacy and efficiency of this index for detecting and mapping distribution of BSCs.

GENERAL DISCUSSION

Influence of the type of soil crust on hydrological processes

Biological soil crusts are very common features in arid and semiarid areas, where they can represent up to or more than 70% of the soil surface cover (Belnap et al., 2005). BSCs play vital roles in hydrological, geomorphologic, biological and ecological processes in drylands, representing a crucial link between atmosphere and soil processes (Belnap et al., 2003b), and becoming an issue essential to understanding soil surface processes. Despite their widely accepted role in numerous soil properties associated with hydrology, the influence of these organisms on processes such as infiltration and runoff has only received special attention in recent years, and their effect on other components of the water balance, such as evaporation and soil moisture, has scarcely been addressed (Belnap, 2006). Moreover, while most research has focused on the influence of total BSC cover on water processes, few studies have investigated the effect of the type of BSC on soil hydrology. This is of utmost importance, as the influence of BSCs on water, as well as on nutrient and sediment redistribution, can be strongly conditioned by BSC cover and composition.

For a clearer understanding of the effect of BSCs on hydrological processes, previous studies have recommended taking a variety of crust types or BSC developmental stages into consideration (Belnap, 2006). In addition, the more widely reported influence of BSCs on infiltration-runoff appears to be conditioned by soil texture (Warren, 2003a). This hypothesis can also be extended to other key components of the water cycle, such as evaporation and soil moisture. In this thesis, we therefore explore the role of BSCs in the major water balance components (infiltration-runoff, evaporation, and soil moisture) considering a gradient of crust types, including physical crusts and BSCs in different stages of development, in two different ecosystems characterised by contrasting soil texture.

Numerous publications have emphasized the importance of BSCs in enhancing soil surface roughness and soil properties, such as aggregate stability, water retention, and C and N content, all of which influence water movement through soil. As documented in this thesis, soil surface roughness increases with the presence of BSCs and their progressive development (Chapter II). Physicochemical soil properties are also better in BSCs than in physical crusts. Soil properties, such as water content at -33 kPa and -1500 kPa, aggregate stability, organic carbon (OC) and N content, and cation exchange capacity, are higher in BSCs than in physical crusts. In addition, all these properties increase in the crust and underlying soils as the BSC develops (Chapter I). All these changes in soil properties have repercussions on a number of well-known drylands ecosystem processes. Increased water retention capacity, OC and N content in more developed BSCs stimulates biological activity and the formation of soil aggregates, both of which increase porosity and thereby, infiltration, and up to a point, soil moisture (Tongway and Ludwig, 1990; Belnap et al., 2005). Increased soil aggregation increases soil stability in turn, which along with improvement in infiltration, strongly contributes to reducing soil erosion (Eldridge and Greene, 1994b; Mazor et al., 1996). Our results also show that the effect of BSC development on soil properties is especially noticeable in the top layer of soil (0.01-m layer of the soil underneath the BSC), and decreases with depth. Thus, in deeper layers (0.01-0.05 m of soil underneath the BSC), the main differences are between physical crusts or less-developed BSCs (incipient cyanobacterial BSCs) and well-developed BSCs (lichens and mosses). The changes in soil properties in the uppermost layer of soil where BSCs are present are significant, as this layer is the most active soil profile and represents the boundary in contact with the atmosphere, where water inputs are controlled and losses into and from the soil take place.

Because of the increased surface roughness, nutrient content, water retention and aggregate stability in soils covered by BSCs, infiltration and soil moisture were expected to be higher and evaporation lower in BSCs than in physical crusts or uncrusted soils. However, the role of BSCs in hydrological processes is complex and results from the interaction of several factors, including ambient conditions, type of substrate and BSC attributes, such as cover, composition, roughness, porosity, and hydrophobicity, apart from the above mentioned effects of BSCs on underlying physicochemical soil properties.

