Inferring the impact of rainfall gradient on biocrusts' developmental stage and thus on soil physical structures in sand dunes

Eli Zaady, Itzhak Katra, Hezi Yizhaq, Shai Kinast, Yosef Ashkenazy

1. Introduction

The transition zone between arid and semi-arid areas is sensitive to precipitation and may be used to model the potential impact of climate change on community structure (Siegal et al., 2013). The effect of climatic change in arid and semi-arid areas is not limited to climatic factors. It is often accompanied by a parallel change in the properties of the soil surface (Almog and Tair, 2007). Desert ecosystems are subject to short wet intervals and long periods of drought. Shifts in moisture availability in the soil environment and water movement in these systems are critical processes affecting the biochemical and physical properties of the soil surface (Schlesinger et al., 1996). In sandy environments, climatic changes can be also associated with winds that expose roots, bury vegetation and biological soil crusts (biocrust), reduce vegetation cover and increase evapotranspiration.

Biocrusts are the common component that covers the soil surface in vast areas arid and semi-arid lands worldwide (Belnap and Lange, 2003; West, 1990). The developmental stage of biocrust is susceptible to climate changes. The annual rainfall affects the successional stage of the biocrust, which is reflected by the biocrust composition. This cryptogamic, biogenic or microphytic crust community varies markedly from typical two mm thick, relatively homogeneous cyanobacterial crusts to complex crust communities about 15 mm thick (Zaady et al., 1997). The biocrust and its components are considered to be “ecosystem engineers,” as their formation plays an important ecological role in key processes in the development of dry ecosystems (Belnap and Lange, 2003; Zaady et al., 2013). In the successional pathway of the crust communities, the pioneers in colonizing the soil surface after disturbances are the cyanobacteria, which are followed by green algae, mosses and lichens (Eldridge and Greene, 1994; Johansen, 1993; West,
1990; Zaady et al., 2000). Different factors can modify successional pathways from the same initial state of the system. Physical influences, such as soil structure, granulometry and soil types, radiation intensity, and topographic traits influence the successional pathways and the soil crust community (Veste et al., 2001, 2011). For example, the slope aspect affects water availability and soil moisture in arid systems (Katrab et al., 2007a,b; Yair, 1990; Yair et al., 2008). When physical conditions are similar, disturbances are the key factors that determine a specific successional stage (Yair and Verrecchia, 2002; Zaady et al., 1997, 2000; Zaady and Offer, 2010).

Sand dune areas are considered to be dry habitats and are characterized by their extremely low particle cohesion. The sand grains on the surface are available for transport by wind speeds greater than 6 m/s (Tsoar et al., 2008; Tsoar and Møller, 1986). Sand dunes can be stabilized due to colonization by filamentous cyanobacteria, which may constitute a prominent crust (Danin, 1996). The results of the interactions between sand, vegetation and biocrust that lead to dune stabilization are not yet fully understood (Kinast et al., 2013). Since crust organisms have the ability to activate their photosynthetic systems for short periods, even at low levels of water availability, such as fog, dew and atmospheric water vapor (Lange et al., 1992), they are often the first organisms to colonize sand dune environments. The polysaccharides that are produced by these cyanobacteria and by soil algae (Bertocchi et al., 1990; Mager and Thomas, 2011) form a mucilaginous sheath on the soil surface that lightly binds the soil surface particles (Baily et al., 1973; Metting and Rayburn, 1983; Schulten, 1985). Thus, the polysaccharides play an essential role in sand stabilization, in limiting water infiltration and in significantly reducing wind erosion (Eldridge and Kinnell, 1997; Neuman et al., 1996). A high moisture holding capacity, typical of polysaccharides, enhances further crust development and facilitates colonization by other organisms, such as surface cyanobacteria, soil algae, mosses and lichens. Furthermore, it has been suggested that the fine material, accumulated by biocrust activities, increases the soil depth by adhering to the soil particles and plays a key factor in gluing to the materials (e.g., polysaccharides) secreted by the cyanobacteria (Belnap and Lange, 2003; Veste et al., 2011; Zaady et al., 2013; Zaady and Offer, 2010). It has been shown that biocrust may limit infiltration (Yair et al., 2011). Different assessments exist on how biocrust affects infiltration, soil moisture and overland runoff generation (Belnap, 2006). It was reported, in sandy dune areas that are stabilized by semi-stable and stable vegetated linear dunes, that the biological topsoil crust plays an important role in the local water regime, as it affects rainwater infiltration, runoff generation and the spatial redistribution of water resources and, consequently, leads to spatial differences in the soil water regime (Yair, 1990, 2001; Almog and Yair, 2007; Yair et al., 2011). Biocrust may limit infiltration (Yair et al., 2011). Runoff and soil moisture data, obtained from hydrological investigations in a sand dune area, highlight the important role of the crusted soil surface (Yair, 1990). Several research projects conducted at the Nizzana research site, located in the southern part of the sandy area in the northeastern Negev Desert, have reported on the important role that biocrusts play in the hydrological and spatial redistribution of water resources within a dune system. Yair et al. (2011) showed that the composition of the topsoil crust is highly dependent on the local soil moisture regime. The wettest area is characterized by a moss-dominated crust, while the driest area is characterized by the predominance of cyanobacteria (Kidron et al., 2003; Almog and Yair, 2007).

