Journal of Hydrology 452–453 (2012) 130–138

Contents lists available at SciVerse ScienceDirect

Journal of Hydrology

journal homepage: www.elsevier.com/locate/jhydrol

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

Sonia Chamizo [a,*], Yolanda Cantón [b], Emilio Rodríguez-Caballero [b], Francisco Domingo [a], Adrián Escudero [c]

[a] *Estación Experimental de Zonas Áridas (EEZA-CSIC), Carretera de Sacramento s/n, 04120 La Cañada de San Urbano, Almería, Spain*
[b] *Departamento de Edafología y Química Agrícola, Universidad de Almería, Carretera de Sacramento s/n, 04120 La Cañada de San Urbano, Almería, Spain*
[c] *Departamento de Biología y Geología, Universidad Rey Juan Carlos, c/Tulipán, 28933 Móstoles, Madrid, Spain*

ARTICLE INFO

Article history:
Received 29 March 2012
Received in revised form 11 May 2012
Accepted 19 May 2012
Available online 27 May 2012
This manuscript was handled by Konstantine P. Georgakakos, Editor-in-Chief, with the assistance of Efrat Morin, Associate Editor

Keywords:
Cyanobacteria
Lichen
Runoff
Microplot scale
Hillslope scale
Structural equation modelling

SUMMARY

Runoff in arid and semiarid areas is characterized 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 analyzed 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 analyzed 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.

1. 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., in press). Publications on their role in infiltration and runoff have reported contradictory results (reviewed in Warren (2003a)), 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 hypothesized 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., 2012a).

* Corresponding author. Tel.: +34 950281045.
E-mail address: schamizo@eeza.csic.es (S. Chamizo).

0022-1694/$ - see front matter © 2012 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.jhydrol.2012.05.045

However, several studies have pointed out the role of BSCs as runoff-source areas in some arid and semiarid areas, and the relevance of this water supply for the survival and maintenance of perennial vegetation downstream (Almog and Yair, 2007; Cantón et al., 2011; Li et al., 2008; Ludwig et al., 2005; Yair et al., 2011).

On the other hand, BSCs are fragile structures that are 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., 2012a). 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 characterized by high spatial and temporal variability, which results from the interaction of different factors acting at each scale (Calvo-Cases et al., 2003; Cammeraat, 2002; Mayor et al., 2011; Puigdefábregas et al., 1999). 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; Arnau-Rosalén et al., 2008; Cantón et al., 2011; Lavee et al., 1998; Solé-Benet et al., 1997). 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 (Greene and Hairsine, 2004; Yair, 2003). 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; Chamizo et al., 2012a; Herrick et al., 2010), and few studies have examined responses at coarser spatial scales, such as hillslopes (e.g., Almog and Yair, 2007; Yair, 2003; 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 analyzed their influence under natural rain conditions (e.g., Almog and Yair, 2007; Cantón et al., 2001, 2002; Kidron and Yair, 1997; 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 2 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 hypothesized 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; Chamizo et al., 2012a; Eldridge et al., 2010; Warren, 2003a). 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).

2. Materials and methods

2.1. Study site

Runoff was monitored in microplots and small hillslope plots at the El Cautivo experimental site in the Tabernas Desert (SE Spain). This area is a badlands catchment surrounded by the Alhamilla, Filabres, Nevada and Gador mountain ranges and developed on gypsum-calcareous mudstones and calcaric sandstones. The mudstone is composed of 80% silt grains with the following predominant mineralogical composition: muscovite (35%), calcite (20–35%), gypsum (5–20%), paragonite (10%) and quartz (9%) (Cantón et al., 2001).The climate is characterized by dry and hot summers with mild temperatures the rest of the year, and rain falling mostly in winter (mean annual rainfall of 235 mm). Soil types are classified as Epileptic, Endoleptic or Calcaric Regosols and Eutric Gypsisols (Cantón et al., 2003) and soil texture is silty loam. Ground cover is strongly controlled by topographic attributes. The area is a mosaic of surfaces characterized by discontinuous perennial plant cover, some patches of annuals in favourable years and widespread physical and biological soil crusts. Physical crusts and BSCs appear as the only soil cover in many landforms, covering almost 80% of the soil surface (Cantón et al., 2004a). Fine soil texture combined with poor structure, low aggregate stability and low organic matter content of the soils in this area make them very prone to physical crusting from raindrop impact. Thus BSCs are usually associated with rain-impact or physical crusts. In early successional stages, cyanobacteria species colonise these physical crusts. Then, as the succession advances, later-successional species, such as lichens, install and replace the earlier cyanobacteria-dominated BSCs (Lázaro et al., 2008).