Influence of BSCs on infiltration-runoff

We found higher infiltration in BSCs than in physical crusts, and as a general trend, an increase in infiltration with BSC development, that is, as cyanobacteria biomass increased and later successional species, such as lichens and mosses, colonised the soil (Chapter II). However, this is not universally true, and there are exceptions to this general pattern that are conditioned by other factors such as rainfall characteristics or the spatial scale under study (Chapter III). In low-intensity rainfall, which is the most common in our study areas, the higher microtopography (Rodríguez-Caballero, 2012; Chapter II) as well as water retention capacity (Chapter I) and porosity (Miralles-Mellado et al., 2011) promoted by better developed BSCs (lichens) causes infiltration to increase compared to less developed BSCs (cyanobacterial crusts) (Chapter III). Under high intensity rainfalls, which cause the most important geomorphological changes in landscape, BSCs appear to have no significant effect on runoff yield (Chapter III). In these intense events, water is stored in soil microdepressions only for a very short time until runoff is generated, and overland flow runs downslope, so the effect of BSCs on microtopography is overridden by the effect of rainfall intensity. Even under long extreme rainfall intensities, blocking of soil pores and hydrophobic properties in well-developed BSCs such as lichens cause more runoff than in less developed ones (cyanobacterial BSCs), or even generate runoff similar to physical crusts (Chapter II). Nevertheless, although under certain conditions BSCs can generate runoff similar to physical crusts, the role of BSCs in soil stability and their essential protection against erosion is unquestionable (Chapter II).

Monitoring runoff in biologically crusted soils under natural rains for over two years has shown that the influence of BSCs on infiltration-runoff greatly depends on such rainfall characteristics. These findings are important, as most previous studies on this topic have employed rainfall simulations (Herrick et al.,

2010) or infiltrometer measurements (Eldridge et al., 2010) to explore the relationship between BSCs and infiltration-runoff. These methods have important limitations, as they either do not reproduce the crusting that occurs under natural rainfalls (infiltrometer methods), or do not reproduce the same conditions in terms of variability in rainfall intensity and size, distribution and kinetic energy of drops of natural rain (rainfall simulations and infiltrometer methods).

Another important factor that must be taken into consideration is the spatial scale at which infiltration-runoff processes are surveyed. So far, most studies on the role of BSCs in infiltration and runoff have been concentrated at small spatial scales (<1 m^2). At these scales, the effect of microtopography on infiltration can be underestimated (Álvarez-Mozos et al., 2011), making other factors associated with BSCs, such as water repellence of some species or blocking of soil pores due to swelling of cyanobacteria upon wetting, become more relevant than the increased roughness promoted by BSCs, and infiltration rates in more developed BSCs (lichen BSCs) are less than expected (Chapter II). The larger the spatial scale is, the more roughness in more developed BSCs (lichens) leads to increased infiltration and reduced runoff relative to less-developed and smoother cyanobacterial BSCs or physical crusts (Rodríguez-Caballero et al., 2012). Thus, at coarse spatial scales, microtopography might become the key variable explaining the response of BSCs to runoff. We also found that the effect of other factors influencing runoff such as topography varies with the spatial scale considered. At very small spatial scales, topography seems to have no significant effect on runoff yield (Chapter II; Chapter III), as also previously reported (Calvo-Cases et al., 1991; Solé-Benet et al., 1997). At coarser spatial scales, increased slope gradients increase runoff generation (Chapter III).

In summary, our findings demonstrate the high spatial and temporal variability of infiltration and runoff in biologically crusted soils. This high variation in space and time has important implications for upscaling their hydrological effects, and modelling infiltration-runoff in semiarid areas, where BSCs represent important ground cover. Thus, future studies should take into account the temporal and spatial scale effect when analysing the influence of BSCs on hydrological processes.

