J. Hydrol. Hydromech., 64, 2016, 2, 133–140
DOI: 10.1515/johh-2016-0001

# Biological soil crusts cause subcritical water repellency in a sand dune ecosystem located along a rainfall gradient in the NW Negev desert, Israel

Hannes Keck[1, 2*], Vincent John Martin Noah Linus Felde[1], Sylvie Laureen Drahorad[1], Peter Felix-Henningsen[1]

[1] Institute of Soil Science and Soil Conservation, Justus Liebig University Giessen, Heinrich-Buff-Ring 26-32, 35392 Giessen, Germany.
[2] Present address: Hermann-Reusch-Strasse 1, 71522 Backnang, Germany.
[*] Corresponding author. Tel.: +49 1578 8495008. Fax: +49 641 99 37109. E-mail: hkeck@posteo.de

**Abstract:** The biological soil crusts (BSCs) in the NW Negev cause local water redistribution by increasing surface runoff. The effects of pore clogging and swelling of organic and inorganic crust components were intensively investigated in earlier studies. However, the effect of water repellency (WR) was not addressed systematically yet. This study investigates subcritical WR of BSCs in three different study sites in the NW Negev. For this purpose, three common methods to determine soil WR were used: (i) the repellency index (RI) method (ii) the water drop penetration time (WDPT) test and (iii) the Wilhelmy plate method (WPM). Furthermore, the potential influence of WR on local water redistribution is discussed and the applied methods are compared. We found the BSC to be subcritically water repellent. The degree of WR may only affect water redistribution on a microscale and has little influence on the ecosystem as a whole. The RI method was clearly the most appropriate to use, whereas the WDPT and the WPM failed to detect subcritical WR.

**Keywords:** Hydrophobicity; Reduced wettability; Surface runoff; Infiltration; Water repellency index.

## INTRODUCTION

Biological soil crusts (BSCs) consist of mineral soil particles, cyanobacteria, green algae, fungi, bacteria, lichens and mosses intertwined by cyanobacterial exopolysaccharides. These crusts cover many soil surfaces in drylands around the world (Belnap, 2006). In the NW Negev desert, Israel, BSCs stabilize the local sand dunes, protecting them from wind and water erosion (Belnap et al., 2007; Rodríguez-Caballero et al., 2012; Tsoar, 2008). In addition they are the main contributors to the local carbon and nitrogen cycles and enhance the fertility and water holding capacity of the dunes by trapping nutrient rich dust (Drahorad et al., 2013a; Verrecchia et al., 1995).

BSCs modify hydrological surface properties thereby altering water infiltration, which increases runoff amounts and frequencies and supports higher vegetation on run-on sites (Eldridge et al., 2000; Kidron et al., 2012; Yair et al., 2011). The modifications in hydrological surface properties are due to a multitude of factors associated with the BSCs, including texture (Fischer et al., 2013), surface roughness (Rodríguez-Caballero et al., 2012), vesicular porosity and capillary barriers (Felde et al., 2014), pore clogging and swelling of organic crust components (Fischer et al., 2010; Kidron et al., 1999) as well as water repellency (WR) (Drahorad et al., 2013b; Fischer et al., 2010). Recently the importance of the single factors have not been characterized systematically, as the complex interactions between them make it difficult to state general claims on their importance.

Most studies on BSCs and their influences on the local hydrological regimes in the NW Negev focused on pore clogging, swelling of organic crust components and strong persistence of WR (Kidron et al., 1999, 2010; Kidron and Büdel, 2014; Yair et al., 2011) whereas the influence of subcritical WR has not yet been investigated. Lamparter et al. (2006) defined a subcritical water repellent soil as a soil with a contact angle between water and soil below 90°. Studies suggest that the impact of subcritical WR on water sorptivity, conductivity and infiltration rates is underestimated (Hallett et al., 2001, 2004; Lamparter et al., 2006; Orfánus et al., 2008) and Lamparter et al. (2006) found subcritically water repellent soils to reduce infiltration rates by a factor of 3 to 170. Overall, the degree of WR mainly depends on the soil texture, quantity and quality of soil organic matter (SOM) and the soil water content (Bisdom et al., 1993; Dekker et al., 2001; Graber et al., 2009; Mataix-Solera et al., 2013; Mirbabaei et al., 2013; Nadav et al., 2013; Woche et al., 2005). These factors influence the amount of soil particle surfaces coated with hydrophobic or amphiphilic organic substances, as well as their orientation (Diehl, 2013; Doerr et al., 2000; Graber et al., 2009). Amphiphilic substances are generally water soluble and possess both hydrophilic, as well as hydrophobic groups. When dry, the hydrophilic ends are attached to inorganic soil particles, leaving the hydrophobic ends exposed, which leads to WR. At wet conditions, a reorientation process takes place so that the hydrophobic ends point at each other, leaving the hydrophilic ends exposed, which makes the soil more wettable (Doerr et al., 2000; Graber et al., 2009). Graber et al. (2009) conclude that a factor influencing the wetting kinetics is the speed of reorientation of amphiphilic molecules, which depends on their properties (e.g. alkyl chain length, alkyl chain saturation, ionized molecules). This may explain the inconsistent results on whether or not the amount of soil organic matter (SOM) has an influence on the occurrence or severity of WR (Aelamanesh et al., 2014; Eynard et al., 2006; Hajnos et al., 2013; Mataix-Solera et al., 2013; Mataix-Solera and Doerr, 2004; Mirbabaei et al., 2013; Varela et al., 2005; Vogelmann et al., 2013; Woche et al., 2005) and the findings of pronounced differences in the effects of a range of organic molecules on WR (de Blas et al., 2013; Doerr et al., 2000; Fischer et al., 2013; Simkovic et al., 2008). WR can be assessed by means of the water drop penetration time (WDPT) test (e.g. Bisdom et al., 1993), by the contact angle methods (e.g. Woche et al., 2005) and the repellency index (RI, e.g. Lichner et al., 2007). The most commonly utilized and fastest method is the WDPT test, which is used to assess the persistence of WR by placing a drop of distilled water on the soil surface and recording the time it takes for complete surface penetration. Since water only enters the soil if the contact angle between water and soil is less than 90°, the WDPT test is a measure of the time required until the contact angle reaches values below 90° and thus, of the stability of WR rather than its intensity (Letey et al., 2000). Contact angle methods determine the wettability of a surface by the contact angle that is formed between water and the soil surface. Using direct methods to measure the contact angle is time consuming, laborious or even impossible, whereas indirect methods, like the Wilhelmy plate method (WPM e.g. Woche et al., 2005), are fast and easy to execute. This analysis is conducted on disturbed samples and reduces effects of surface roughness or heterogeneous distribution of water repellent compounds (Bachmann et al., 2006). It involves immersing a plate that is covered with a one-grain layer of soil particles and connected to an electronic balance into a test liquid (distilled water). The balance measures the forces acting on the plate during immersing and the contact angle is computed according to Bachmann et al. (2006). Laboratory experiments comparing the WDPT test with contact angle methods of Leelamanie et al. (2008) and Bachmann et al. (2003) on soils and soil like materials showed a very narrow sensitive range (contact angle of 85–115°) for WDPT measurements. These studies confirm that the WDPT test is of limited use for the determination of subcritical WR. To elaborate on subcritical WR the RI method is more applicable (Letey et al., 2000). It compares the initial sorptivity of water and ethanol and can be used to measure the soil surface (un)polarity, thus the wettability of the soil at levels below the resolution of the WDPT test. Ethanol wets all soil surfaces with a contact angle equal to zero and is not influenced by soil hydrophobicity. A simultaneous infiltration of water and ethanol is used to compute the initial sorptivity of both liquids. In order to exclude time dependent reductions in WR only the time of infiltration in which a linear relationship between the cumulative infiltration and the square root of time can be observed, often the first 1–3 min. is used to calculate the RI (Hallett, 2008; Schacht et al., 2014). RI values of 1 indicate no WR and a value greater than 1 indicates a water repellent soil (Hallett and Young, 1999). Lamparter et al. (2010) demonstrated the usefulness of ethanol to measure the intrinsic hydrologic properties to exclude the effect of WR on soils. Lichner et al. (2007) showed that the RI method is well suited for a wide range of hydrophobic soils. The RI method was successfully used in several ecosystems to investigate WR on BSCs in a range of studies (Drahorad et al., 2013b; Fischer et al., 2010; Lichner et al., 2013). In the sand dune ecosystems of the NW Negev the content of SOM within the BSC is higher compared to the topsoil (Drahorad et al., 2013a; Yair et al., 2011). Moreover, the living crust components like green algae, cyanobacteria, bacteria, lichens and filamentous fungi produce extracellular polymeric substances that are reported to possess hydrophobic properties (Chamizo et al., 2012; Fischer et al., 2010, 2013; Hakanpää et al., 2004; Rillig, 2005; Young et al., 2012). This led scientists to elaborate on WR of the BSCs within the NW Negev using the WDPT test (Kidron et al., 1999, 2010; Kidron and Büdel, 2014; Yair et al., 2011). Up to now no water repellency was found on the BSCs in the region. However, more sensitive measurements with a resolution beyond the WDPT test and a systematic description of subcritical WR in the NW Negev are still missing.