It was hypothesized that biocrusts' successional stage may be affected by aridity levels and that it is reflected by soil surface properties (e.g., granulometry, the content of the cohesive soil particles of very-fine silt and clay fractions <10 μm, soil surface hardness, water permeability and soil moisture). Moreover, it is possible to infer the developmental stage of the biocrust based on the aridity level (Zaady et al., 2010).

The objectives of this study were: (1) To determine whether the developmental stage of the biocrust, as influenced by aridity levels, affects soil surface properties, pedogenesis and hydrology in sand dunes. (2) To show the differences between treatments within each site. (3) To examine whether measurements at two ends of the rainfall gradient in a sand dune area (arid and semi-arid) can imitate climate change scenarios of biocrusts' successional impact on soil moisture in specific sites. We used a multidisciplinary approach by combining bio-physiological, physical surface properties and hydrological measurements to address the objectives.

The innovation of this work is that by studying the features of the bio-physiological parameters of biocrusts as influenced by aridity levels, it is possible to predict climate change scenarios on soil moisture in specific sites.

2. Methods and materials

2.1. Study area

In the northern Sinai Peninsula (Sinai-Negev erg), the Negev (Israeli) dune field is dominated by semi-stable (active crest) and stable vegetated linear dunes, while the Egyptian side is characterized by active sand dunes due to increased anthropogenic activities, mainly the trampling of goat herds (Karnieli and Tsoar, 1995; Tsoar, 2008). The Negev sand dunes are mostly composed of quartz with very few other minerals, mostly calcite, magnetite, hematite and other silicates (Almagor, 2002).

The stabilization of the northern Sinai Israeli sand dunes is mainly attributed to biocrust and, to a lesser degree, to vegetation (Roskin et al., 2012; Siegal et al., 2013). The climate in the research area is arid to semi-arid; within a range of 25–30-km, the precipitation rate varies from 150 mm/yr in the north to 70 mm/yr in the south (Breckle et al., 2008; Karnieli and Tsoar, 1995; Tsoar, 2008; Tsoar and Møller, 1986). The composition of the biocrust in the area varies from south to north. In the south, the biocrust is composed primarily of cyanobacteria, while moving northward with the rainfall gradient, green algae, mosses and soil lichens also appear. The cyanobacteria are represented by Microcoleus sociatus, Calotris perientina and Nostoc sp.; the Chlorophytes are represented by Chlorococcum sp. and Stichococcus sp. (Lange et al., 1992; Zaady et al., 2000); mosses are represented by Bryum sp., and lichens are represented by Collema spp., Fulgensia fulgens, Squamarina cartilaginea, S. lentigera and Diploschistes diacsapis (Budel and Veste, 2008; Veste et al., 2011).