2.2. 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. 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 cyanobacterial 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 10–100 m. The microplots, located at the top of gentle hillslopes and about 1 m from the watershed, 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 in these plots 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 h 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.

As the plots were open, the contributing area to each plot was estimated from a 1-cm-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.

2.3. 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 (Grace, 2006; Iriondo et al., 2003). 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

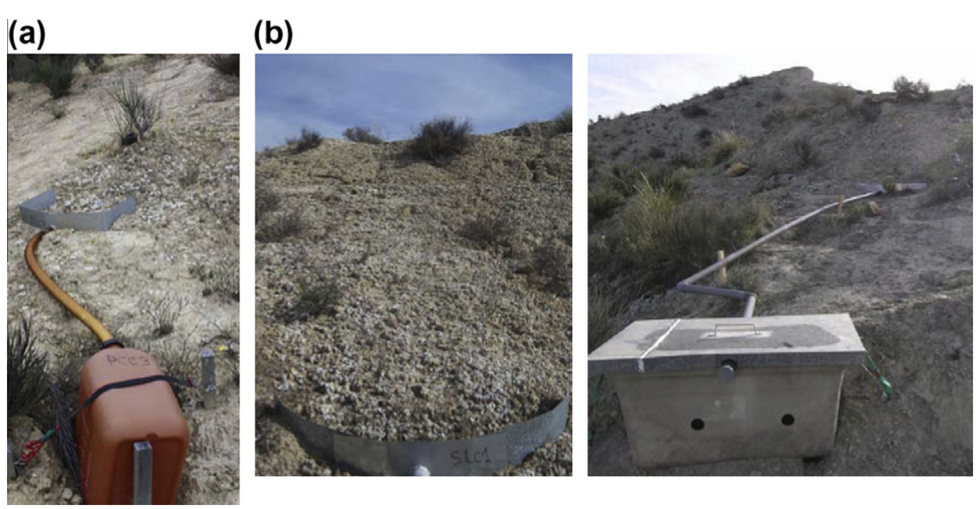

Fig. 1. (a) Microplot on a BSC-dominated crusted surface, connected to a 20 l deposit to collect total runoff. (b) Hillslope plot on a BSC-dominated crusted surface, connected to a tank provided with a 0.5 l tipping-bucket rain gauge to register runoff at high temporal resolution.

structure of data implied by the model with the observed covariance structure of the data (Bollen, 1989; Grace and Pugesek, 1998; McCune and Grace, 2002; Shipley, 2000). 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 plot soil cover and the three covers were correlated, only the cover of the two types of BSC were included in the SEM model (Fig. 2). 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.

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).

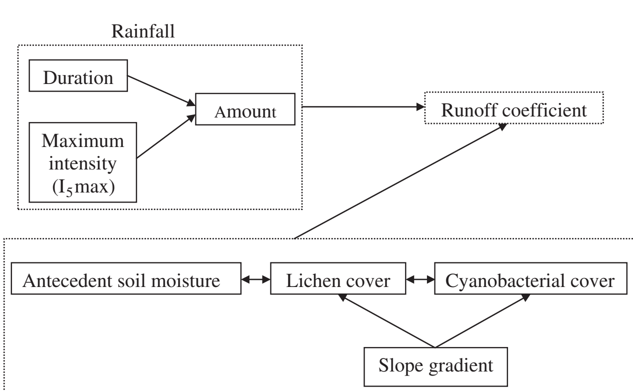

Fig. 2. *A priori* model representing the hypothesized causal relationships among rainfall characteristics, soil-related properties and runoff. I_5max is the maximum 5-min rainfall intensity.

3. Results

3.1. 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 over 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 crusts. 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 5° to 14° in the microplots and from 10° to 24° 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 2-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 mm h^{-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 mm h^{-1} and 57 mm h^{-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).