The aim of this study was to investigate subcritical WR on BSCs in the NW Negev using the RI method and compare it with the WDPT test and the WPM. Due to the elevated SOM contents in the BSC compared to the topsoil we hypothesize that (i) the BSC is water repellent but on a subcritical level that is beyond the sensitivity of the WDPT test and therefore not discovered yet. Furthermore, we hypothesize that (ii) the applied methods show a strong influence on WR detection and that (iii) the RI method is more sensitive thus, capable of detecting WR in the study sites.

## MATERIAL AND METHODS

The three study sites, Nizzana-South (NS), Nizzana-84 (N84) and Nizzana-69 (N69) are located in the NW Negev, Israel and characterized by a steep rainfall gradient with increasing amounts of annual rainfall from south to north (Fig. 1). The mean annual precipitations are approx. 100, 130 and 170 mm respectively and most precipitation events occur between December and February with high interannual variability (Littmann and Berkowicz, 2008). Dew formation is estimated to enhance the annually available moisture by approx. 30 mm in all sites (Littmann and Berkowicz, 2008). The study sites are located in the Sinai sand dune field directly on the border between Egypt and Israel. After 1982 when grazing activities stopped on the Israeli site of the border the formerly mobile sand dunes were colonized and stabilized by BSCs, protecting them from wind erosion (Belnap and Gillette, 1998; Tsoar, 2008). The relief in NS is characterized by 15 to 20 m high linear sand dunes with stabilized slopes, mobile crests and broad interdunal valleys. Further North in N84 and N69 the linear dunes are reduced in height and intersected with barchan-shaped dunes forming narrower basin like interdunes. Despite the close proximity and the uniform quarzitic sandy substratum in the region, crusts differ in their species composition, chemical and physical properties (Drahorad et al., 2013a; Drahorad and Felix-Henningsen, 2013; Kidron et al., 2010; Veste et al., 2001; Yair et al., 2011). The dune slopes and the interdune in NS are colonized by a cyanobacteria dominated BSC with the filamentous genera *Microcoleus, Leptolyngbya* and *Trichocoleus* as the most abundant (Hagemann et al., 2014; Karnieli et al., 1999). These BSCs are smooth, lightly gray colored, thin and fragile (1–2 mm thick) and correspond to the crust type A as classified by Kidron et al. (2010). Only on the north-facing dune slopes, where higher amounts of moisture are available thicker crusts (2–4 mm) with lichens or mosses of type C to E can be found (Kidron et al., 2010; Kidron and Benenson, 2014). Not only within the individual sites the crust types change according to the moisture regime but also along the precipitation gradient (Almog and Yair, 2007; Hagemann et al., 2014; Yair et al., 2011; Zaady et al., 2014). With higher amounts of available water in the interdunes of N84 and N69 BSCs of type C, D and E are more common. The dominating crust of the interdunes in N84 and N69 can be best described by crust type D. BSCs in the interdunes of N84 and N69 are darker colored, rougher and thicker than in NS (Fig. 2, Yair et al. 2011). The abundance of cyanobacterial strains like *Microcoleus, Leptolyngbya* and *Trichocoleus* decreases from the southern to the norther site, whereas the abundance of lichens like *Collema tenax*, *Diploschistes diacapsis*, *Fulgensia fulgens, Squamarina cartilaginea*, *S. lentigera* and mosses of the genera *bryum* sp. increases (Büdel and Veste, 2008; Hagemann et al., 2014; Veste et al., 2011). More lichens can be found in N84 and more mosses in N69. The crust thickness increased from approx. 4–6 mm in N84 to 7–10 mm in N69.

For a characterization of the BSCs and soil properties, three samples were taken of the BSC and the topsoil up to 10 cm beneath the crust. The samples were taken from representative spots in the interdune of each site as close as possible to the infiltration area at the beginning of the dry season in 2012.