The northwestern Negev dune field (about 30 km2) can be subdivided into several sections, based on its geological structure, the wadis that traverse the area and the morphology of the sand dunes (Siegal et al., 2013; Tsoar et al., 2008, Fig. 1). The dunes' height and wavelength decrease as a function of precipitation (and hence stabilization) when moving northward with the rainfall gradient from the more arid site to the semi-arid site (see Table 1). The winter season begins in November–December and ends in April–May. However, the span of this season can vary by about two months.

2.2. Experimental sites

Soil surface sampling commenced in the northernmost semi-arid site (150–170 mm/yr average annual precipitation, 31°9'9"N, 34°18'30"E) and continued in the southernmost arid site (70–90 mm/yr, 30°56'07.24"N, 34°23'39.86"E) (Fig. 1), along the Israel–Egypt border of the northwestern Negev. The distance between the sites was about 30 km. Plots were located at the...
bottom of the northern facing slope of the dune. The line-point method (Rosentreter et al., 2007) was used to determine the locations of two plots (3 × 3 m) at each site. The sand dune transect was selected to minimize the effects of environmental factors, such as altitude and topography, and due to the homogeneity of its texture. Three treatments were performed in each of the two sites: (a) scalping biocrust (2–3 cm depth) at the beginning of the experiment (summer 2010) (labeled below as “scalped”), (b) biocrust (natural crusted soil surface cover, labeled below as “control”) (Fig. 2), (c) biocrust removal at the end of the two consecutive years, exposing the sand dune surface.

2.3. Biocrust samples

Ten biocrust samples were collected from two diagonal cross-sectional lines within each plot in the two sites. Crust samples were collected using an inverted Petri dish to ensure a maximum depth of 1 cm and the same volume for all samples. The crust samples were used as is, with no exclusion of any part or organism. We followed Johansen (1993) and West (1990) and evaluated the crusts with several different bio-physiological methods. These methods complement each other and provide a better view of the processes that occur in the biocrust at the different developmental stages. Bio-physiological parameters (proteins, chlorophyll and polysaccharide contents) and a geomorphological parameter (surface resistance to breaking pressure) were measured from these samples (Zaady and Bouskila, 2002).

2.4. Bio-physiological measurements

Total chlorophyll content (a+b) was determined by extracting with ethanol and measuring the extracts by spectrophotometer (UV–VIS mini-1240 spectrophotometer, Shimadzu, Colombia, MD, USA). The absorbance wavelengths used to measure the total chlorophyll were calculated according to the formula 17.76 (A646.6) + 7.34 (A663.6), where A represents the wavelength used (Castle et al., 2011; Lichtenthaler and Wellburn, 1983). Polysaccharides were measured with the UV–VIS mini-1240 spectrophotometer, using an Anthron reagent and sulfuric acid, based on a method developed by Dische (1962). Protein content was determined by extraction from the soil using the Lowry method with 0.1 N NaOH (Lowry et al., 1951).

2.5. Physical surface properties

Soil surface resistance to biocrust breaking pressure (Zaady and Bouskila, 2002) was measured in each plot, in 2-cm intervals along
each of the cross-sectional lines (50 points) using a field penetrometer (Pocket Penetrometer, Forestry Suppliers, Inc., Jackson, Mississippi USA). The readings reflect the highest pressure (in units of kg cm\(^{-2}\)) that can be applied to the soil surface by the penetrometer before the surface breaks (Zaady and Bouskila, 2002 and Zaady et al., 2010).

Granulometry was performed by ANALYSETTE 22 MicroTec Plus laser diffraction, which measures particles in the range of 0.08–2000 \(\mu\)m, to determine the class weight of the cohesive soil fraction. The preparation of each soil sample included sample splitting by a micro-splitter device and the removal of distinct organic matter. For the analysis, three replicates (4 g) of each sand sample were dispersed in a Na hexametaphosphate solution (at 0.5\%) (Klute, 1986) and by sonication (38 kHz). Grain size distributions were calculated using the Fraunhofer diffraction model (measurement error <5.0%).

2.6. Hydrological measurements

A Mini-Disk Infiltrometer (Decagon Devices – Pullman, WA, USA, 2007) was used to measure infiltration rates at five random points along each plot (15 for each site) (Zhang, 1997).