3.2. 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%

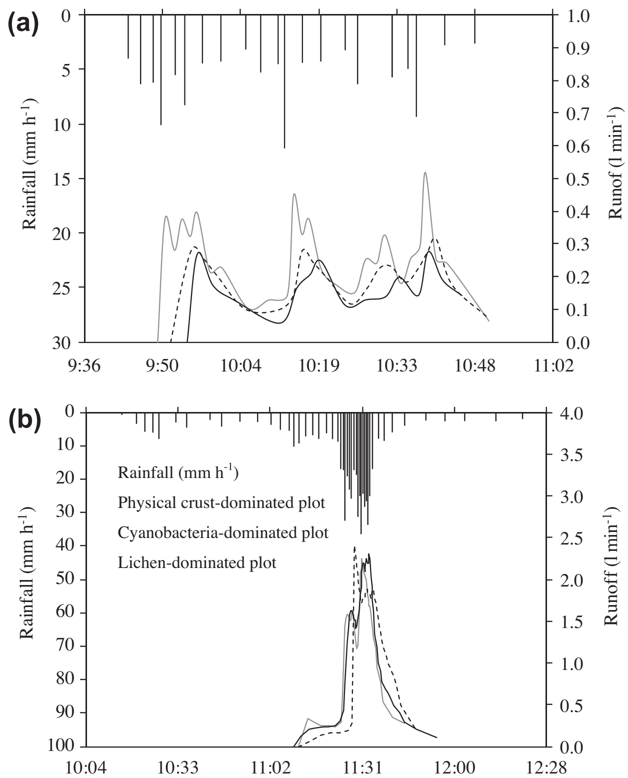

Fig. 3. Hydrograph of a physical-dominated, cyanobacteria-dominated and lichen-dominated hillslope plot, for a low-intensity rainfall (I_5max = 9.8 mm h^{-1}; rainfall amount = 7.5 mm) (a) and a high-intensity rainfall (I_5max = 27.9 mm h^{-1}; rainfall amount = 19.8 mm) (b).

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.

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.

3.3. 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).

4. 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.

4.1. 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; Cantón et al., 2011; Li et al., 2008; Maestre et al., 2011). After monitoring runoff under natural rainfall in plots with varying cover of lichens and cyanobacteria for over 2 years, we found that runoff decreased with increased lichen cover at both microplot and small hillslope scales, when rainfall intensity was low (Figs. 4 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; Chamizo et al., 2012a; Eldridge et al., 2010; Warren, 2003a). Previous high-intensity rainfall simulations (50 mm h^{-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., 2012a). 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,

