Ecosystems (2012) 15: 148–161
DOI: 10.1007/s10021-011-9499-6

ECOSYSTEMS
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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 study was to analyze 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 southeast Spain characterized 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 (BSC) showed higher infiltration rates than physical soil crusts (PSC). Within BSC, infiltration increased as cyanobacterial biomass increased and was the highest in moss crusts. However, late-successional crustose and squamulose lichen crusts 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.

Key words: physical soil crust; biological soil crust; developmental stage; infiltration; trampling; scraping.

Received 13 June 2011; accepted 7 October 2011;
published online 3 November 2011

Author Contributions: YC, RL conceived the study; FD contributed original ideas; SC, YC, RL, AS, FD performed the research; SC, RL, YC analyzed the data; SC, YC wrote the paper.

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Introduction

Semiarid areas are heterogeneous landscapes characterized by patches of vegetation and open spaces between the scattered vascular plants usually occupied by physical soil crusts (PSC) and biological soil crusts (BSC). 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 and others 1990; Ludwig and others 2005; Li and others 2008; Cantón and others 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 and others 2006). Therefore, the knowledge of how crusts and their disturbance affect runoff generation and thereby influence nutrient cycling, erosion, and vegetation patterns in drylands is of vital importance.

Physical and biological crusts are widespread in arid and semiarid areas, which comprise over 40% of the world's land surface (Reynolds and others 2007). Although PSC and BSC are an almost negligible portion of the soil profile (from less than one to a few millimeters in thickness), they play multiple roles, especially where water is scarce (Maestre and others 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 and others 2003a). 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 PSC and BSC on runoff and infiltration at the plot scale but, whereas there is general agreement regarding the negative impact of PSC on infiltration from reducing hydraulic conductivities and infiltration rates (Römkens and others 1990; Singer and Bissonnais 1998; Neave and Rayburg 2007), the role of BSC in regulating water flow into soils is not well understood (Eldridge and Greene 1994). Some studies indicate that the presence of BSC increases infiltration, and consequently, decreases runoff (for example, Harper and St. Clair 1985; Greene and Tongway 1989; Eldridge 1993), whereas others have found that it has no effect on either of them (for example, Eldridge and others 1997). Still other studies suggest that both PSC and BSC decrease infiltration and increase runoff (for example, Solé-Benet and others 1997; Eldridge and others 2000; Cantón and others 2002). Part of this controversy was interpreted by Warren (2003a), who concluded from the literature that BSC decrease infiltration on soils where the sand content exceeds 80% and do not frost, due to blocking of soil pores by filaments of BSC, 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 BSC, and the consequent improvement in porosity. According to a review by Belnap (2006), the contradicting results on the hydrological role of the BSC 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 (for example from early to late successional BSC) 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 BSC to swell upon wetting can cause pore clogging (Kidron and others 1999; Fischer and others 2010) and induce important differences in runoff generation. Furthermore, BSC 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 BSC or convert late-successional BSC into early ones (Barger and others 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 1994; Mazor and others 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 and others 2010).

Derived from the reasons mentioned above, we designed an experiment to analyze 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 PSC and BSC was investigated by rainfall simulation in two Mediterranean ecosystems in southeast 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, characterized by disperse patches of vegetation and interplant spaces occupied by soil crusts; (2) successional dynamics of BSC (that is, from poorly developed BSC such as cyanobacteria to well-developed BSC such 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 behavior 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 PSC and BSC are interspersed in many semiarid ecosystems, few studies have considered both jointly (for example, see Solé-Benet and others 1997; Cantón and others 2002).

The specific objectives of this article were to: (1) analyze the influence of different crust types, representing a development gradient, on infiltration, (2) analyze 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 PSC than in the BSC and within these, infiltration would increase from the least to the most developed BSC, as a result of increased biomass and roughness with the higher development of the crust (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 PSC and BSC, on two different soil types and also considering different crust disturbance conditions.