Influence of BSCs on evaporation and soil moisture

As mentioned above, water infiltration increases with the presence of BSCs. In addition, they control soil water loss. The water budget is strongly dominated by evapotranspiration in arid and semiarid ecosystems. Thus another important objective of this thesis was to analyse the influence of BSCs on soil evaporation. We found that even though infiltration was higher in BSCs than in physical crusts, and that infiltration increased with BSC development, there was little difference in evaporation between the crust types during the time that evaporation measurements were conducted (Chapter IV). However, this was in late spring when ambient conditions were quite warm and all crust types lost water very quickly. Soil moisture monitored throughout the year shows differences in moisture content and soil water loss among types of BSCs depending on the soil moisture status. When it rains, lichen BSCs enhance infiltration more than cyanobacterial BSCs or bare soils (Chapter III). Under saturation of the upper soil layer, higher polysaccharide content in lichen than in cyanobacterial BSCs (Chapter IV) and swelling of polysaccharides upon wetting could clog soil pores in lichen more effectively than in cyanobacterial BSCs, thereby reducing evaporation. Both effects combined (increased infiltration and reduced evaporation) result in increased soil moisture under lichen than in cyanobacteria-crusted soils (Chapter V). In contrast, during long periods of drying, soil pores unblock and porosity is larger in soils covered by lichens (Miralles-Mellado et al., 2011), resulting in faster loss of soil water and decreased soil moisture in lichen-crusted than in cyanobacteria-crusted soils (Chapter V). Moreover, previous work in our study areas has shown that soils occupied by physical crusts show drier moisture regimes than soils covered by lichen BSCs (Cantón et al., 2004b). BSCs therefore have a more important effect than physical crusts on increasing water availability in water-poor interplant spaces. More available soil moisture increases biological activity and C and N fixation by BSC organisms, which is used for synthesis of carbohydrates through photosynthesis. This enhanced soil organic matter content contributes to the formation of larger and more stable soil aggregates, and consequently, to the formation of larger soil pores, which in turn increases infiltration, and thereby, soil moisture. In view of the effects of the different types of soil crusts on water processes, we can affirm that BSCs increase water inputs and reduce water outputs compared to physical crusts, and that water inputs also increase with development of BSCs.

Consequences of BSC disturbance on hydrological processes

BSCs are quite fragile and susceptible to disturbances caused by activities such as grazing, hunting or tracked-vehicle traffic (Warren, 2003b). Disturbance can lead to loss of species diversity, BSC biomass and cover, and the replacement of well-developed BSCs composed of a rich community of a variety of species of cyanobacteria, lichens and mosses by a simple community composed of a few species of cyanobacteria (Belnap and Eldridge, 2003). Disturbance of BSCs has profound effects on water processes. Trampling causes the deterioration of BSCs and soil compaction, thus reducing infiltration (Chapter II). On the contrary, removal of BSCs apparently increases infiltration compared to intact surfaces covered by BSCs. However, according to our findings, this effect is only significant at first. Over time, infiltration in the scalped soils is reduced as raindrop impact reseals the surface (Chapter II). After successive rainfall events, a physical crust is expected to form in unprotected BSC-devoid soils that generate much higher runoff than soils covered by BSCs. Because fine-textured soils are more susceptible to physical crusting and development of vesicular horizons than coarse-textured soils (Warren, 2003a), disturbance of BSCs has more negative impact on infiltration in fine than in coarse-textured soils (Chapter II). In addition to the negative effect on infiltration, deterioration or loss of BSCs dramatically increases erosion (Chapter II). This effect also depends on the type of soil texture. As shown by our results, loss of BSCs leads to much faster erosion in fine-textured than in coarse-textured soils.