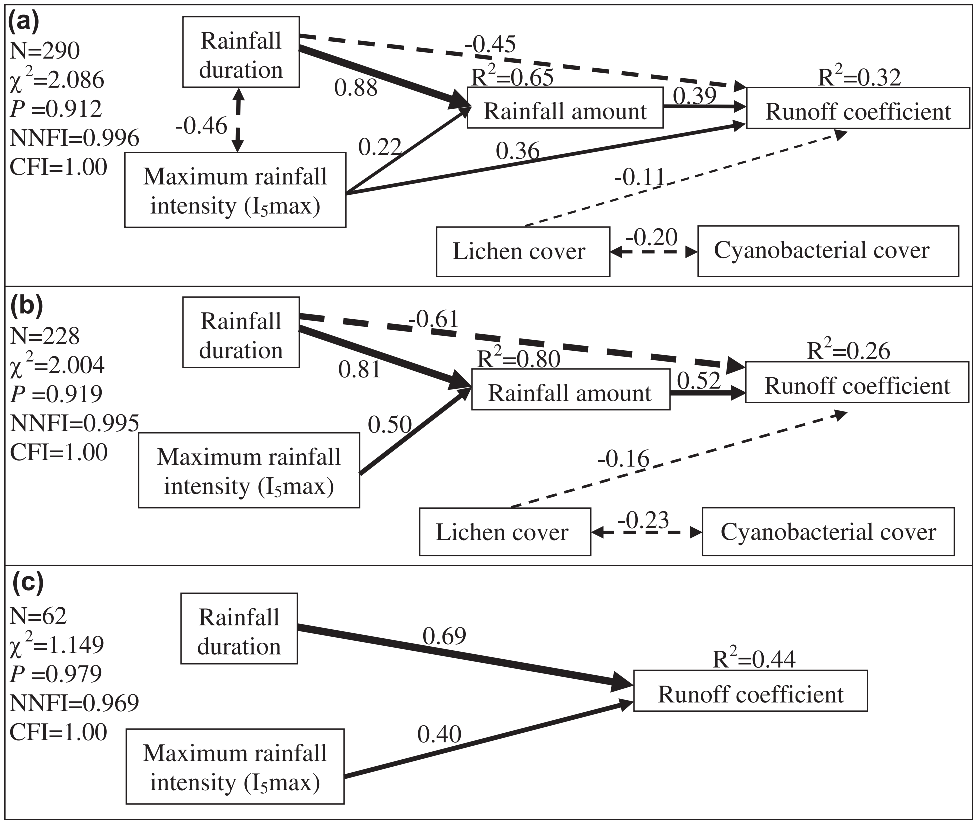

Fig. 4. Microplot runoff SEM model, including (a) all the events registered during the study period (September 2008–December 2010), (b) low-intensity events, and (c) high-intensity events. Continuous lines show positive effects. Dashed lines show negative effects. Arrow widths are proportional to adjacent 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.

these BSCs can reduce runoff by three mechanisms: (1) more developed lichen BSCs have a higher water retention capacity than less developed cyanobacterial BSCs (Chamizo et al., 2012b); (2) lichen surfaces are discontinuous, and when they dry, they crack, allowing water to infiltrate. Although *D. diacapsis* and *S. lentigera* are known to almost completely cap the soil surface, they also present some discontinuities when dry that contribute to increased infiltration. Such effect would be enhanced at coarser spatial scales, as the possibility for runoff infiltration along the soil surface increases (Cantón et al., 2011; Mayor et al., 2011; Puigdefábregas et al., 1998; Wilcox et al., 2003). 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. 4 and 5a); (3) Infiltration is controlled by the interaction of water residence time on a soil surface and the permeability of that surface (Eldridge and Greene, 1994). In this sense, lichen BSCs could enhance infiltration by increasing soil surface roughness and water storage capacity (Rodríguez-Caballero et al., 2012). In hyperarid hot regions, where BSCs are smooth, water retention time is shorter and the area for water infiltration is lower than in BSCs from cold desert regions, which have a high roughness, thus lengthening the path for water infiltration and decreasing runoff (Belnap, 2006). In our areas, with BSCs having a moderate roughness between those of hyperarid and cold regions, lichens (about 1 cm height from the soil) generate rougher surfaces than cyanobacteria (about 0.5 cm height from the soil) and thus, are more effective in reducing runoff than the smoother cyanobacterial BSCs (Rodríguez-Caballero et al., 2012). This seems especially feasible in the presence of frequent squamulose and foliose lichens in our study areas such as *Squamarina lentigera* or *Cladonia convoluta* which present a rougher 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). Moreover, as the spatial scale increases, spatial heterogeneity of soil surface cover increases and it is more likely the alternation of patches of physical, cyanobacterial and lichen BSCs, which increases the possibility for water to transfer from runoff-trigger surfaces to runoff-sink surfaces. This would also explain the lower variance in runoff explained at microplot (26%) than at small hillslope scales (37%) in low-intensity rainfalls. On the other hand, 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 (Figs. 4 and 5b), but no significant effect on runoff in high-intensity rainfall (Figs. 4 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