Soil moisture was determined 12 times during the study (every one to two months) by a Portable Neutron Scattering moisture meter (Troxler Model 4300 Soil Moisture Gauge). Measurements were taken at five depths (13, 38, 68, 88 and 113 cm) through aluminum pipes sunk vertically into the soil in the center of each plot. The measured volumetric soil water content was within the range of one to two months by a Portable Neutron Scattering moisture meter (Pocket Penetrometer, Forestry Suppliers, Inc., Jackson, Mississippi USA). The readings reflect the highest pressure (in units of kg cm\(^{-2}\)) that can be applied to the soil surface by the penetrometer before the surface breaks (Zaady and Bouskila, 2002 and Zaady et al., 2010).

2.7. Physical surface properties

Two years after applying the scalping disturbance (summer 2010 to summer 2012), the protein content in the upper soil surface layer was found to be higher in the naturally crusted control plots at both sites. Furthermore, the moving sand measurements had lower protein content at the northern site than at the arid southern site (\(p < 0.01\)) (Fig. 3).

The chlorophyll content values, in the southern site, were lower in the control plots than in the scalped and the sand plots, while in the northern site, the chlorophyll content was higher in the control plots than in the scalped and the sand plots (\(p < 0.01\)) (Fig. 4). When comparing between the sites, the chlorophyll content results showed contrasting trends. Specifically, there was a high content in the north control plot and a lower content in the south control plot, while the value was higher in the south scalped and south sand plots than in the north scalped and north sand plots.

A lower polysaccharide content was found in the moving sand plots than in the natural crusted-control and the scalped plots in the southern site (\(p < 0.001\)) (Fig. 5). A similar pattern was found in the northern site. In addition, the northern plots had higher polysaccharide contents, compared to the southern site, as expected from the more developed biocrust there, due to the higher precipitation rate.

3. Results and discussion

3.1. Bio-physiological measurements

Two years after applying the scalping disturbance (summer 2010 to summer 2012), the protein content in the upper soil surface layer was found to be higher in the naturally crusted control plots at both sites. Furthermore, the moving sand measurements had lower protein content at the northern site than at the arid southern site (\(p < 0.01\)) (Fig. 3).

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3.2. Physical surface properties

The northern site showed low breaking pressure in the case of the moving sand plots (less than 0.3 kg cm\(^{-2}\)) (\(p < 0.001\)) (Fig. 6), while the reclaimed scalped treatments presented intermediate results (an average of 2.4 kg cm\(^{-2}\)) in comparison with the natural crusted plots (with an average of 4.2 kg cm\(^{-2}\)). Similar result patterns were obtained in the southern site. The moving sand plots showed lower breaking pressure (less than 0.25 kg cm\(^{-2}\)) (\(p < 0.001\)) (Fig. 6), while the reclaimed scalped treatments presented intermediate results (an average of 0.95 kg cm\(^{-2}\)) in comparison with the natural crusted plots (with an average of 1.45 kg cm\(^{-2}\)). A comparison between the sites showed that the natural crusted plot of the southern site presented a lower resistance to breaking pressure—about one-third (1.45 kg cm\(^{-2}\)) of the resistance to breaking pressure of the natural crusted plot of the northern site (semi-arid area) (\(p < 0.01\)) (4.2 kg cm\(^{-2}\)) (Fig. 6).

Grain size distributions of the biocrust samples are presented in Fig. 7. The samples of the semi-arid northern site are characterized by bi-modal distributions, while in the south, there are tri-modal distributions. In all the samples, the coarse mode was found in the medium-sand fraction. The values of all the southern site treatments are slightly higher than those of the northern site (Mode 1 in Table 2). The second mode in the southern site ranged from 102.7 to 125.3 \(\mu\)m (fine-sand fraction). However, the finest modes of both sites were in found the fine-silt fraction (14.1 \(\mu\)m). Overall, the samples of the southern site were coarser than those of the northern site. A smaller amount of sand fraction (>50 \(\mu\)m) was obtained in the more humid northern site than in the more arid southern site (Table 2). The fractions of silt (2–50 \(\mu\)m) and clay (<2 \(\mu\)m) in the control plots showed the opposite trend, with higher values in the northern site than in the southern site.
3.3. Hydrological measurements

As described in Section 2.4, the soil water content was measured by a neutron scattering probe at five depths during the time of the experiment; here, we focus on the results from the depth of 65 cm, which is the average depth suggested for the local perennial shrub root systems (Siegal et al., 2013). We compared the scalped crusted plots with the natural crust plots. Winter rainfall was similar at the two sites (about 100 mm) during winter 2009–10, whereas during winter 2010–11, the annual rainfall was similar to the long-term annual mean (i.e., 80 mm at the southern site and 150 mm at the northern site).