Removal of BSCs also results in decreased soil moisture, especially in the uppermost layer of the soil, during periods of high soil moisture content. During these wet periods, removal of better-developed BSCs such as lichens leads to a greater decrease in soil moisture than removal of less-developed ones such as cyanobacterial BSCs. This effect is more noticeable in fine-textured soils, where the presence of BSCs has a stronger influence on increasing porosity and infiltration, than in coarse-textured soils (Chapter V). Soil water loss after rain is also faster in BSC-scalped than in crusted soils. BSC organisms are able to absorb large amounts of water after rain and strongly increase water retention at the soil surface (Verrecchia et al., 1995). In addition, swelling of cyanobacterial polysaccharide sheaths and algal and cyanobacteria filaments block soil pores upon wetting (Kidron et al., 1999), leading to a reduction in evaporation and conservation of soil moisture (Verrecchia et al., 1995). During dry periods, soil moisture is similar in BSC-crusted and scalped soils (Chapter V). This is in agreement with the similar total evaporative losses found in late spring in soils with BSCs and the respective soils without BSCs under dry soil conditions (Chapter IV).

In summary, disturbance of BSCs results in decreased infiltration and increased runoff, reduction of soil moisture and increased soil water losses through evaporation, thereby leading to an overall negative effect on the local water balance. In addition, loss of BSCs causes a dramatic increase in erosion (Chapter II). In arid and semiarid ecosystems, where vegetation cover is low and soil is often exposed, resistance of soil to erosion by water and wind is the most important driver for the reduction of resource losses out of the ecosystem (Bowker et al., 2008). The protection created by the network of cyanobacteria filaments and anchoring structures of lichen and mosses, and the secretion of sticky polysaccharides by BSC organisms that increase soil organic matter and soil aggregation provide soils with enormous resistance to erosive forces (Belnap and Gardner, 1993; Mazor et al., 1996). Consequently, a major role of BSCs in drylands is preventing soil erosion and the subsequent loss of sediment and nutrients out of the ecosystem. Changes in soil hydrology, in addition to the noticeable increase in sediment yield as a consequence of BSC disturbance, are likely to affect spatial redistribution of water and nutrient resources and their availability for plants. In addition, lowered soil water availability in interplant spaces due to BSC disturbance would cause important changes in biogeochemical processes in drylands, where water is the most important limiting factor. Thus, changes in soil moisture availability would affect rates of C and N fixation, decomposition of organic compounds, mineralization of N, and soil microbe activity, all of which would lead to changes in the composition and structure of plant communities (Schwinning and Sala, 2004). Ultimately, such alterations would result in modification of general ecosystem functioning (Belnap et al., 2005; Ludwig et al., 2005).

Needs for future research

This thesis demonstrates that the presence of BSCs has a positive effect on the local water balance. This effect increases with advancing BSC development. However, it is been reported that, compared to vegetation, BSCs are considered as sources of runoff and that this water surplus can represent a critical resource for survival of nearby vegetation patches. As emphasized in the discussion above, the effect of BSCs on hydrological processes is temporal and spatial scale-dependent. Thus, transfer of runoff, nutrient and sediment resources from crusted interplant spaces to plant patches is greatly conditioned by the spatial and temporal scale at which hydrological and erosive processes are studied.

This thesis provides an initial approach to the effect of BSCs on infiltration and runoff at a fine spatial scale (microplot and small hillslope scale), but further investigation is required to find out how BSCs affect these processes at coarser spatial scales such as hillslope and catchment.