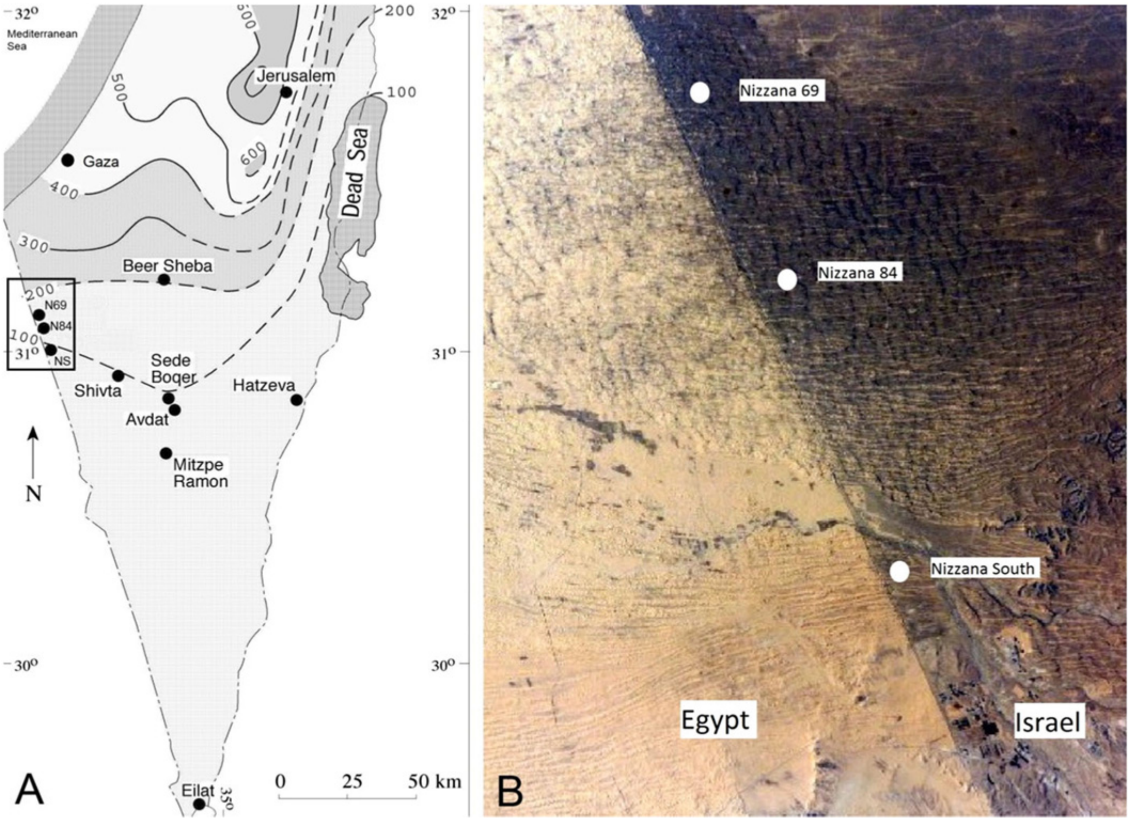


**Fig. 1.** (**A**) Location of the three study sites Nizzana-South (NS, 30°56'22.2"N 34°22'45.4"E), Nizzana-84 (N84, 31°02'28.2"N 34°20'52.9"E) and Nizzana-69 (N69, 31°06'25"N 34°18'50"E) on a map of south Israel and Gaza Strip with average annual rainfall (mm) indicated by isohyets (after Israel Meteorological Service). **(B)** Satellite image of the research area, note the strong difference in color between the light colored, grazed and disturbed sand dunes in Egypt and the dark, undisturbed sand dunes with BSC cover in Israel (adapted from NASA, taken on June 3, 2002).


**Fig. 2.** Photographs of the biological soil crusts in the interdunes of Nizzana-South (NS), Nizzana-84 (N84) and Nizzana-69 (N69).

Physico-chemical characteristics of the samples were determined as described in Hagemann et al. (2014). Particle size analysis was conducted according to DIN ISO 11277. Water content was measured in the field with a Thetaprobe ML2x (Delta-T Devices, Cambridge, UK) and one out of 5 measurements was validated gravimetrically. To assess the water repellent characteristics of the BSC three different methods were applied: (i) the repellency index (RI) method (ii) the water drop penetration time (WDPT) test and (iii) the Wilhelmy plate method (WPM). In the interdunes of each study site infiltration measurements were carried out (n = 5) using the method described by Lichner et al. (2007). Unsaturated hydraulic conductivity (K), sorptivity (S) and RI were obtained by simultaneous infiltration of water and ethanol using two mini disc infiltrometers (Decagon Devices, Pullman, USA) at a distance of 20 cm (according to Schacht et al. (2011), see Fig. 3). For each measurement a thin layer of medium textured, non-repellent sand was applied on the BSC or topsoil surface to ensure a good and even contact of the infiltrometers' steel disk. To make sure this contact sand contained no organic substances that could influence the measurements, this sand was collected from the mobile dune crest in the southernmost site. A pressure head of $h_0$ = –3 cm was chosen to exclude macro pores from the infiltration process and prevent very rapid infiltration into the coarse sandy substrate. Veste et al. (2001) observed that a dew formation exceeding 0.1 mm triggers BSC organisms to get active and Heusinkveld et al. (2006) found an average dew event to contribute 0.1 to 0.2 mm to the ecosystem in NS. In order to observe a possible influence of a dew event on WR due the excretion of water repellent compounds by an active crust, the measurements were repeated after wetting the crust (wet) at next to the dry measurement on the same crust type representative for the inder-

**Fig. 3.** Infiltration experiment in the interdune of Nizzana-84. Water infiltration (left), ethanol infiltration (right).

dune to ensure comparability but avoid influences of the infiltration fluids from the previous measurements. For the wet treatment we applied approximately 0.2 mm of distilled water to the area of infiltration with a sprayer. The infiltration was started 10 min. after wetting to ensure the organic and inorganic crust components had time to swell, the crust time to get active. In order to examine the influence of the BSC on infiltration as a whole, we also measured at a depth of 10 cm on the bare soil devoid of crust (bare). The measurements were recorded with the small compact camera Nikon Coolpix S6200 and the videos were processed in the lab, intervals of 10 s were chosen.