Moisture was higher in the scalped than in the crusted control plots in the southern site, whereas in the northern site, moisture was similar in both. Differences between years were seen in the crusted plots, in which the southern crusts showed higher moisture levels than the northern crusts during the first year but similar moisture levels during the second year (Fig. 8).

Higher infiltration rates were obtained in the moving sand plots than in the scalped and the natural control plots in the southern site \( (p < 0.001) \) (Fig. 9).

Similar patterns were obtained in the northern site. A comparison between the two sites showed that the natural control crusts had a higher resistance to water infiltration (Fig. 9).

4. Discussion

4.1. Determination of the developmental stage of the biocrust

The composition of the topsoil crust highly depends on the local soil moisture regime (Almog and Yair, 2007; Kidron et al., 2010; Zhang et al., 2010). As the soil moisture increases, the cyanobacteria that dominate the dry arid southern areas (~75 mm/yr) are replaced by green algae, mosses (~150 mm/yr) and lichens (>200 mm/yr) (Almog and Yair, 2007; Eldridge and Greene, 1994; Yair et al., 2011).

We used three bio-physiological parameters (protein, chlorophyll and polysaccharide contents) to characterize the bio-physiological parameters of biocrusts as affected by aridity levels. Protein content may reflect the total biomass of soil microorganisms, in general, that may include, in addition to cyanobacteria, bacteria, fungi and other soil organisms. Polysaccharides may be derived not only from photosynthetic organisms, but also from soil particles aggregated by bacterial and root exudates in the upper 5 cm of the soil profile (Paul and Clark, 1996). Chlorophyll content is the parameter that reflects the photosynthetic organisms that colonize and produce the crust and, therefore, is considered a reliable and successful indicator of the photosynthetic activity of the biocrust organisms (Beinap et al., 2008; Johansen, 1993; Lange et al., 1992; West, 1990). However, a combination of the three bio-physiological parameters can serve as a good
Consequently, the developmental stages of the biocrust was reflected by the fact is that all trends of these three parameters showed, in common, a decrease in magnitude from the northern site that had a well-developed cyanobacterial and moss biocrust to the southern site with cyanobacterial biocrust (West, 1990; Zaady and Bouskila, 2002).

As for the differences between treatments in the same area, the chlorophyll content in the control natural crusts was lower than in the other treatments in the southern site. One of the explanations could be that sand, although not visually identifiable, presented an important cover of cyanobacteria, while the higher chlorophyll content in the scalped crusts, as compared with the control crusts, could be due to colonization by biocrust since the crust was scalped in 2010. By the beginning of 2014, the scalped and natural control plots seemed visually very much the same.

### 4.2. Physical surface properties

Surface resistance to breaking pressure may reflect the hardness and the thickness of the crusted soil surface of the biocrusts. However, in the case of the biocrust, it is closely related to the content of the polysaccharides that glue the soil particles together, and therefore, an increase in resistance is related to higher developmental stages of the biocrust.

Surface dune stabilization often occurs due to the development of topsoil crusts, rich in fine-grained particles (Danin, 1996; Yair et al., 2011). The main source for fine-grained particles is the

### Table 2

Statistical parameters and soil fractions calculated from the particle size analysis by the laser diffractometer.