Material and Methods

Study Sites

Two sites representing key spatial distributions of BSC in Mediterranean semiarid ecosystems were chosen: El Cautivo, in the Tabernas desert, with crusts (PSC and BSC) occupying most of the ground cover and located on fine-textured soils, and Las Amoladeras, with crusts (mainly BSC) representing almost a third of the soil cover, occupying intershrub spaces and on coarser-textured soils. Both the sites are located in the province of Almeria in southeast Spain (Figure 1).

(a) El Cautivo (N37°00′37″, W2°26′30″) is located in the Neogene–Quaternary Tabernas depression. Several studies on its geomorphology, hydrology, and erosion provide a good general description of the area (see for example, Solé-Benet and others 1997; Cantón and others 2002, 2003; Lázaro and others 2008). The climate is semiarid thermo-Mediterranean, with a mean annual rainfall of 235 mm, falling mostly in winter. The main soil types at the site identified by Cantón and others (2003) are Epileptic and Endoleptic Leptosols, Calcaric Regosols, and Eutric Gypsisols (FAO 1998), and soil texture is silty loam. Soil under BSC 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 area is a mosaic of three main surface types, each occupying about a third of the total area: zones dominated by vascular plants (*Macrochloa tenacissima* (L.) Kunth, *Helianthemum almeriense* Pau, *Artemisia barrelieri* Besser, *Salsola genistoides* Juss. ex Poir., *Euzomodendron bourgaeanum* Cosson), zones dominated by BSC with very sparse vascular plants, and zones with eroded soil and very low vegetation or BSC cover, where PSC strongly dominate. In summary, PSC (30%) and BSC (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 and others 2004).

(b) Las Amoladeras (N36°48′34″, W2°16′6″) is located in Cabo de Gata-Níjar Natural Park. It is an exposed, dissected caliche area in the distal, flat part of an alluvial fan system. The climate is also semiarid, with a mean annual rainfall of 200 mm. 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 BSC has average percentages of sand, silt, and clay of 61.5 ± 5.1, 28.4 ± 4.8,