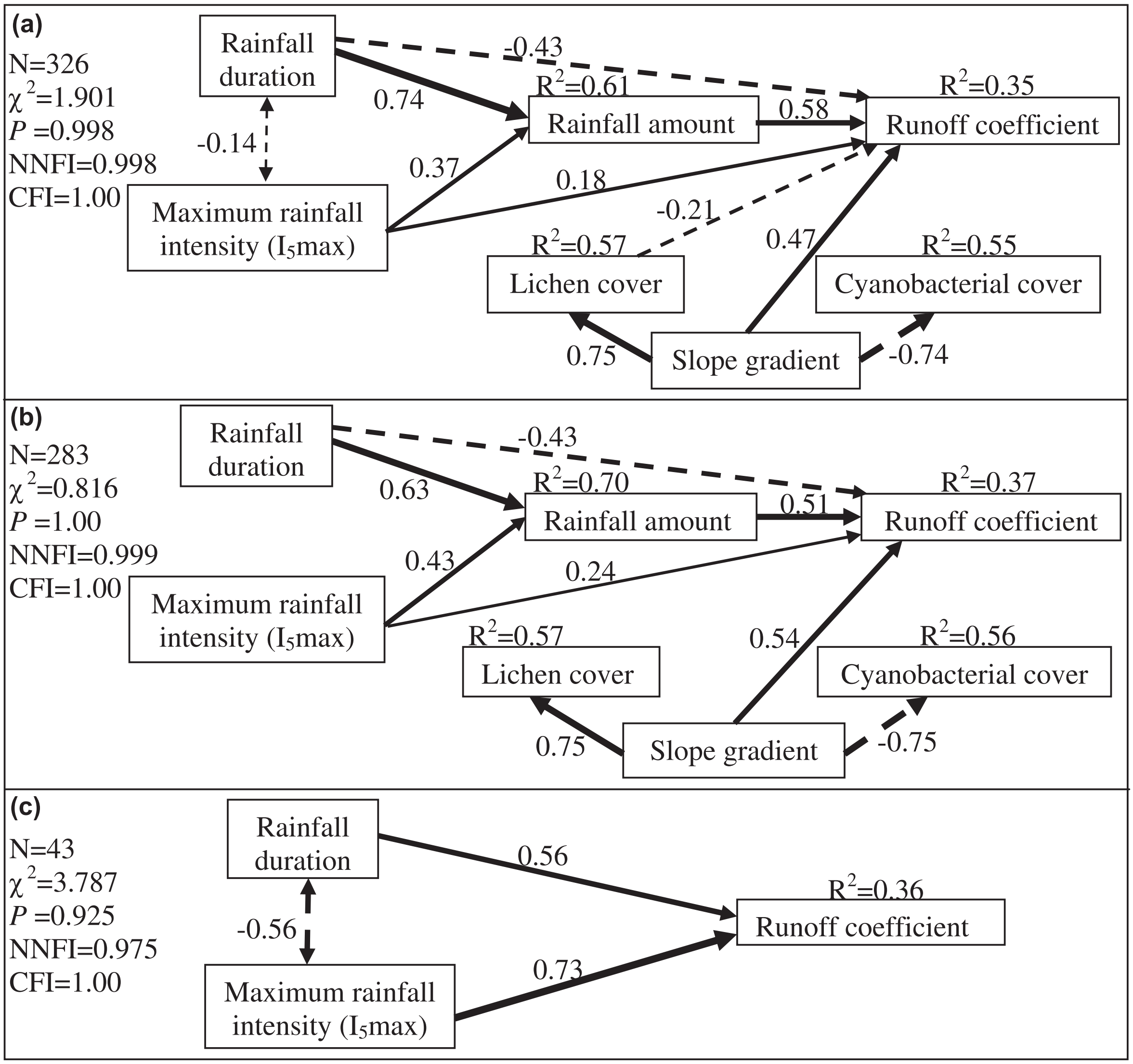

Fig. 5. Small hillslope runoff SEM model, including (a) all the events registered during the study period (September 2008–December 2010), (b) low-intensity events, and (c) high-intensity events. Continuous lines show positive effects. Dashed lines show negative effects. Arrow widths are proportional 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.

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).

4.2. Relationship between the slope gradient and runoff

The influence of slope gradient on runoff depended on the spatial scale analyzed. It had a significant influence on runoff at small hillslope scales (Fig. 5), but not significantly 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). 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, 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.

4.3. 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. 4 and 5a and b), 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. 4 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 5a and b), 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 characterized 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. 4 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. 4 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 many 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 (Chamizo et al., 2012a; Mayor et al., 2009), others have found no relationship between antecedent moisture and runoff at micro-catchment 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.

Acknowledgements

This work has been supported by research Projects: BACARCOS (CGL2011-29429) and CARBORAD (CGL2011-27493), funded by the Ministerio de Ciencia e Innovación and including European Union ERDF funds, and COSTRAS (RNM-3614) and GEOCARBO (P08-RNM-3721) funded by the Consejería de Innovación, Ciencia y Empresa de la Junta de Andalucía, also including European Union ERDF funds. The DESIRE (037046) Project (EC-DG RTD-6th Framework Research Programme) funded the laser scanner that allowed the estimation of the contributing areas of the plots. The first author is funded by a FPI fellowship from the Spanish Government (BES-2007-15218). We thank Alfredo Durán and Iván Ortiz for their indispensable help during the field work, Roberto Lázaro for his help on the installation of the plots, and Ashraf Afana and Albert Solé for their assistance with the laser scanner measurements. We are grateful to three anonymous reviewers for valuable suggestions that have helped to greatly improve the paper. The Cautivo site's owner, the Viciana family, is thanked for ceding their land as a "scientific experimental site".

References

Abrahams, A.D., Parsons, A.J., Wainwright, J., 1995. Effects of vegetation change on interrill runoff and erosion, Walnut Gulch, Southern Arizona. Geomorphology 13, 37–48.