<table>
<thead>
<tr>
<th>Sample</th>
<th>South scalped</th>
<th>South control</th>
<th>South sand</th>
<th>North scalped</th>
<th>North control</th>
<th>North sand</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Statistical parameters (µm)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>178.2</td>
<td>266.0</td>
<td>203.2</td>
<td>133.1</td>
<td>122.8</td>
<td>139.0</td>
</tr>
<tr>
<td>Mode 1</td>
<td>277.5</td>
<td>373.9</td>
<td>277.5</td>
<td>206.0</td>
<td>186.5</td>
<td>206.0</td>
</tr>
<tr>
<td>Mode 2</td>
<td>102.7</td>
<td>125.3</td>
<td>113.5</td>
<td>14.1</td>
<td>14.1</td>
<td>14.1</td>
</tr>
<tr>
<td>Mode 3</td>
<td>14.1</td>
<td>14.1</td>
<td>14.1</td>
<td>–</td>
<td>8.5</td>
<td>8.2</td>
</tr>
<tr>
<td>D₁₀</td>
<td>15.9</td>
<td>48.9</td>
<td>15.1</td>
<td>7.9</td>
<td>8.5</td>
<td>8.2</td>
</tr>
<tr>
<td>D₅₀</td>
<td>169.8</td>
<td>288.2</td>
<td>217.7</td>
<td>140.3</td>
<td>122.5</td>
<td>148.1</td>
</tr>
<tr>
<td>D₉₀</td>
<td>334.0</td>
<td>450.9</td>
<td>347.2</td>
<td>246.4</td>
<td>233.7</td>
<td>255.3</td>
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<tr>
<td><strong>Soil fractions (%)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Clay (&lt;2 µm)</td>
<td>1.9</td>
<td>1.5</td>
<td>1.8</td>
<td>3.0</td>
<td>2.9</td>
<td>2.8</td>
</tr>
<tr>
<td>Fine-silt (2-20 µm)</td>
<td>9.4</td>
<td>7.8</td>
<td>9.6</td>
<td>18.2</td>
<td>17.0</td>
<td>18.2</td>
</tr>
<tr>
<td>Coarse-silt (20-50 µm)</td>
<td>2.8</td>
<td>1.0</td>
<td>0.9</td>
<td>2.9</td>
<td>4.5</td>
<td>2.9</td>
</tr>
<tr>
<td>Sand (&gt;50 µm)</td>
<td>85.9</td>
<td>89.7</td>
<td>87.7</td>
<td>75.8</td>
<td>75.6</td>
<td>76.2</td>
</tr>
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</table>

**Fig. 8.** The changes of the volumetric soil water content during the experimental period as measured by the neutron scattering probe at 65 cm depth, in the natural control plots and in the scalped plots. Each point represents a replicate.

**Fig. 9.** Water infiltration rates in the natural biocrust and reclaimed biocrust, in comparison with the moving sand at the two sites. The gray columns indicate the mean, and the white columns indicate the median.

indicator for the developmental stages of the biocrust (West, 1990; Zaady and Bouskila, 2002).
entrapment of dust. Soil-surface biocrusts are effective dust traps (Belnap, 2003; Zaady and Offer, 2010). Dust inputs have enriched the sediments in many elements, including P, Mg, Na, K, and Mo, as well as Ca, at sites where the bedrock lacks calcite cement (Reynolds et al., 2001). It has been reported that dust was best incorporated into Microcoleus spp., (filamentous cyanobacteria) crust and appeared to increase the growth of the cyanobacteria as well as to strengthen the cohesion of the crust (Almog and Yair, 2007; Belnap and Lange, 2001; Zaady and Offer, 2010). Microbial crust cohesion was mainly attributed to cyanobacterial and green soil agal aggregation, while lichens, fungi and mosses had more effect on the soil structure and physico-chemical properties (Chunxiang et al., 2002). Increasing the amounts of silt and clay (Table 2) may help to seal the soil surface and reduce the infiltra-
tion rates. Furthermore, it was found that the biocrust incorporated large quantities of deposited atmospheric particles, leading to a significantly enhanced rate of increase in soil depth in windy and arid environments (Zaady and Offer, 2010). While the biocrust in the arid southern site is mainly dominated by cyanobacteria and a 2–3 mm crust thickness, the semi-arid northern site has a crust thickness of 5–11 mm to 15 mm with a heavy cover of mosses and lichens (Almog and Yair, 2007; Veste et al., 2001, Yair et al., 2011; Williams et al., 2013). The mosses and lichens protruding from the soil surface layer affect the surface micro-topography and help to incorporate deposited atmospheric particles, mainly fine-silt and clay. The magnitude of dust capture and the mecha-
nisms of dust accretion change with biocrust succession. Biocrusts uniquely facilitate the accumulation, morphology, and ecosystem function of dust and should, therefore, be considered critical agents in arid pedogenesis and landscape development (Williams et al., 2012).