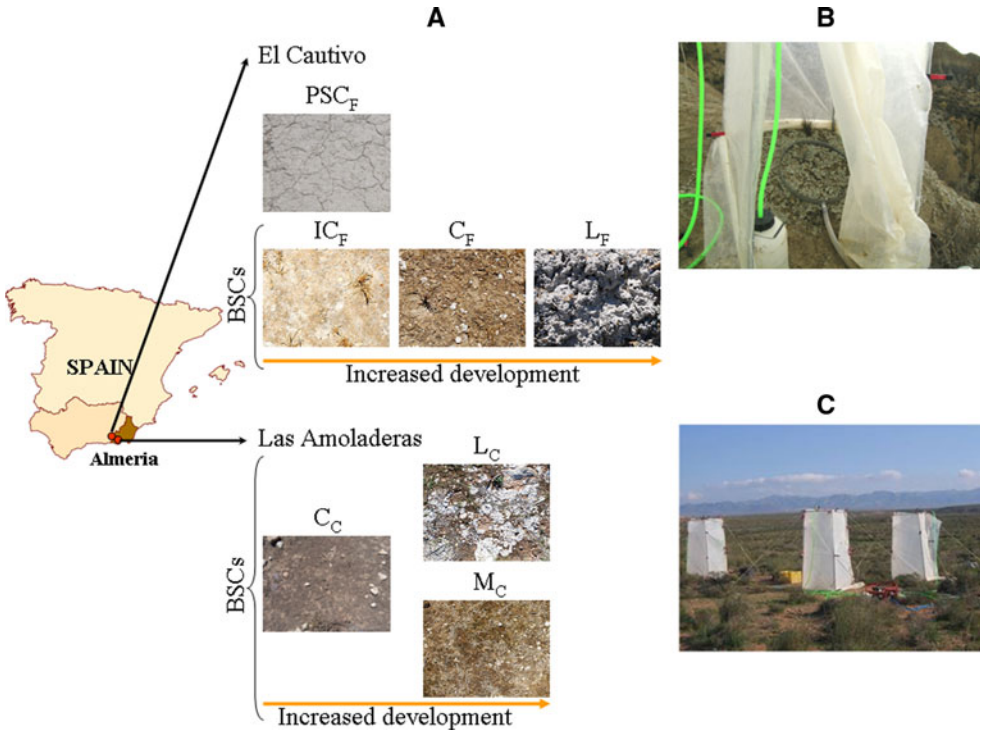

Figure 1. Location map and photographs of the most representative soil crusts at each site. **A** The different crust types in the two study sites. *PSC* = physical soil crust; *IC* = incipient-cyanobacterial crust; *C* = cyanobacterial crust; *L* = lichen crust; *M* = moss crust. The subscripts indicate the soil texture below the crust: *F* = fine; *C* = coarse. **B** Rain simulation microplot bounded by a metal ring and the pipe to collect water runoff. **C** The three rainfall simulators, one for every treatment, running simultaneously. Rainfall simulations were done on every soil crust type.

and 10.1 ± 2.1, respectively. Livestock grazing is frequent in the area. 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. BSC 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, PSC are not frequent in this area and most soil crusts are BSC.

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 and others (2008), who classified the main types in our study areas based on the crust development stage, using crust composition and color as indicators. The most representative crust types in El Cautivo area, on fine-textured soils (indicated by subscript F), were (Figure 1A): (1) physical soil crust (PSC_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 (Figure 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 BSC, whereas the lichen and moss crusts represent late-successional stages.

It should be pointed out that at both sites, except for the ''physical crust'' and the ''incipient cyanobacterial crust'' at El Cautivo, the other crust types are complex communities, which even at the microplot scale, do not imply a ''pure'', constant kind of soil surface, but represent the predominant ground cover in the microplot. 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* spp., particularly, *F. fulgida* (Nyl.) Szatala. The lichen or white crust also includes considerable cyanobacterial cover in addition to large terricolous lichens, such as *Diploschistes diacapsis* (Ach.) Lumbsch, *Squamarina lentigera* (Weber) Poelt, *Buellia zoharyi* Galun and *B. epigea* (Pers.) Tuck., *Lepraria crassissima* (Hue) Lettau, and *Acarospora nodulosa* (Dufour) Hue. Other lichen species, such as *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.

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 50-cm long chain with 0.3-cm 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 (Figure 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 × 3 treatments × 2 antecedent soil moisture conditions × 4 repetitions) and 72 in Las Amoladeras (3 crust types × 3 treatments × 2 antecedent soil moisture conditions × 4 repetitions). The rainfall simulator used, described by Calvo-Cases and others (1988) and Cerdá and others (1997), has been successfully applied in numerous studies on the effect of surface on infiltration (Solé-Benet and others 1997; Cerdá 1999a, b; Mayor and others 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 center delimited by the ring, where rainfall is uniform. The rain (deionized 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 (Figure 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 and others 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 and others 1997; Cantón and others 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 (1933).

Generalized Linear Models (GLM) were used to test for differences in the dependent variables: total infiltration rate (In, mm h^{-1}) and steady state infiltration rate (fc, mm h^{-1}). First, a series of GLM (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 GLM was done separately for each study site. The factors (categorical predictors for the dependent variables) were crust type (PSC_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 STATISTICA 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 with increased crust development such 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

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

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

PSC_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.
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).

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 GLM 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 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 to 3.84 mm

Table 2. *P* Values from the Generalized Linear Models (GLM) to Test the Influence of the Categorical Predictors and their Interactions (Rows): Site (Only in the First Series of GLM, 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)

	Both areas		Badlands area		Caliche area	
	In (mm h^{-1})	fc (mm h^{-1})	In (mm h^{-1})	fc (mm h^{-1})	In (mm h^{-1})	fc (mm h^{-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	–

Third order interactions were not significant and are not shown in the table.
*Significant P values at ** 95% and * 90% confidence interval.*

Table 3. Mean Infiltration Rates (After 1-h 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

Crust type	Total infiltration rates (mm h^{-1})			Steady state infiltration rates (mm h^{-1})		
	Undisturbed	Trampled	Scraped	Undisturbed	Trampled	Scraped
PSC_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	$^{C}44.4 \pm 3.0^{b}$	$^{B}41.6 \pm 3.7^{ab}$	$^{A}34.1 \pm 9.4^{a}$	$^{A}35.8 \pm 8.2^{A}$	$^{A}25.4 \pm 3.4^{B}$	$^{A}22.1 \pm 4.8^{B}$

PSC_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.
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).