Information about the effect of BSCs on evaporation, soil moisture or dew deposition is scarce, although the few existing studies highlight their importance. We have analysed the influence of BSCs on evaporation and soil moisture at small spatial scales, as well as temporal variability in soil moisture. Future research should examine the effects of BSCs on these components at coarser spatial scales in more detail, as well as their temporal variability, and integrate them with those of other patch scale components such as bare soil and vegetation. Results from all these studies should be incorporated in current hydrological models in order to improve their capabilities and their usefulness as a resource management tool in arid and semiarid areas. Reliable cartography of BSC distribution in semiarid areas is necessary for this. Analysis of the spectral response of vegetation, physical crusts and various types of BSCs has demonstrated that their distinctive spectral features make their classification possible, as well as BSCs subjected to different disturbances (Chapter VI). We propose a spectral classification system, which applied to multispectral or hyperspectral images, provides a promising tool for mapping this common ground cover in semiarid areas. Specifically, it would enable monitoring spatial distribution and temporal changes in BSCs, and provide essential information about soil surface conditions, C and N stocks, and hydrological and erosive dynamics in arid and semiarid lands. Furthermore, the relationships of BSC type or developmental stage with soil physicochemical properties and hydrological and erosive processes could potentially be used to develop a qualitative/quantitative indicator of soil or ecosystem quality, based on total BSC cover, the presence of well-developed BSCs, or on attributes associated with BSCs.

CONCLUSIONS

1. BSCs improve physicochemical soil properties associated with soil hydrology, stability and fertility, such as water content, aggregate stability, organic carbon and total nitrogen compared to physical crusts, more so the higher the BSC developmental stage is. The influence of BSCs on underlying physicochemical soil properties is especially noticeable in the upper layer of the soil and decreases with depth.

2. The role of soil crusts on hydrological processes shows high temporal variability and is conditioned by the interaction of several factors, such as site characteristics (type of underlying soil, topography, land use), rainfall characteristics, and inherent crust properties, such as roughness, hydrophobicity and porosity. Crust infiltration is higher in coarse than in fine-textured soils. BSCs increase infiltration relative to physical crusts and, within BSCs, infiltration generally increases with more developed BSCs. However, there are exceptions to this general pattern depending on the type of rainfall and the spatial scale considered. At very small spatial scales (0.25 m^2) and under simulated high-intensity rainfall, well-developed lichen BSCs generate lower infiltration rates than less-developed cyanobacterial BSCs. At larger spatial scales (1-10 m^2) under intense natural rainfall, neither BSC type nor cover show significant effect on infiltration. However, under low-intensity natural rainfall, rougher lichen BSCs increase infiltration compared to cyanobacterial BSCs. This effect of lichen BSCs on infiltration is enhanced at coarser spatial scales, as the possibility for runoff to infiltrate along the soil surface increases.

3. The influence of BSCs on soil moisture and evaporation varies depending on soil water content. Under hot wet ambient conditions, both physical crusts and BSCs, as well as the soils underneath them, lose water very quickly, so no significant differences are found in evaporation losses among the types of surfaces. However, during long cold wet periods, BSC-crusted soils maintain more soil moisture and lose water more slowly than BSC-scalped soils. In addition, higher infiltration and slower evaporative losses in lichen than in cyanobacterial BSCs results in higher moisture content in lichen-crusted than in cyanobacteria-crusted soils. In contrast, during long drying periods, larger porosity in lichen-crusted soils results in faster evaporative losses and decreased soil moisture than in cyanobacteria-crusted soil.

4. Disturbance of BSCs has a negative effect on water processes. Disturbance alters infiltration of BSCs in different ways depending on the type of disturbance and the texture of underlying soil. Trampling causes infiltration to decrease, especially under wet conditions and in fine-textured soil. Removal of BSCs increases infiltration at first, but this enhancement diminishes over time as raindrop impact forms a physical crust. In addition to decreasing infiltration, disturbance of BSCs by trampling, and especially by scalping, dramatically increases erosion. Moreover, disturbance of well-developed BSCs induces more erosion than disturbance of less-developed BSCs. During wet periods, removal of BSCs results in decreased soil moisture, especially in the upper layer of the soil. This decrease in soil moisture is more noticeable in fine-textured than in coarse-textured soils. BSC-scalped soils also lose water more quickly than crusted ones. However, during dry periods, the removal of BSCs does not lead to significant changes in soil moisture content compared to soils occupied by BSCs.