For a quick analysis of the persistence of WR we used the WDPT test. Due to the sensitivity of WR on the water content, we measured the WDPT on field-dry samples in the field, as well as on samples, which were oven-dried in the laboratory at 65 and 105°C to investigate on the potential WR as introduced by Dekker et al. (2001). For the WDPT test, a water drop of 50 (± 5) µL was placed on the crust with a pipette at approx. 10 mm height, ten repetitions were made. To classify the level of WR persistence the classification according to Bisdom et al. (1993) was used. The contact angle was measured using the Wilhelmy plate method (WPM) on disturbed samples in the laboratory with three repetitions using a contact angle tensiometer (DCAT 11, DataPhysics, Filderstadt, Germany) according to Woche et al. (2005). Both methods were used to obtain a higher spatial resolution of water repellent properties in each site, including slope positions, where infiltrometer measurements were not feasible. WDPT and WPM analyses were made on BSCs along transects running from the south-facing and the interdune to the north-facing slope at three positions. It was taken care that the analyses in the interdunes were conducted on the same BSCs and as close as possible to the area of infiltration, making sure that they represent the typical BSC of each site. Infiltration experiments were not possible on the dune slopes because of the infiltrometers' unstable stand on a slope and the associated difficulties of ensuring a consistent tension level at infiltration (Walker et al., 2006).

For data processing and statistical analysis, LibreOffice Calc 4.2. and SAS Studio 3.1 were used. The K, S and RI were calculated according to Lichner et al. (2007). A one-sample t-test was used to compare the RI values of the bare soil with the theoretical value of a completely non-repellent soil (RI = 1), a two-way ANOVA was used to test the influence of the treatments (dry, wet and bare) and the sites (NS, N84 and N69) on RI and a subsequent Bonferroni comparison to distinguish between the means of the covariates treatment and site. The same statistical model and test was used to distinguish the means of the total nitrogen, organic carbon ($C_{org}$) and fine contents in the BSC and in the topsoil.

## RESULTS AND DISCUSSION

The $C_{org}$ and total nitrogen concentrations are higher ($p < 0.05$) in the BSC than in the topsoil, which is in accordance with Drahorad et al. (2013a) (Table 1). The increase ($p < 0.05$) of $C_{org}$, total nitrogen and fines (< 63 µm) from the southernmost to the northernmost sampling site is in accordance with Hagemann et al. (2014) and Yair et al. (2011). The maximum initial soil water content was found in N69 of 2.38 vol-% (Table 1).

Data analysis of the infiltration measurements showed that there was no significant difference between the treatments "wet" and "dry" for the RI, K and S for water and ethanol (Table 2). No significant interaction between the site and the treatment was found. A significantly lower ($p < 0.05$) RI and significantly higher ($p < 0.05$) K and S was observed on the bare soil compared to the BSC (wet and dry). This demonstrates that the BSC in the NW Negev is water repellent and illustrates the importance of the BSC for the local redistribution of water, supporting earlier findings that show the reduction in infiltration by the BSC in the NW Negev (Eldridge et al., 2000; Yair, 1990). Furthermore, the RI on the bare soil did not differ significantly ($P > 0.05$) from the theoretically expected value of RI = 1, thus no WR was present there. In NS the RI of 0.86 (±0.18) on the bare soil suggests an better wetting by water than by ethanol and is possibly due to interactions of infiltration fluids with complex pore structure (Lichner et al., 2007) and the RI of 1.30 (±0.84) and 1.11 (±0.48) on bare soil in N84 and N69 indicates an insignificantly reduced wettability by water. The lack of WR on the bare soil may be explained by the very low $C_{org}$ concentrations measured in the topsoil. These low concentrations of organic substances are insufficient to coat the inorganic soil particles in a way that induces WR. Also,

**Table 1.** Soil characteristics of the three study sites. Organic carbon ($C_{org}$) and total nitrogen ($N_{tot}$) content, C/N ratio, content of fines (<63 µm) and soil pH at the three sites of the biological soil crust (BSC), and the topsoil (TS). Soil water content (SWC) under field-dry conditions. With n = 3, standard deviation in parentheses and significances ($p < 0.05$) indicated with letters.

| Site | (n = 3) | $C_{org}$ [%] | $N_{tot}$ [%] | C/N | Fines [%] | pH | SWC [vol-%] |
|---|---|---|---|---|---|---|---|
| NS | BSC | $0.331^A$ (±0.012) | $0.041^A$ (±0.006) | $7.98^A$ (±2.17) | $19.40^A$ (±3.32) | $7.77^A$ | 2.08 (±0.19) |
| | TS | $0.087^D$ (±0.024) | $0.007^D$ (±0.001) | $12.97^A$ (±2.91) | $6.26^D$ (±0.71) | $8.71^B$ | |
| N84 | BSC | $0.686^B$ (±0.202) | $0.076^B$ (±0.020) | $8.93^A$ (±0.50) | $22.84^B$ (±9.16) | $7.64^A$ | 1.24 (±0.17) |
| | TS | $0.076^D$ (±0.032) | $0.012^D$ (±0.001) | $6.71^A$ (±3.21) | $4.61^D$ (±1.30) | $8.65^B$ | |
| N69 | BSC | $1.155^C$ (±0.056) | $0.124^C$ (±0.016) | $9.41^A$ (±0.82) | $42.83^C$ (±8.65) | $7.62^A$ | 2.38 (±0.11) |
| | TS | $0.086^D$ (±0.021) | $0.010^D$ (±0.001) | $8.30^A$ (±1.60) | $8.79^D$ (±1.42) | $8.59^B$ | |

**Table 2.** Soil hydrological parameters of the three study sites. Repellency index (RI); sorptivity of water ($S_W$); sorptivity of ethanol ($S_E$); unsaturated hydraulic conductivity of water ($K_W$); unsaturated hydraulic conductivity of ethanol ($K_E$) at a pressure head of –3 cm. With n = 5; on the bare soil (bare) and the dry crust (dry) conducted under field-dry conditions and the wet crust (wet) conducted after wetting; standard deviation in parentheses and significances ($p < 0.05$) indicated with letters.