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.

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 BSC, infiltration increased with crust development (IC_F–C_F and C_C–L_C–M_C), except for the lichen crust, 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 BSC and infiltration rates similar to the PSC. The steady state infiltration rates (fc) followed the same pattern as total infiltration rates, that is, higher as crust development increased, except for the lichen crust on fine-textured soils, which generated steady state infiltration rates similar to the PSC.

Effects of Antecedent Soil Moisture

Infiltration rates significantly varied depending on antecedent soil moisture (Table 2). Figure 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).

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 Figure 3. 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 crust in Figure 3B).

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-h simulated rain between the trampled and the respective undisturbed crust type was not statistically significant (Table 3). As shown in Figure 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 crust, where crust 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

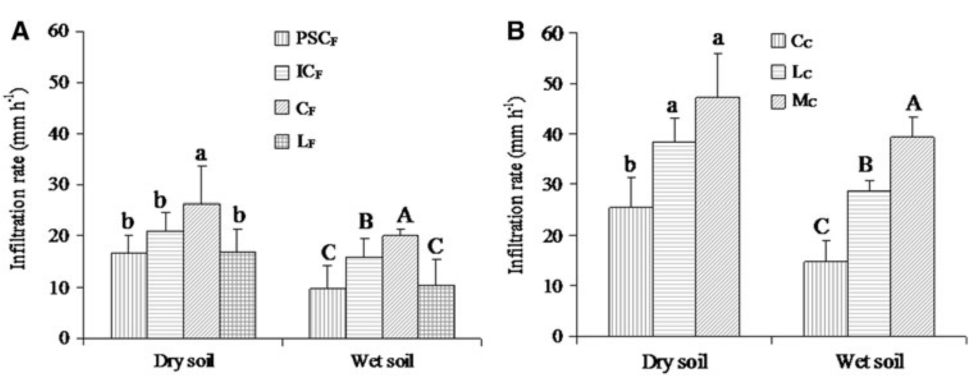

Figure 2. Mean infiltration rates (average of the four plots), with their standard deviations, in the different crust types on fine-textured soil (El Cautivo) (**A**): PSC_F = physical soil crust, IC_F = incipient-cyanobacterial crust; C_F = cyanobacterial crust; L_F = lichen crust; and on coarse-textured 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*).

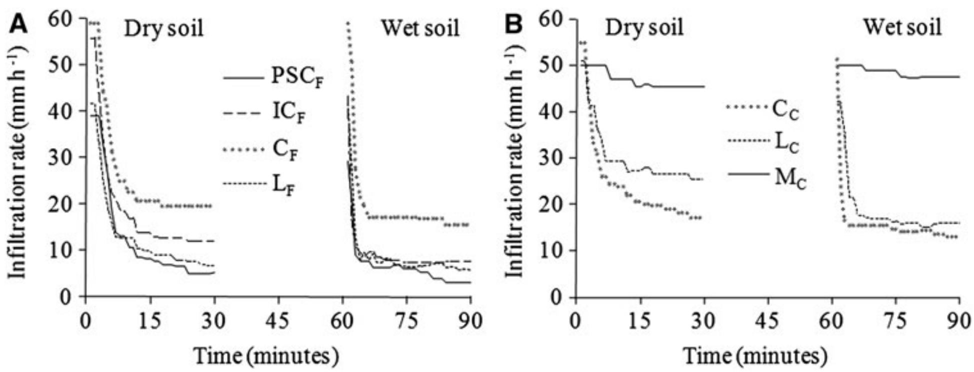

Figure 3. Infiltration curves in plots of each undisturbed crust type under dry and wet antecedent soil moisture, on fine- (El Cautivo) (**A**) and coarse-textured (Las Amoladeras) (**B**) soil.