5. A quantitative analysis of spectral features of vegetation, physical crusts and BSC developmental stages has demonstrated the possibility of classifying these common ground covers in semiarid areas based on the absorption by pigments at about 500 and 680 nm and by water at about 1450 nm, as well as steepness of the spectral curves between 680-750 and 750-980 nm. The application of the classification system we propose to remote sensing data provides the possibility for future mapping of BSCs in semiarid areas, which is crucial to monitoring spatial and temporal changes in BSCs and incorporating crusted surfaces in current hydrological and erosion models.

6. BSCs increase water input and reduce water output compared to physical crusts or uncrusted soils, and water input increases with more advanced BSC developmental stages. Thus, the presence of BSCs and, especially the presence of well-developed BSCs, have an overall positive effect on the local water balance in semiarid ecosystems.

RESUMEN

En zonas áridas y semiáridas, los espacios libres entre las plantas suelen estar cubiertos por costras físicas y biológicas. Estas costras, aunque representan una parte muy pequeña del perfil del suelo, juegan un papel ecológico importante, ya que constituyen el límite entre la biosfera y la atmósfera, por lo que regulan el intercambio de gases, agua y nutrientes desde y hacia el suelo (Belnap et al., 2003b). En los últimos años, el estudio de las costras biológicas del suelo ha atraído la atención de numerosos investigadores debido al importante papel que éstas desempeñan en numerosos procesos cruciales para los ecosistemas donde aparecen. A diferencia de las costras físicas, las costras biológicas protegen el suelo frente a la erosión por el agua y el viento (Eldridge y Greene, 1994b; Cantón et al., 2001), aumentan el contenido en nutrientes mediante la fijación de carbono atmosférico y la síntesis de polisacáridos, la fijación de nitrógeno atmosférico, reducen las pérdidas de suelo y nutrientes por escorrentía y erosión (Housman et al., 2006; Li et al., 2008), y juegan un papel clave en procesos hidrológicos como la infiltración y escorrentía, humedad del suelo y evaporación, a través de su influencia en numerosas propiedades que afectan al movimiento del agua en el suelo como son la rugosidad, la porosidad, el agrietamiento, el albedo, etc. (Alexander y Calvo, 1990; Malam Issa et al., 2009; Miralles et al., 2011; Rodríguez-Caballero et al., 2012). Además, debido a los cambios que imprimen en las propiedades del suelo, las costras biológicas son capaces de afectar la emergencia, establecimiento y supervivencia de las plantas vasculares (Eldridge y Greene, 1994a; Belnap et al., 2003c; Escudero et al., 2007).

Concretamente, en cuanto al papel de las costras del suelo en los procesos hidrológicos, es ampliamente conocida la influencia de las costras físicas en la reducción de la porosidad y conductividad hidráulica del suelo, disminuyendo así la infiltración (Römkens et al., 1990). La capacidad de retención de agua y conservación de la humedad del suelo también es baja en estas costras (Cantón et al., 2004b). Sin embargo, existe bastante controversia en cuanto al papel de las costras biológicas en los diferentes componentes del balance de agua. Según

algunos estudios, las costras biológicas aumentan la infiltración (Greene y Tongway, 1989; Eldridge, 1993), mientras que según otros, aumentan la escorrentía superficial (Eldridge et al., 2000) o no tienen efecto sobre estos procesos (Eldridge et al., 1997). Por otra parte, el efecto de las costras biológicas en otros componentes del balance de agua como la evaporación o la humedad del suelo apenas se ha estudiado y los escasos trabajos existentes también muestran resultados controvertidos.