| Site | (n = 5) | RI | $S_W$ (–3 cm) [cm $s^{-1/2}$] | $S_E$ (–3 cm) [cm $s^{-1/2}$] | $K_W$ (–3 cm) [cm $s^{-1}$] | $K_E$ (–3 cm) [cm $s^{-1}$] |
|---|---|---|---|---|---|---|
| NS | bare | $0.86^A$ (±0.18) | $0.891^A$ (±0.287) | $0.379^A$ (±0.115) | $0.0678^A$ (±0.0236) | $0.0255^A$ (±0.0083) |
| | dry | $1.89^B$ (±0.58) | $0.148^B$ (±0.063) | $0.144^B$ (±0.067) | $0.0046^B$ (±0.0018) | $0.0053^B$ (±0.0028) |
| | wet | $2.13^B$ (±0.62) | $0.077^B$ (±0.027) | $0.078^B$ (±0.014) | $0.0028^B$ (±0.0012) | $0.0024^B$ (±0.0007) |
| N84 | bare | $1.30^A$ (±0.84) | $0.393^A$ (±0153) | $0.249^A$ (±0.143) | $0.0289^A$ (±0.0108) | $0.0160^A$ (±0.0086) |
| | dry | $5.40^C$ (±1.12) | $0.078^C$ (±0.016) | $0.216^B$ (±0.066) | $0.0018^C$ (±0.0006) | $0.0077^B$ (±0.0032) |
| | wet | $5.70^C$ (±1.63) | $0.062^C$ (±0.012) | $0.176^B$ (±0.038) | $0.0016^C$ (±0.0006) | $0.0069^B$ (±0.0013) |
| N69 | bare | $1.11^A$ (±0.48) | $0.618^A$ (±0,213) | $0.329^A$ (±0.089) | $0.0423^A$ (±0.0171) | $0.0211^A$ (±0.0060) |
| | dry | $3.26^B$ (±0.86) | $0.134^B$ (±0.030) | $0.218^B$ (±0.051) | $0.0050^B$ (±0.0017) | $0.0080^B$ (±0.0029) |
| | wet | $2.28^B$ (±1.04) | $0.156^B$ (±0.071) | $0.159^B$ (±0.033) | $0.0058^B$ (±0.0029) | $0.0065^B$ (±0.0013) |

infiltration rates on BSCs were reported to depend on the soil water content. Chamizo et al. (2012) found a decrease in infiltration rates from dry to wet crusts, indicating the clogging of pores. We could not observe significant differences in RI or K between the dry and the wet crusts. This indicates that the water added to simulate dew formation has a limited effect on the hydrological surface properties of the BSCs in the NW Negev. The added water may have led to an activation of the crust organisms and an excretion of hydrophobic substances, thus increasing the WR. But wetting can also lead to reorientation processes of amphiphilic substances from a dry and hydrophobic state to a moist and more hydrophilic state. Thus, these two processes have an opposite effect and can compensate each other. Furthermore, fast drying processes after water application and insufficient time for swelling or some degree of persistent subcritical WR could have contributed to the results as well. Compared to other values of RI measurements from BSCs around the world, ranging from a RI of 4.4 to 210 (cf. Drahorad et al., 2013b; Fischer et al., 2010; Lichner et al., 2013, 2007) the values measured for the crust in the NW Negev are located in the lower RI range with the highest RI values on wet crust in N84 of 5.70 (see Table 2).

The comparison of the RIs between the three sites showed that WR is significantly higher in N84 compared to NS and N69 ($p < 0.05$). The K and S values for water followed a reverse trend (Table 2). In NS highest S (water) and K (water) were observed and in N84 the lowest, but both sites were not different to N69 ($p = 0.05$). There was no effect of the different sites on S (ethanol) or K (ethanol). The increase of RI from NS to N84 can be explained by an increase in $C_{org}$. However, WR in the NW Negev is not linearly increasing from the southern to the northern study site in accordance with our results of the $C_{org}$ measurements (Table 1). This suggests that other factors contribute to the development of WR. Some studies showed that development stages of BSCs are responsible for strongly varying hydrological behavior (Drahorad et al., 2013b; Rodríguez-Caballero et al., 2012; Yair et al., 2011; Zaady et al., 2014). Lichner et al. (2013) showed that species composition had a strong effect on the development of WR. Fischer et al. (2010) described an increase of WR in the first successional stages that where dominated by cyanobacteria and green algae and a decrease with further succession that introduced bryophytes. Lichens were reported to possess WR properties (Chamizo et al., 2012; Rodríguez-Caballero et al., 2013). Thus, a higher abundance of lichens in N84 can lead to an increase in WR. The decrease of RI values from N84 to N69 contradicts the further increase in $C_{org}$ but this may be overcompensated by higher amounts of fines (Woche et al., 2005) (Table 1) and a reduced number of lichens in N69. Furthermore, the increasing abundance of heterotrophic organisms (Hagemann et al., 2014) and changes in structure and composition of SOM (Drahorad et al., 2013a) in the northern site may additionally influence the level of WR. Drahorad et al., (2013a) found a total increase of carbohydrates, peptides, alkylaromates, and N-compounds in the upper 2 mm of the crust from the driest study site NS to N84 followed by a decrease towards N69 as well as a maximum in fatty acid concentration in N84 in the lower 2–40 mm of the crust. This indicates an SOM composition with higher amounts of stable SOM constituents and an enrichment of more decomposed, perhaps partly "humified" components for N84 in the upper millimeters and a higher concentration of fatty acids as WR compounds in the lower millimeters of the crust related to higher WR values measured in this study.

We found a decrease in infiltration rates form the cyanobacterial dominated crusts in the southern most site, to the lichen dominated crust in N84 and an increase for the more developed and thicker crusts consisting mainly of cyanobacteria, lichens and some mosses in the northern most site. This agrees with Eldridge et al. (2010), Maestre et al. (2011) and Rodríguez-Caballero et al. (2013) describing lichens as runoff promoters and mosses as infiltration promoters for arid ecosystems, but may contradict results of Drahorad et al. (2013b) describing a negative relation of infiltration rate and a positive relation of WR with successional stages of moss dominated BSCs under humid climate conditions. Here, vegetation (coniferous trees) plays an important role in the development of WR (Lichner et al., 2007), but this can be ruled out in the Negev desert since there is no sufficient plant cover present that may contribute significantly to WR development.