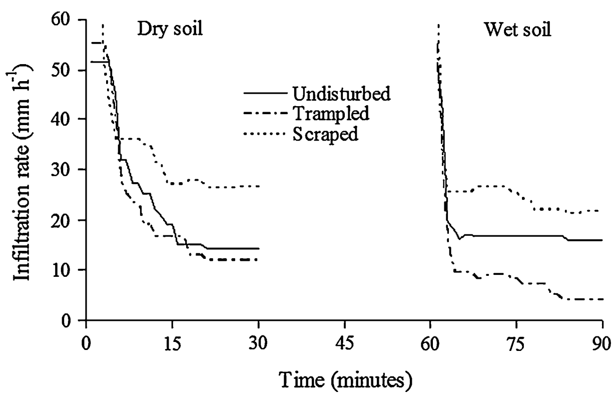

Figure 4. Infiltration curve of a lichen microplot on fine-textured soil (El Cautivo), for the three disturbance conditions and under dry and wet antecedent soil moisture.

the scraped crusts approached those recorded in the respective undisturbed crust types (Figure 4). Hence, differences in infiltration between the undisturbed and the respective scraped crusts after the 1-h 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).

Discussion

The role of BSC on 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 analyzed the influence on these processes of various crust types, including PSC and different developmental stages of BSC, 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 characterized by large pores and rapid infiltration, whereas fine-textured soils are characterized 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 BSC increased infiltration compared to PSC, and that infiltration generally increased with greater development of the BSC (Table 3; Figure 2). These results agree with the hypothesis suggested by Warren (2003a) regarding the positive effect of BSC on infiltration in soils with a sand content less than 80%, where pore formation by BSC has a larger impact on infiltration rates than pore blocking by them.

Physical crusts are known to reduce infiltration by blocking soil matrix pores (Römkens and others 1990). Miralles and others (2011) reported these crusts to be characterized by small rounded pores, most of the 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. Biological crusts 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, BSC can enhance infiltration by their effect on microtopography (Eldridge and Greene 1994) 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 crust had low biotic crust biomass and little roughness (Table 1) and also low porosity due to the predominance of vesicle pores (Miralles and others 2011), explaining the lower infiltration rates than the cyanobacterial crust, which was rougher (Table 1) and has higher meso- and macroporosity (Miralles and others 2011), thus promoting higher infiltration rates (Table 3; Figure 2). The lichen crust, although more developed and, consequently, rougher than the other crust types (Table 1), showed similar infiltration rates to PSC (Table 3; Figure 2). These low infiltration rates in the lichen crusts 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 and others (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 crust mainly consisted of *Diploschistes diacapsis* and *Squamarina lentigera* that have been described as having hydrophobic features in the soil interface (Souza-Egipsy and others 2002). Souza-Egipsy and others (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 and others (2011) reported for these lichen crusts 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 favor infiltration. Hydrophobicity in BSC can be generated also chemically, due to metabolites of some fungi and polysaccharide secretions of some algae and cyanobacteria (Mazor and others 1996; Kidron and others 1999; Warren 2003a; Fischer and others 2010). As shown in Table 3, infiltration remained low even after removal of the lichen crust, 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 crusts 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 and others 2010) and, along with frequent cracks in the lichens from trampling, explains the higher infiltration rates compared to the cyanobacterial crusts. Mosses are highly permeable and have high water-holding capacity and microroughness which slows runoff flux, thus lengthening the beginning of runoff by absorbing large amounts of water after a rain (Maestre and others 2002; Eldridge 2003). Moss crusts 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 crusts than in lichens or in cyanobacterial crusts (Brotherson and Rushforth 1983; Eldridge and others 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 (Figure 2) and steady state infiltration rates were reached sooner (Figure 3).