Con el objetivo de esclarecer el papel que tienen las costras en el balance de agua en ambientes semiáridos, esta tesis ha analizado la influencia de diferentes tipos de costras, físicas y biológicas, éstas últimas en distintas etapas de su desarrollo, sobre los componentes clave del balance de agua, como son la infiltración, la evaporación y la humedad del suelo, a pequeña escala. Además, para comprender la respuesta hidrológica de estas costras, se ha analizado como influyen el tipo y grado de desarrollo de la costra en diferentes propiedades físico-químicas del suelo que influyen a su vez sobre el movimiento y contenido de agua en el suelo. Por último, se han analizado las características espectrales de los diferentes tipos de costras, así como de la vegetación, con la intención de desarrollar un índice basado en características espectrales distintivas de estos tipos de cubierta comunes en áreas semiáridas que permita su posterior cartografía y la modelización de los efectos de las áreas encostradas en los procesos hidrológicos y erosivos a escalas espaciales mayores (ladera y cuenca).

Para la consecución de nuestros objetivos, se eligieron dos áreas de estudio en el sureste español, El Cautivo (desierto de Tabernas) y Las Amoladeras (Parque Natural de Cabo de Gata-Níjar), donde abundan diferentes tipos de costras biológicas y que son representativos de los tipos de distribución espacial más común de las costras biológicas en ecosistemas semiáridos.

Nuestros resultados muestran que las costras biológicas mejoran la estabilidad de los agregados del suelo, tienen una mayor capacidad de retención de agua y contenido en carbono orgánico y nitrógeno que las costras físicas, y dentro de estas costras biológicas, a medida que la costra es más evolucionada (en términos de biomasa y composición de especies más tardías de la sucesión), estas propiedades se ven favorecidas tanto en la costra como en el suelo subyacente. La mejora que la presencia de las costras biológicas confiere al suelo es sobre todo notable en la capa más superficial del suelo (0.01 m) y disminuye en profundidad (Capítulo I).

Así, a través del aumento de la rugosidad superficial y la mejora en las propiedades físico-químicas del suelo, las costras biológicas aumentan la infiltración y reducen la escorrentía en comparación con costras físicas. En general, el aumento en la infiltración es mayor cuanto mayor es el grado de desarrollo de la costra biológica (Capítulo II). Sin embargo, existen excepciones a este patrón general que vienen condicionadas por otros factores como son la escala espacial de estudio y el tipo de evento lluvioso. A escalas muy pequeñas (0.25 m^2) y bajo una lluvia simulada de 1h de alta intensidad (50 mmh^{-1}), encontramos que las costras más desarrolladas, costras liquénicas, generan mayores tasas de escorrentía que costras menos desarrolladas como las costras dominadas por cianobacterias, e incluso tasas similares a las costras físicas (Capítulo II). Así, a escala de microparcela y en eventos extremos, el efecto positivo en la infiltración debido a la rugosidad promovida por las costras biológicas más desarrolladas puede ser anulado por la capacidad de la costra para bloquear los poros del suelo cuando está mojada, aumentando así la escorrentía. Sin embargo, cuando se estudia la respuesta de las costras biológicas sobre la infiltración y escorrentía en condiciones de lluvia natural y a mayores escalas espaciales (parcelas de 1 a 10 m^2), encontramos que la escorrentía disminuye a medida que aumenta la cobertura de las costras más desarrolladas (líquenes), y que este efecto es mayor a escalas espaciales mayores (Capítulo III). Esta disminución de la escorrentía se debe probablemente a la rugosidad que las costras biológicas bien desarrolladas confieren al suelo (Rodríguez-Caballero et al., 2012). No obstante, de acuerdo con nuestros resultados, este efecto sólo es notable en eventos de lluvia de baja intensidad. En eventos de alta intensidad, la cobertura de costra biológica no tiene una influencia significativa sobre la escorrentía y el principal factor que determina la generación de escorrentía es la intensidad de la lluvia (Capítulo III).