Our results of very small WDPT values are in accordance with those published by Kidron et al. (1999; 2010) for a sandy substrate. After drying, we observed a slight increase in WDPT that was most pronounced in NS, which may indicate that the cyanobacterial dominated BSCs possess more amphiphilic substances than the crusts from the other sites. A possible explanation is that the higher abundance of heterotrophic organisms (Hagemann et al., 2014) increases the consumption of the amphiphilic organic substances. However, this change was not significant and values are still below those of soils classified as hydrophobic according to Bisdom et al. (1993). The fact that drying at two temperature levels had only a small effect on WDPTs leads to the assumption that BSCs from the NW Negev are only to a small extent covered by amphiphilic compounds, whose orientation may be influenced by drying. Therefore, this process is of no ecological relevance for hydrological processes in the NW Negev. The results of both the WDPT and contact angle measurements along the transects in all sites yielded a maximum value of 1.51 s and 46.07° respectively (Table 3). This finding is in accordance with Lamparter et al. (2006) who found contact angles below 90° were associated with WDPT values below 2 s. Furthermore, the variations within the repetitions of our measurements were too high to detect clear trends of spatial differences, but indicate neither the presence of high WR, nor its persistence. In contrast the RI results for the interdunes of the study sites, the respective contact angle and WDPT results failed to detect WR. This is in accordance with findings of Fischer et al. (2010). Since the WDPT was unable to detect WR and the contact angles are clearly below 90° (Table 3) the WR we detected by means of the RI method is on a subcritical level and to our knowledge the first documentation of subcritical WR on BSCs of the sand dunes in the NW Negev. The comparison of the three methods shows that the RI method is still capable of detecting WR when the WDPT and the WPM method fail to do so. As stated earlier, the reason for the insensitivity of the WDPT test is that this method only measures the time that it takes to reduce the contact angle from its original value to values below 90° after a drop of water was placed on the soil, thus it does not account for subcritical WR (Lamparter et al., 2006; Letey et al., 2000). The WPM is theoretically capable of measuring contact angels from 0° to 180° (Bachmann et al., 2003). However, our high standard deviations suggest a detection limit for subcritical WR for the WPM, which is in agreement with Woche et al. (2005) who found high variability in contact angles below 70°. It is worthwhile to note that the soil water contents for each of the analysis was below 2.4 vol-% thus, outside the transition zone between a wettable and non-wettable soil state for dune sand as found by Dekker et al. (2001) and therefore of no relevance for the comparison.

**Table 3.** Results of water drop penetration time (WDPT) test (n = 10) and the contact angle (CA) method (n = 3) along transects in each site on south-facing (SF) slope, interdune (ID), north-facing (NF) slope conducted under field-dry conditions. Standard deviation in parentheses.

| Site | | WDPT [s] (n=10) | CA [degrees] (n=3) |
|---|---|---|---|
| NS | SF | 0.92 (±0.59) | 0.00 (±0.00) |
| | ID | 0.69 (±0.21) | 8.45 (±10.59) |
| | NF | 0.77 (±0.32) | 18.01 (±15.12) |
| N84 | SF | 0.44 (±0.06) | 12.79 (±14.34) |
| | ID | 0.91 (±0.37) | 16.56 (±28.69) |
| | NF | 0.30 (±0.04) | 22.73 (±22.77) |
| N69 | SF | 0.62 (±0,19) | 19.00 (±18.30) |
| | ID | 0.49 (±0.13) | 6.01 (±10.40) |
| | NF | 1.51 (±1.40) | 46.07 (±2.17) |

In the complex interactions of factors leading to runoff creation in the NW Negev, surface sealing properties of the crust like higher amounts of fines, pore clogging, swelling of organic and inorganic crust components, the presence of capillary boundaries and vesicular pores in combination with subcritical WR can explain the significant lower K (water) and S (water) values on the crust compared to the bare soil (Felde et al., 2014; Fischer et al., 2010; Kidron et al., 1999). Furthermore, WR can affect water redistribution on small scales and on local hot spots of hydrophobicity depending on biotic crust components and their influence on WR, leading to water reallocation from run-off promoters to infiltration promoters (Eldridge et al., 2010; Maestre et al., 2011). The variability in our RI results may be due to spatial variability in crust components promoting hydrophilic or others promoting hydrophobic soil properties (Eldridge et al., 2010; Young et al., 2012). This would be in accordance with Orfánus et al. (2008) reporting a highly variable WR on sandy soils at sample scales of 22 cm² and Hallett and Young (1999) with similar results at millimeter scaled measurements on soil aggregates. WR not only varies spatially but also in time due to seasonal changes and the strongly varying precipitation patterns in the NW Negev (Doerr et al., 2000). Thus, for a detailed evaluation of the ecological relevance of WR for runoff it would be necessary to monitor the WR over one or multiple hydrological years.

## CONCLUSION

This study shows for the first time that the BSCs in the NW Negev desert are subcritically water repellent. The degree of WR may only affect water redistribution on a microscale and has little influence on the ecosystem as a whole. The comparison of the three methods WDPT, WPM and RI clearly showed that the RI method is the most sensitive and should be preferred when studying soils with subcritical levels of WR. Furthermore, it is unlikely that a wetting event (e.g. dew) changes the WR and infiltration capacity of the crust. Unexpectedly, WR and infiltration capacity neither related linearly to an increasing $C_{org}$ content nor to an increase in mean annual precipitation from south to north. We believe that the quality of SOM and the species composition of the crust play an important role for the development of WR and the infiltration capacity in the region, however this will need further investigations.

*Acknowledgement*. We thank the German Research Foundation (DFG) for funding this research in the framework of their Trilateral Project "Biotic and abiotic factor affecting biological soil crust formation and recovery in a semiarid dune ecosystem, Gaza and NW Negev" (Project FE 218/14-2), and the Arid Ecosystems Research Center of the Hebrew University of Jerusalem. Special thanks go to Simon Berkowicz for his great support during field work, Laura Williams for editing and to two anonymous reviewers which helped to increase the clarity of this manuscript. Thanks are due to Mrs. Elke Schneidenwind and Mrs. Elke Müller for the analysis of C, N and the grain size distribution.

## REFERENCES

Aelamanesh, P., Mosaddeghi, M.R., Mahboubi, A.A., Ahrens, B., Sinegani, A.A.S., 2014. Water repellency in calcareous soils under different land uses in Western Iran. Pedosphere, 24, 378–390.

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.

Bachmann, J., Woche, S.K., Goebel, M.-O., Kirkham, M.B., Horton, R., 2003. Extended methodology for determining wetting properties of porous media: Determining wetting properties of soil. Water Resour. Res., 39, doi: 10.1029/2003WR002143

Bachmann, J., Arye, G., Deurer, M., Woche, S.K., Horton, R., Hartge, K.-H., Chen, Y., 2006. Universality of a surface tension—contact-angle relation for hydrophobic soils of different texture. J. Plant Nutr. Soil Sci., 169, 745–753.

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

Belnap, J., Gillette, D.A., 1998. Vulnerability of desert biological soil crusts to wind erosion: the influences of crust development, soil texture, and disturbance. J. Arid Environ., 39, 133–142.

Belnap, J., Phillips, S.L., Herrick, J.E., Johansen, J.R., 2007. Wind erodibility of soils at Fort Irwin, California (Mojave Desert), USA, before and after trampling disturbance: implications for land management. Earth Surf. Process. Landf., 32, 75–84.

Bisdom, E.B.A., Dekker, L.W., Schoute, J.F.T., 1993. Water repellency of sieve fractions from sandy soils and relationships with organic material and soil structure. Geoderma, 56, 105–118.

Büdel, B., Veste, M., 2008. Biological crusts. In: Breckle, S.-W., Yair, A., Veste, M. (Eds.): Arid Dune Ecosystems. The Nizzana Sands in the Negev Desert. Springer, Berlin, pp. 149–155.