4.3. Hydrological measurements

Biocrust affects soil moisture at the sub-surface. Regardless of the sandy dune texture along the rainfall gradient (Tsoar et al., 2008), in the less arid northern plot, a thick biocrust of cyanobacteria, mosses and lichens developed. Such a relatively thick bioc-
rust may affect water infiltration and limit the soil moisture due to its hydrophobic characters (Almog and Yair, 2007). In the southern, arid site, the thin biocrust layer of cyanobacteria can absorb only limited amounts of rain water at the surface, consequently resulting in higher soil moisture in the deep layers (Fig. 8). Our findings demonstrate the important role played by different types (developmental stages) of biocrust in a sand erg with a rainfall gra-
dient. These results challenge the widely held belief that an increase in rainfall amount directly increases the soil moisture both in the sub-surface and in the deep layers of sands. This belief may, therefore, be limited to scoured or uncrusted sandy areas Our results are in accordance with Almog and Yair (2007) and Yair et al. (2011) who suggested that higher precipitation results in a more developed biocrust and, thus, may reduce soil moisture. In a recent study, Siegal et al. (2013) reported results that somewhat contra-
dict those of Yair et al. (2011). While our results support the observ-
ations of the latter, they cannot rule out the results of Siegal et al. (2013), as we have focused on the bottom flat area of the northern face of the dune (that generally contains the most developed biocrust), while Siegal et al. (2013) performed a more extended study that included the four different faces of the sand dunes.

The research period may be divided into two periods—in the first period, the annual precipitation at the two sites was almost the same, and in the second period, the annual precipitation resembled the climatic rainfall gradient, with a low precipitation rate at the arid southern site and a higher precipitation rate at the semi-arid northern site. The cyanobacterial crust of the southern site is thin, and thus, the high rate of precipitation enabled the infiltration of more water in comparison with the northern site, which received the same amount of precipitation but had a thicker cyanobacterial-moss-lichen crust that prevented the infiltration of water. In the second research period, we observed almost the same soil water content in all sites, despite the significantly higher annual precipitation in the northern site. This supports our hypoth-

Fig. 10. Suggested trend for the climate change scenario from our observed biocrust succession on soil moisture along a rainfall gradient. As the biocrust becomes more developed, it decreases the water infiltration into the soil.
depending on the rate of the changes (Fig. 10): (1) In slow changes toward drought, the ecosystems will simply shift to the balance that occurs in the more arid areas, and the areas will become drier, but the biocrust permeability will increase while increasing the soil moisture. (2) In slow changes toward a humid climate, the ecosystems will shift to the balance that occurs in the more semi-arid areas, and the areas will become wetter; as a result the biocrust permeability will decrease, increase in soil moisture within the biocrust layer and less in deeper soil layers while decreasing the soil moisture. Furthermore, when the rate of change toward drought (or humidity) is expected to be rapid, in relation to the rate at which the ecosystems can adapt to the new regime, it could lead to a negative impact on ecosystem resilience (Almag and Yair, 2007; Maestre et al., 2012; Siegal et al., 2013).

5. Conclusions

Our findings demonstrate the important role played by different types of biocrust in a sand erg with a rainfall gradient. Our results challenge the common belief that a high amount of wet precipitation directly affects the soil water regime in sand dunes. The cyanobacterial crust of the southern site is thin, and thus, the high amount of precipitation enabled the infiltration of more water in comparison with the northern site, which received the same amount of precipitation but had a thicker cyanobacterial-moss-lichen crust. It should be noted that when annual precipitation was significantly higher in the northern site than in the southern site, the same water content was observed in the soil depth. Furthermore, in this study, by characterizing the bio-physiological parameters of biocrusts as affected by aridity levels, it is possible to imitate climate change scenarios in soil moisture in specific sites.

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