Alexander, R.W., Calvo, A., 1990. The influence of lichens on slope processes in some Spanish badlands. In: Thornes, J.B. (Ed.), Vegetation and Erosion. John Wiley, New York, pp. 385–398.

Almog, R., Yair, A., 2007. Negative and positive effects of topsoil biological crusts on water availability along a rainfall gradient in a sandy arid area. Catena 70, 437–442.

Álvarez-Mozos, J., Campo, M.A., Giménez, R., Casalí, J., Leibar, U., 2011. Implications of scale, slope, tillage operation and direction in the estimation of surface depression storage. Soil. Till. Res. 111, 142–153.

Arnau-Rosalén, E., Calvo-Cases, A., Boix-Fayos, C., Lavee, H., Sarah, P., 2008. Analysis of soil surface component patterns affecting runoff generation. An example of methods applied to Mediterranean hillslopes in Alicante (Spain). Geomorphology 101, 595–606.

Barger, N.N., Herrick, J.E., Zee, J.V., Belnap, J., 2006. Impacts of biological soil crust disturbance and composition on C and N loss from water erosion. Biogeochemistry 77, 247–263.

Belnap, J., 2006. The potential roles of biological soil crusts in dryland hydrologic cycles. Hydrol. Process. 20, 3159–3178.

Belnap, J., Welter, J.R., Grimm, N.B., Barger, N., Ludwig, J.A., 2005. Linkages between microbial and hydrologic processes in arid and semiarid watersheds. Ecology 86, 298–307.

Bentler, P.M., 1989. EQS Structural Equations Program Manual. BMDP Statistical Software, Los Angeles, CA, USA.

Bentler, P.M., Bonet, D.G., 1980. Significance tests and goodness of fit in the analysis of covariance structures. Psychometrika 45, 289–308.

Bollen, K.A., 1989. Structural Equations with Latent Variables. Wiley-Interscience, New York, New York, USA.

Bollen, K.A., Stine, R.A., 1992. Bootstrapping goodness-of-fit measures in structural equation models. Sociol. Method. Res. 21, 205–229.

Calvo-Cases, A., Harvey, A.M., Paya-Serrano, J., Alexander, R.W., 1991. Response of the badland surfaces in the south east Spain to simulated rainfall. Cuaternario y Geomorfología 5, 3–14.