Chamizo, S., Cantón, Y., Lázaro, R., Solé-Benet, A., Domingo, F., 2012. Crust composition and disturbance drive infiltration through biological soil crusts in semiarid ecosystems. Ecosystems, 15, 148–161.

de Blas, E., Almendros, G., Sanz, J., 2013. Molecular characterization of lipid fractions from extremely water-repellent pine and eucalyptus forest soils. Geoderma, 206, 75–84.

Dekker, L.W., Doerr, S.H., Oostindie, K., Ziogas, A.K., Ritsema, C.J., 2001. Water repellency and critical soil water content in a dune sand. Soil Sci. Soc. Am. J., 65, 1667–1674.

Diehl, D., 2013. Soil water repellency: Dynamics of heterogeneous surfaces. Colloids Surf. Physicochem. Eng. Asp., 432, 8–18.

Doerr, S.H., Shakesby, R.A., Walsh, R.P.D., 2000. Soil water repellency: its causes, characteristics and hydro-geomorphological significance. Earth-Sci. Rev., 51, 33–65.

Drahorad, S.L., Felix-Henningsen, P., 2013. Application of an electronic micropenetrometer to assess mechanical stability of biological soil crusts. J. Plant Nutr. Soil Sci., 176, 904–909.

Drahorad, S.L., Felix-Henningsen, P., Eckhardt, K.-U., Leinweber, P., 2013a. Spatial carbon and nitrogen distribution and organic matter characteristics of biological soil crusts in the Negev desert (Israel) along a rainfall gradient. J. Arid Environ., 94, 18–26.

Drahorad, S.L., Steckenmesser, D., Felix-Henningsen, P., Lichner, Ľ., Rodný, M., 2013b. Ongoing succession of biological soil crusts increases water repellency – a case study on Arenosols in Sekule, Slovakia. Biologia, 68, 1089–1093.

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.

Eynard, A., Schumacher, T.E., Lindstrom, M.J., Malo, D.D., Kohl, R.A., 2006. Effects of aggregate structure and organic C on wettability of Ustolls. Soil Tillage Res., 88, 205–216.

Felde, V.J.M.N.L., Peth, S., Uteau-Puschmann, D., Drahorad, S., Felix-Henningsen, P., 2014. Soil microstructure as an under-explored feature of biological soil crust hydrological properties: case study from the NW Negev Desert. Biodivers. Conserv., 23, 1687–1708.

Fischer, T., Veste, M., Wiehe, W., Lange, P., 2010. Water repellency and pore clogging at early successional stages of microbiotic crusts on inland dunes, Brandenburg, NE Germany. Catena, 80, 47–52.

Fischer, T., Yair, A., Veste, M., Geppert, H., 2013. Hydraulic properties of biological soil crusts on sand dunes studied by 13C-CP/MAS-NMR: A comparison between an arid and a temperate site. Catena, 110, 155–160.

Graber, E.R., Tagger, S., Wallach, R., 2009. Role of divalent fatty acid salts in soil water repellency. Soil Sci. Soc. Am. J., 73, 541–549.

Hagemann, M., Henneberg, M., Felde, V.J.M.N.L., Drahorad, S.L., Berkowicz, S.M., Felix-Henningsen, P., Kaplan, A., 2014. Cyanobacterial diversity in biological soil crusts along a precipitation gradient, Northwest Negev Desert, Israel. Microb. Ecol., doi:10.1007/s00248-014-0533-z

Hajnos, M., Calka, A., Jozefaciuk, G., 2013. Wettability of mineral soils. Geoderma, 206, 63–69.

Hakanpää, J., Paananen, A., Askolin, S., Nakari-Setälä, T., Parkkinen, T., Penttilä, M., Linder, M.B., Rouvinen, J., 2004. Atomic resolution structure of the HFBII hydrophobin, a self-assembling amphiphile. The Journal of Biological Chemistry, 279, 534–539.

Hallett, P.D., 2008. A brief overview of the causes, impacts and amelioration of soil water repellency – a review. Soil Water Res., 3, 21–29.

Hallett, P.D., Young, I.M., 1999. Changes to water repellence of soil aggregates caused by substrate-induced microbial activity. Eur. J. Soil Sci., 50, 35–40.

Hallett, P.D., Baumgartl, T., Young, I.M., 2001. Subcritical water repellency of aggregates from a range of soil management practices. Soil Sci. Soc. Am. J., 65, 184–190.

Hallett, P.D., Nunan, N., Douglas, J.T., Young, I.M., 2004. Millimeter-scale spatial variability in soil water sorptivity: scale, surface elevation, and subcritical repellency effects. Soil Sci. Soc. Am. J., 68, 352–358.

Heusinkveld, B.G., Berkowicz, S.M., Jacobs, A.F.G., Holtslag, A.A.M., Hillen, W.C.A.M., 2006. An automated microlysimeter to study dew formation and evaporation in arid and semiarid regions. J. Hydrometeorol., 7, 825–832.

International Organization for Standardization (ISO), 1998. Soil quality -- Determination of particle size distribution in mineral soil material -- Method by sieving and sedimentation. ISO 11277:1998-05-15.

Karnieli, A., Kidron, G.J., Glaesser, C., Ben-Dor, E., 1999. Spectral characteristics of cyanobacteria soil crust in semiarid environments. Remote Sens. Environ., 69, 67–75.

Kidron, G.J., Benenson, I., 2014. Biocrusts serve as biomarkers for the upper 30 cm soil water content. J. Hydrol., 509, 398–405.

Kidron, G.J., Büdel, B., 2014. Contrasting hydrological response of coastal and desert biocrusts. Hydrol. Process., 28, 361–371.

Kidron, G.J., Yaalon, D.H., Vonshak, A., 1999. Two causes for runoff initiation on microbiotic crusts: hydrophobicity and pore clogging. Soil Sci., 164, 18–27.

Kidron, G.J., Vonshak, A., Dor, I., Barinova, S., Abeliovich, A., 2010. Properties and spatial distribution of microbiotic crusts in the Negev Desert, Israel. Catena, 82, 92–101.

Kidron, G.J., Monger, H.C., Vonshak, A., Conrod, W., 2012. Contrasting effects of microbiotic crusts on runoff in desert surfaces. Geomorphology, 139–140, 484–494.

Lamparter, A., Deurer, M., Bachmann, J., Duijnisveld, W.H.M., 2006. Effect of subcritical hydrophobicity in a sandy soil on water infiltration and mobile water content. J. Plant Nutr. Soil Sci., 169, 38–46.

