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Biocrusts serve as biomarkers for the upper 30 cm soil water content

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SUMMARY

Knowledge regarding the spatial distribution of moisture in soil is of great importance especially in arid regions where water is scarce. Following a previous research that showed a significant relationship between daylight surface wetness duration and the average chlorophyll content of 5 biocrusts in the Negev Desert (Israel), and the resultant outcome that pointed to the possible use of biocrusts as biomarkers for surface wetness duration, we hypothesize that biocrusts may also serve as biomarkers for the moisture content of the upper soil layer. Toward this end, daylight surface wetness duration was measured at 5 crust types following rain events during 1993–1995 along with periodical soil sampling of the upper 30 cm (at 5 cm intervals) of the soil profiles underlying these biocrusts. The findings showed a positive linear relationship between daylight surface wetness duration and the chlorophyll content of the crusts ($r^2 = 0.96$–0.97). High correlations were also found between daylight surface wetness duration and the available water content ($r^2 = 0.96$) and duration ($r^2 = 0.85$–0.88) of the upper 30 cm soil and between the chlorophyll content of the crust and the available water content ($r^2 = 0.93$–0.96) and duration ($r^2 = 0.78$–0.84). Topography-induced shading and slope position (which determined additional water either by runoff or subsurface flow) are seen responsible for the clear link between subsurface moisture content, daylight surface wetness duration and chlorophyll content of the crust. This link points to the possible use of biocrusts as biomarkers for subsurface water content and highlights the importance of crust typology and mapping for the study of the spatial distribution of water and their potential use for the study of ecosystem structure and function.

1. Introduction

Knowledge regarding the spatial distribution of moisture in soil is of great importance for hydrologists, pedologists and ecologists. This is more so in arid regions where water is scarce. Antecedent moisture may affect runoff (Kidron, 1999) and subsurface flow (Warsta et al., 2013), which in turn may impact solute transport (Yu et al., 2012) and sediment yield (Kidron, 2001; Wine et al., 2012). It may dictate soil forming processes (Dan et al., 1982) as well as microorganism and plant activity (Noy-Meir, 1973) and subsequently nutrient cycling and mineralization. Moisture may also dictate biocrust activity.

Biocrusts (known also as microbiotic crusts or biological soil crusts) play an important role in arid regions. Being composed of cyanobacteria, green algae, lichens, mosses, fungi and bacteria, they provide the ecosystem with C (Lange et al., 1992) and N (Evans and Lange, 2001; Mayland and McIntosh, 1966). They may also affect the water regime of habitats by either promoting or hindering runoff (Kidron et al., 2012b).

In the Nizzana research site (NRS) of the Hallamish dune field (western Negev Desert), biocrusts cover all mid and lower slopes of the longitudinal dunes and all the sandy interdunes, being absent only from elevated dune crests, where wind velocity is too high to facilitate their establishment. Five crusts were defined in NRS, four cyanobacteria-dominated crusts (crusts A–D with *Microcoleus vaginatus* predominating), and one (crust E) moss-dominated crust (Kidron et al., 2010). When various variables such as rain, maximal water-holding capacity or dust (which also implies addition of nutrients) were examined, none of these variables yielded significant correlations with the chlorophyll content of the crusts (Kidron et al., 2009). High correlations with r^2 ranging between 0.92 and 0.99 were however found between the crust's chlorophyll content and daylight surface wetness duration during a three-year study. The study highlighted the fact that under relatively stable conditions, daylight surface wetness duration determines crust biomass and hence crust type (Kidron et al., 2010), with daylight surface wetness duration increasing with $A < B < C < D < E$ (Kidron et al., 2009). The findings pointed out that chlorophyll content may thus serve as a good proxy for daylight surface wetness duration.

Following these findings, we hypothesize that crust biomass may also serve as a biomarker for the moisture content of the

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upper soil layer. Advancing from the atmosphere–pedosphere interface to depth, it is hypothesized that the desiccation rate that determines surface wetness duration may point to dry and wet subsurface soil profiles. We therefore assume that long wet surface conditions may require long subsurface wetness conditions. Subsequently, we hypothesize that biocrusts that may serve as biomarkers for surface wetness duration may also serve as biomarkers for the underlying moisture content of the upper 30 cm soil layer. This hypothesis is examined herein.

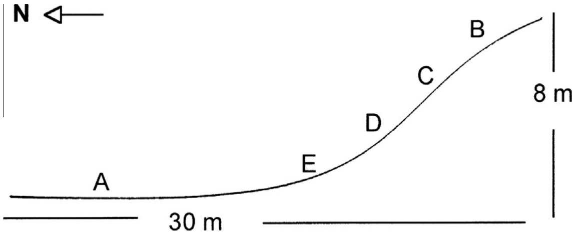

Fig. 1. A schematic cross section of the transect, showing the crusted habitats A, B, C, D and E.

2. The research site and methodology

The Nizzana research site (NRS) lies within the Hallamish dune field at the western Negev Desert, Israel (34°23′E, 30°56′N). Long-term mean precipitation is 95 mm falling during November to April (Rosenan and Gilad, 1985). Mean annual temperature is 20 °C; it is 26 °C during the hottest month of July and 8 °C during the coldest month of January. Annual potential evaporation is ~2600 mm (Evenari, 1981).