Calvo-Cases, A., Boix-Fayos, C., Imeson, A.C., 2003. Runoff generation, sediment movement and soil water behaviour on calcareous (limestone) slopes of some Mediterranean environments in southeast Spain. Geomorphology 50, 269–291.
Cammeraat, L.H., 2002. A review of two strongly contrasting geomorphological systems within the context of scale. Earth. Surf. Proc. Land. 27, 1201–1222.
Cantón, Y., Domingo, F., Solé-Benet, A., Puigdefábregas, J., 2001. Hydrological and erosional response of a badlands system in semiarid SE Spain. J. Hydrol. 252, 65–84.
Cantón, Y., Domingo, F., Solé-Benet, A., Puigdefábregas, J., 2002. Influence of soil surface types on the overall runoff of the Tabernas badlands (SE Spain). Field data and model approaches. Hydrol. Process. 16, 2621–2643.
Cantón, Y., Solé–Benet, A., Lázaro, R., 2003. Soil–geomorphology relations in gypsiferous materials of the Tabernas desert (Almería, SE Spain). Geoderma 115, 193–222.
Cantón, Y., Del Barrio, G., Solé-Benet, A., Lázaro, R., 2004a. Topographic controls on the spatial distribution of ground cover in a semiarid badlands area. Catena 55, 341–365.
Cantón, Y., Solé-Benet, A., Domingo, F., 2004b. Temporal and spatial patterns of soil moisture in semiarid badlands of SE Spain. J. Hydrol. 285, 199–214.
Cantón, Y., Solé-Benet, A., de Vente, J., Boix-Fayos, C., Calvo-Cases, A., Asensio, C., Puigdefábregas, J., 2011. A review of runoff generation and soil erosion across scales in semiarid south-eastern Spain. J. Arid. Environ. 75, 1254–1261.
Castillo-Monroy, A., Maestre, F., 2011. La costra biológica del suelo: avances recientes en el conocimiento de su estructura y función ecológica. Rev. Chil. Hist. Nat. 84, 1–21.
Chamizo, S., Cantón, Y., Lázaro, R., Solé-Benet, A., Domingo, F., 2012a. Crust composition and disturbance drive infiltration through biological soil crusts in semiarid ecosystems. Ecosystems 15, 148–161.
Chamizo, S., Cantón, Y., Miralles, I., Domingo, F., 2012b. Biological soil crust development affects physicochemical characteristics of soil surface in semiarid ecosystems. Soil. Biol. Biochem. 49, 96–105.
Chamizo, S., Cantón, Y., Domingo, F., Belnap, J., in press. Evaporative losses from soils covered by physical and different types of biological soil crusts. Hydrol. Process. doi:10.1002/hyp.8421.
Eldridge, D.J., Greene, R.S.B., 1994. Microbiotic soil crusts: a review of their roles in soil and ecological processes in the rangelands of Australia. Aust. J. Soil. Res. 32, 389–415.
Eldridge, D.J., Tozer, M.E., Slangen, S., 1997. Soil hydrology is independent of microphytic crust cover: further evidence from a wooded semiarid Australian rangeland. Arid. Soil. Res. Rehab. 11, 113–126.
Eldridge, D.J., Zaady, E., Shachak, M., 2000. Infiltration through three contrasting biological soil crusts in patterned landscapes in the Negev, Israel. Catena 40, 323–336.
Eldridge, D.J., Bowker, M.A., Maestre, F.T., Alonso, P., Mau, R.L., Papadopoulos, J., Escudero, A., 2010. Interactive effects of three ecosystem engineers on infiltration in a semi–arid Mediterranean grassland. Ecosystems 13, 499–510.
Faust, W.T., 1970. The effect of algal-mold crusts on the hydrologic processes of infiltration, runoff, and soil erosion under simulated conditions. MS Thesis, University of Arizona, Tucson, Arizona.
Finch, J.F., West, S.G., MacKinnon, D.P., 1997. Effects of sample size and nonnormality on the estimation of mediated effects in latent variable models. Struct. Equat. Model. 4, 87–107.
Gómez-Plaza, A., Martínez, M., Albaladejo, J., Castillo, V.M., 2001. Factors regulating spatial distribution of soil water content in small semiarid catchments. J. Hydrol. 253, 211–226.
Grace, J.B., 2006. Structural Equation Modeling and Natural Systems. Cambridge University Press, UK.
Grace, J.B., Pugesek, B.H., 1998. On the use of path analysis and related procedures for the investigation of ecological problems. Am. Nat. 152, 151–159.
Greene, R.S.B., Hairsine, P.B., 2004. Elementary processes of soil–water interaction and thresholds in soil surface dynamics: a review. Earth. Surf. Proc. Land. 29, 1077–1091.
Greene, R.S.B., Tongway, D.J., 1989. The significance of (surface) physical and chemical properties in determining soil surface condition of red earths in rangelands. Aust. J. Soil. Res. 27, 213–225.
Hatcher, L., 1994. A Step-by-Step Approach to Using SAS for Factor Analysis and Structural Equation Modelling. SAS Institute Inc., Cary, NC, USA.
Herrick, J.E., Van Zee, J.W., Belnap, J., Johansen, J.R., Remmenga, M., 2010. Fine gravel controls hydrologic and erodibility responses to trampling disturbance for coarse–textured soils with weak cyanobacterial crusts. Catena 83, 119–126.