Lamparter, A., Bachmann, J., Deurer, M., Woche, S.K., 2010. Applicability of ethanol for measuring intrinsic hydraulic properies of sand with various water repellency levels. Vadose Zone J., 9, 445–450.

Leelamanie, D.A.L., Karube, J., Yoshida, A., 2008. Characterizing water repellency indices: Contact angle and water drop penetration time of hydrophobized sand. Soil Sci. Plant Nutr., 54, 179–187.

Letey, J., Carrillo, M.L., Pang, X., 2000. Approaches to characterize the degree of water repellency. J. Hydrol., 231–232, 61–65.

Lichner, L., Hallett, P.D., Feeney, D.S., Ďugová, O., Šír, M., Tesař, M., 2007. Field measurement of soil water repellency and its impact on water flow under different vegetation. Biologia, 62, 537–541.

Lichner, L., Hallett, P.D., Drongová, Z., Czachor, H., Kovacik, L., Mataix-Solera, J., Homolák, M., 2013. Algae influence the hydrophysical parameters of a sandy soil. Catena, 108, 58–68.

Littmann, T., Berkowicz, S.M., 2008. The regional climatic setting. In: Breckle, S.-W., Yair, A., Veste, M. (Eds.): Arid Dune Ecosystems. The Nizzana Sands in the Negev Desert. Springer, Berlin, pp. 49–63.

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.

Mataix-Solera, J., Doerr, S., 2004. Hydrophobicity and aggregate stability in calcareous topsoils from fire-affected pine forests in southeastern Spain. Geoderma, 118, 77–88.

Mataix-Solera, J., Arcenegui, V., Tessler, N., Zornoza, R., Wittenberg, L., Martínez, C., Caselles, P., Pérez-Bejarano, A., Malkinson, D., Jordán, M.M., 2013. Soil properties as key factors controlling water repellency in fire-affected areas: Evidences from burned sites in Spain and Israel. Catena, 108, 6–13.

Mirbabaei, S.M., Shahrestani, M.S., Zolfaghari, A., Abkenar, K.T., 2013. Relationship between soil water repellency and some of soil properties in northern Iran. Catena, 108, 26–34.

Nadav, I., Tarchitzky, J., Chen, Y., 2013. Induction of soil water repellency following irrigation with treated wastewater: effects of irrigation water quality and soil texture. Irrig. Sci., 31, 385–394.

Orfánus, T., Bedrna, Z., Lichner, Ľ., Hallett, P.D., Kňava, K., Sebíň, M., 2008. Spatial variability of water repellency in pine forest soil. Soil Water Res., 3, 123–129.

Rillig, M.C., 2005. A connection between fungal hydrophobins and soil water repellency? Pedobiologia, 49, 395–399.

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.

Rodríguez-Caballero, E., Cantón, Y., Chamizo, S., Lázaro, R., Escudero, A., 2013. Soil loss and runoff in semiarid ecosystems: a complex interaction between biological soil crusts, micro-topography, and hydrological drivers. Ecosystems, 16, 529–546.

Schacht, K., Gönster, S., Jüschke, E., Chen, Y., Tarchitzky, J., Al-Bakri, J., Al-Karablieh, E., Marschner, B., 2011. Evaluation of soil sensitivity towards the irrigation with treated wastewater in the Jordan River Region. Water, 3, 1092–1111.

Schacht, K., Chen, Y., Tarchitzky, J., Lichner, L., Marschner, B., 2014. Impact of treated wastewater irrigation on water repellency of Mediterranean soils. Irrig. Sci., 32, 369–378.

Simkovic, I., Dlapa, P., Doerr, S.H., Mataix-Solera, J., Sasinkova, V., 2008. Thermal destruction of soil water repellency and associated changes to soil organic matter as observed by FTIR spectroscopy. Catena, 74, 205–211.

Tsoar, H., 2008. Land use and its effect on the mobilization and stabilization of the North-Western Negev sand dunes. In: Breckle, S.-W., Yair, A., Veste, M. (Eds.): Arid Dune Ecosystems. The Nizzana Sands in the Negev Desert. Springer, Berlin, pp. 79–89.

Varela, M.E., Benito, E., de Blas, E., 2005. Impact of wildfires on surface water repellency in soils of northwest Spain. Hydrol. Process., 19, 3649–3657.

Verrecchia, E., Yair, A., Kidron, G.J., Verrecchia, K., 1995. Physical properties of the psammophile cryptogamic crust and their consequences to the water regime of sandy soils, north-western Negev Desert, Israel. J. Arid Environ., 29, 427–437.

Veste, M., Littmann, T., Breckle, S.-W., Yair, A., 2001. The role of biological soil crusts on desert sand dunes of the north-western Negev (Israel). In: Breckle, S.-W., Veste, M., Wucherer, W. (Eds.): Sustainable Land-Use in Deserts. Springer, Heidelberg-New York-Tokyo, pp. 357–367.

Veste, M., Breckle, S.-W., Eggert, K., Littmann, T., 2011. Vegetation pattern in arid sand dunes controlled by biological soil crusts along a climatic gradient in the Northern Negev desert. Basic Appl. Dryland Res., 5, 1–16.

Vogelmann, E.S., Reichert, J.M., Prevedello, J., Consensa, C.O.B., Oliveira, A.É., Awe, G.O., Mataix-Solera, J., 2013. Threshold water content beyond which hydrophobic soils become hydrophilic: The role of soil texture and organic matter content. Geoderma, 209–210, 177–187.

Walker, C., Lin, H.S., Fritton, D.D., 2006. Is the tension beneath a tension infiltrometer what we think it is? Vadose Zone J., 5, 860–866.

Woche, S.K., Goebel, M.-O., Kirkham, M.B., Horton, R., Van der Ploeg, R.R., Bachmann, J., 2005. Contact angle of soils as affected by depth, texture, and land management. Eur. J. Soil Sci., 56, 239–251.

Yair, A., 1990. Runoff generation in a sandy area - The Nizzana sands, Western Negev, Israel. Earth Surf. Process. Landf., 15, 597–609.

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.

Young, I.M., Feeney, D.S., O'Donnell, A.G., Goulding, K.W.T., 2012. Fungi in century old managed soils could hold key to the development of soil water repellency. Soil Biol. Biochem., 45, 125–127.

Zaady, E., Katra, I., Yizhaq, H., Kinast, S., Ashkenazy, Y., 2014. Inferring the impact of rainfall gradient on biocrusts' developmental stage and thus on soil physical structures in sand dunes. Aeolian Res., 13, 81–89.

Received 28 April 2015
Accepted 28 September 2015