La eliminación de la costra biológica produce un aumento inicial de la infiltración. Sin embargo, este efecto se reduce con el tiempo ya que, con el transcurso de la lluvia y debido al impacto de las gotas de lluvia, se sella nuevamente la superficie del suelo (Capítulo II). Tras varios eventos lluviosos, se forma una costra física que genera tasas de escorrentía superiores a la de los suelos cubiertos por costras biológicas. Además, la alteración de la costra biológica por pisoteo y sobre todo su eliminación, produce un aumento notable de la erosión (Capítulo II). El grado de desarrollo de la costra biológica también influye sobre la erosión, de forma que costras biológicas desarrolladas (líquenes y musgos) protegen mejor frente a la erosión que costras menos desarrolladas (cianobacterias) (Capítulo II).

Respecto a la influencia de las costras en la evaporación, la medida de la pérdida de agua, usando microlisímetros, en los distintos tipos de costra y suelos en los que se eliminó la costra biológica, demuestra que, bajo condiciones de saturación del suelo y elevadas temperaturas ambientales, la pérdida de agua en todos los microlisímetros es rápida, de forma que la pérdida total de agua durante el ciclo evaporativo completo (desde saturación hasta suelo seco) es similar en los tipos de superficies estudiadas (Capítulo IV). Sin embargo, el registro en continuo de la humedad del suelo durante un año con sensores de humedad instalados a dos profundidades (0.03 y 0.10 m) bajo costras biológicas y suelos en lo que se eliminó dicha costra demuestra que, bajo condiciones ambientales menos cálidas, las pérdidas evaporativas tras una lluvia son más rápidas en suelos sin costras biológicas que en los cubiertos por dichas costras (Capítulo V). Así, en épocas húmedas, la humedad del suelo se mantiene más alta en los primeros centímetros de suelo en suelos con costras biológicas que en suelos adyacentes donde se eliminó la costra. A profundidades mayores (0.10 m), el contenido en humedad es similar en suelos con y sin costra biológica (Capítulo V). Por otro lado, la eliminación de la costra biológica causa una disminución mayor de la humedad en los suelos de textura franco-limosa (Cautivo) que en los suelos de textura franco-arenosa (Amoladeras), probablemente debido al mayor efecto que tienen las costras biológicas en el aumento de la porosidad y con ello, en la infiltración, en suelos de textura fina que en suelos de textura gruesa. La disminución del contenido en humedad del suelo también es mayor cuando se eliminan costras biológicas más desarrolladas (aquellas dominadas por líquenes) que cuando se eliminan costras menos desarrolladas (dominadas por cianobacterias). En condiciones de baja humedad del suelo, la humedad del suelo es similar en suelos con y sin costras biológicas (Capítulo V).

Por último, el estudio de las características espectrales de los tipos de costra, así como de la vegetación, ha permitido identificar ciertas características espectrales distintivas entre los tipos de cubiertas (Capítulo VI). A partir de estas características, se ha generado un índice espectral para discriminar diferentes tipos de costra biológica y éstas del suelo desnudo (costra física) y de la vegetación, que podría potencialmente aplicarse a imágenes multi e hiperespectrales para cartografiar la distribución espacial y dinámica temporal de las costras biológicas y poder incorporar así sus efectos en la modelización hidrológica y erosiva a escalas espaciales mayores, esto es, a escala de ladera y cuenca.

En resumen, la presencia de costras biológicas del suelo, comparado con costras físicas, mejora las propiedades físico-químicas del suelo subyacente, especialmente en los primeros centímetros de suelo, siendo la mejora mayor a medida que la costra biológica es más desarrollada. Debido a estas mejores propiedades del suelo y a la mayor rugosidad que las costras biológicas confieren a la superficie de los suelos, la presencia de dichas costras aumenta las entradas de agua a través de la mejora en la infiltración y aumento del contenido de humedad del suelo, y reduce las salidas de agua a través de la disminución de las pérdidas de agua por evaporación. Así, la presencia de costras biológicas frente a costras físicas y, especialmente la presencia de costras biológicas desarrolladas, tiene un efecto global positivo sobre el balance de agua local. Además, las costras biológicas tienen un papel crucial en la protección del suelo frente a la erosión por el agua y el viento.

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