Housman, D.C., Powers, H.H., Collins, A.D., Belnap, J., 2006. Carbon and nitrogen fixation differ between successional stages of biological soil crusts in the Colorado Plateau and Chihuahuan Desert. J. Arid. Environ. 66, 620–634.
Iriondo, J.M., Albert, M.J., Escudero, A., 2003. Structural equation modelling: an alternative for assessing causal relationships in threatened plant populations. Biol. Conserv. 113, 367–377.
Kidron, G.J., Yair, A., 1997. Rainfall-runoff relationships over encrusted dune surface, Nizzana, western Negev Israel. Earth. Surf. Proc. Land. 22, 1169–1184.
Lavee, H., Imeson, A.C., Sarah, P., 1998. The impact of climate change on geomorphology and desertification along a Mediterranean-arid transect. Land. Degrad. Dev. 9, 407–422.
Lázaro, R., Rodrigo, F.S., Gutiérrez, L., Domingo, F., Puigdefábregas, J., 2001. Analysis of a 30-year rainfall record (1967–1997) in semi–arid SE Spain for implications on vegetation. J. Arid. Environ. 48, 373–395.
Lázaro, R., Cantón, Y., Solé-Benet, A., Bevan, J., Alexander, R., Sancho, L.G., Puigdefábregas, J., 2008. The influence of competition between lichen colonization and erosion on the evolution of soil surfaces in the Tabernas badlands (SE Spain) and its landscape effects. Geomorphology 102, 252–266.
Li, X.J., Li, X.R., Song, M., Gao, Y.P., Zheng, J.G., Jia, R.L., 2008. Effects of crust and shrub patches on runoff, sedimentation, and related nutrient (C, N) redistribution in the desertified steppe zone of the Tengger Desert, Northern China. Geomorphology 96, 221–232.
Ludwig, J.A., Wilcox, B.P., Breshears, D.D., Tongway, D.J., Imeson, A.C., 2005. Vegetation patches and runoff-erosion as interacting ecohydrological processes in semi-arid landscape. Ecology 86, 288–297.
Maestre, F.T., Bowker, M.A., Cantón, Y., Castillo-Monroy, A.P., Cortina, J., Escolar, C., Escudero, A., Lázaro, R., Martínez, I., 2011. Ecology and functional roles of biological soil crusts in semi-arid ecosystems of Spain. J. Arid. Environ. 75, 1282–1291.
Mayor, A.G., Bautista, S., Bellot, J., 2009. Factors and interactions controlling infiltration, runoff, and soil loss at the microscale in a patchy Mediterranean semiarid landscape. Earth. Surf. Proc. Land. 34, 1702–1711.
Mayor, A.G., Bautista, S., Bellot, J., 2011. Scale-dependent variation in runoff and sediment yield in a semiarid Mediterranean catchment. J. Hydrol. 397, 128–135.
McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MJM Software Design, Gleneden Beach, Oregon.
Puigdefábregas, J., Barrio, G., Boer, M., Gutierrez, L., Solé, A., 1998. Differential responses and channel elements to rainfall events in a semi-arid area. Geomorphology 23, 337–351.
Puigdefábregas, J., Solé, A., Gutierrez, L., Barrio, G., Boer, M., 1999. Scales and processes of water and sediment redistribution in drylands: results from the Rambla Honda field site in Southeast Spain. Earth. Sci. Rev. 48, 39–70.
Rodríguez-Caballero, E., Cantón, Y., Chamizo, S., Afana, A., Solé-Benet, A., 2012. Effects of biological soil crusts on surface roughness and implications for runoff and erosion. Geomorphology 145–146, 81–89.
Shipley, B., 2000. Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference. Cambridge University Press, Cambridge, UK.
Solé-Benet, A., Calvo, A., Cerdá, A., Lázaro, R., Pini, R., Barbero, J., 1997. Influence of micro–relief patterns and plant cover on runoff related processes in badlands from Tabernas (SE Spain). Catena 31, 23–38.
Souza-Egipsy, V., Ascaso, C., Sancho, L.G., 2002. Water distribution within terricolous lichens revealed by scanning electron microscopy and its relevance in soil crust ecology. Mycol. Res. 106, 1367–1374.
Warren, S.D., 2003a. Synopsis: influence of biological soil crusts on arid land hydrology and soil stability. In: Belnap, J., Lange, O.L. (Eds.), Biological Soil Crusts: Structure, Function and Management. Springer-Verlag, Berlin, pp. 349–360.
Warren, S.D., 2003b. Biological soil crusts and hydrology in North American deserts. In: Belnap, J., Lange, O.L. (Eds.), Biological Soil Crusts: Structure, Function and Management. Springer-Verlag, Berlin, pp. 327–337.
Wilcox, B.P., Breshears, D.D., Allen, C.D., 2003. Ecohydrology of a resource conserving semiarid woodland: effects of scale and disturbance. Ecol. Monogr. 73, 223–239.
Yair, A., 2003. Effects of biological soil crusts on water redistribution in the Negev desert, Israel: a case study in longitudinal dunes. In: Belnap, J., Lange, O.L. (Eds.), Biological Soil Crusts: Structure, Function and Management. Springer-Verlag, Berlin, pp. 303–314.
Yair, A., Almog, R., Veste, M., 2011. Differential hydrological response of biological topsoil crusts along a rainfall gradient in a sandy arid area: Northern Negev desert, Israel. Catena 87, 326–333.