Effects of Crust Disturbance on Infiltration

Given the vulnerability of BSC to disturbance, in addition to analyzing the role of different developmental stages of BSC on infiltration, disturbance treatments were included to provide information on the consequences of a possible land-use change (for example, 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 (Figure 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 and others 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 the well-developed lichen and moss crusts, but not the earlier cyanobacterial crusts (Table 3). In contrast, Herrick and others (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 crusts on coarse-textured soil, probably because these BSC promoted the highest infiltration rates (Table 3). Unlike them, the cyanobacterial crust 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 and others 2000; Barger and others 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 (Figure 4). Besides, the formation of PSC occurs 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 PSC 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 the average erosion rate after the 1-h simulated rainfall on the undisturbed and disturbed crust types, at both sites. Sediment yields strongly decreased from the physical to cyanobacterial and to lichen and moss crusts and were much lower on the flat coarse soil than on the steeper fine soil. It is important to emphasize that despite the fact that the lichen crusts on fine soil generated similar infiltration rates to PSC, there were marked differences in erosion rates between them. The lichen crusts generated the lowest erosion rates whereas the PSC exhibited the highest. The removal of the lichen BSC also induced the highest increase in erosion.

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 and others (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 BSC contribute to increased water infiltration (Table 3) and reduced

Table 4. Mean Erosion Rate, and Standard Deviation (g m^{-2}), After 1-h Simulated Rainfall on the Undisturbed, Trampled, and Scraped Crust Types

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

PSC_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.

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 (Table 4) compared to PSC or poorly developed BSC. This absorbed water triggers microbial activity and stimulates C and N fixation by BSC that is used to produce more BSC biomass (Belnap and others 2005). Increased biomass contributes to increase in 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 increases the formation of macropores in the soil, thereby enhancing infiltration (Ludwig and others 2005). Nevertheless, infiltration rates found in the BSC are lower than those commonly reported for vascular plants (Cantón and others 2011), which highlights the relevance of BSC 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 and others 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 (Figure 2). Moreover, unlike PSC, BSC strongly contribute to reduction of soil erosion and thus, to nutrient retention and maintaining of fertility in the interplant spaces, also creating a more favorable habitat for soil microbiota (Belnap 2003) and vascular vegetation (Belnap and others 2003b).

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 BSC. Belnap and others (2004) reported that alterations in precipitation frequency could reduce the cover of late-successional BSC. The expected consequences of a replacement of late-successional by early successional BSC, 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 such as grazing, hunting, or recreational uses in private and public lands have the potential to cause deterioration or destruction of BSC (Barger and others 2006), leaving the soil surface unprotected and, as shown by our results, facilitating the formation of PSC, which increase runoff and erosion (Tables 3, 4). The loss of BSC would be implicated in a decrease of soil stability, an increase in water and wind erosion (Eldridge and Greene 1994), and a reduction in the capacity of soils to trap nutrient-enriched dust (Reynolds and others 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 and others 2003; Ludwig and others 2005; Li and others 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 PSC 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 and others 2005; Ludwig and others 2005). Therefore, it can be expected that disturbance of ecosystems where BSC 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, BSC 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 such 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 BSC than in PSC. Within the BSC, infiltration increased as cyanobacterial biomass increased and was the highest in the late-successional moss BSC, but late-successional crustose and squamulose lichen BSC showed very low infiltration rates. Therefore, infiltration does not always linearly increase with crust 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 PSC formed again from raindrop impact. Even in further rainfall events the formation of a new well-developed PSC over the scraped surfaces may generate higher runoff than over undisturbed biologically crusted surfaces. Moreover, destruction of BSC 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.

ACKNOWLEDGMENTS

This work has been supported by several research projects: PROBASE (CGL2006-11619/HID), BACARCOS (CGL2011-29429) and PREVEA (CGL2007-63258/BOS), funded by the Ministerio de España de Ciencia e Innovación and including European Union ERDF funds, and COSTRAS (RNM–3614) and GEOCARBO (RNM-3721) funded by the Consejería de Innovación, Ciencia y Empresa de la Junta de Andalucía, including European Union ERDF funds. The first author is funded by a FPI fellowship from the Spanish Government (BES–2007–15218). We thank Alfredo Durán, Luis Villagarcía, Ana Were, Laura Morillas, Carlos Asensio and Ashraf Afana for their indispensable help during the field work. Adrián Escudero is especially thanked for valuable comments to improve this manuscript. The Cautivo site's owner, the Viciana family, is thanked for ceding their land as a ''scientific experimental site.'' We also thank anonymous reviewers for their constructive comments to improve this manuscript.

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