The Hallamish sand dune is comprised of 15–20 m high longitudinal dunes which trend west-east and are separated by 50–200 m wide interdunes. The dunes and the interdunes consist of >90% of sand (63–2000 μ) and <10% of fine content, i.e., silt (2–63 μ) and clay (<2 μ). The most xeric crust at the sandy dunes, crust A, occupies the south-facing slopes and the sandy interdunes, whereas crusts B, C, D and E occupy the northern aspects of the dunes. On a low stabilized dune which is entirely covered by biocrusts, crust B was found at the upper slope, crust C the upper-middle slope, crust D the midslope and crust E at the interface between the bottom slope and the interdune. The crusts differed in their chlorophyll, protein and carbohydrate content. They also differ in their species composition and their physical variables such as thickness and compressional strength (Kidron et al., 2010). Some of the crust properties are shown in Table 1.

Surface wetness duration and soil moisture measurements took place during the growing seasons of 1993/94 and 1994/95. Measurements took place along a transect in which a pair of plots (2–6 m^2) was demarcated at each of the biocrusts (A–E). A schematic cross section of the transect is shown in Fig. 1.

Surface wetness duration was monitored in 1–3 h intervals following rainstorms during which the relative cover of the wet surfaces, as visually estimated, was monitored, as also described elsewhere (Kidron et al., 2009). Plots which over 50% of their surface was wet were considered wet. In addition, periodical moisture sampling in 1–3 week intervals (with a total of 13 and 16 samplings for 1993/94 and 1994/95 growing periods, respectively) was carried out. Measurements were confined to the upper 30 cm, following previous findings that indicated that >90% of the roots of the annual plants concentrate at the upper 30 cm (Kidron, unpub.). Excavation took place adjacent (westward) to each plot. In order to avoid the impact of the wet crust upon the subsurface moisture content, sampling of the crust was avoided. Soil sampling was carried out in pairs (for each habitat) at 1–5, 5–10, 10–15, 15–20, 20–25 and 25–30 cm. Approximately 20–30 g of soil were taken from each depth. The samples were placed in pre-weighed glass flasks, sealed hermetically and taken to a nearby lab for measurements. The samples were oven-dried at 105 °C until reaching a constant weight and then re-weighed, and their gravimetric moisture content was calculated. The volumetric water content was then determined following the equation:

$$Wv = Ww * Db/Dw$$

where Wv (cm^3/cm^3) is the volumetric water content, Ww (g) the gravimetric water content, Db (g/cm^3) is the soil bulk density and Dw (g/cm^3) is the water density (≈1).

Yet, in order to determine the actual moisture that may potentially be available to the plants, the volumetric water content was subtracted from the wilting-point water content, as determined by pressure plates (Kidron et al., 2002). This water fraction, available to plants and microorganisms, will be referred to hereafter as available water content, AWC (Hillel and Tadmor, 1962). Similarly, the time during which water above the wilting point will be available will be termed as available water duration (AWD).

Following the growing period, the chlorophyll a content (hereafter chlorophyll) of the different crusts was determined. By measuring the chlorophyll content of the crusts at the conclusion of the growing season, chlorophyll fluctuation in accordance with the daily precipitation was avoided (Kidron et al., 2012a). Nevertheless, since the chlorophyll content of the crust gradually decreases as the surface dries out to a base level that reflects the winter precipitation (being higher and lower following a wet and dry year, respectively; see Kidron et al., 2008), the crust's chlorophyll content during the summer may reflect the precipitation regime during the previous winter. Consequently, the chlorophyll content of the crusts was measured in 18–24 samples, 1.2 cm in diameter, taken from each plot in the end of each growing season. Chlorophyll was extracted by hot methanol (70 °C, 20 min) in the presence of $MgCO_3$ (0.1% w/v) in sealed test tubes and assayed according to Wetzel and Westlake (1969).

Three-way ANOVA was performed using SPSS version 11 software (IL, Chicago, USA) in order to determine the effect of rain (above and below 5 mm per week prior to sampling), year, and the habitat location (i.e., crust type) on the moisture content. In

Table 1
Crust properties. Standard deviation in parenthesis (after Kidron et al., 2010).

Crust	Aspect and angle (degree)[a]	Thickness (mm)	Chlorophyll (mg/m^2)	Organic matter (%)[b]	Moss cover (%)
A	H, 0-3 SF, 3-30	1.1 (0.3)	16.7 (9.9)	0.5 (0.1)	<0.1
B	NF, 3-7	1.5 (0.3)	20.7 (10.5)	0.6 (0.1)	<0.1
C	NF, 7-15	2.0 (0.4)	28.5 (16.7)	0.75 (0.1)	~1
D	NF, 15-30	2.8 (0.3)	43.4 (27.6)	0.9 (0.15)	15.1 (3.5)
E	NF, 0-30	10.3 (1.4)	53.2 (25.8)	2.6 (0.95)	85.3 (6.4)

[a] H stands for flat horizontal surface, SF for south-facing and NF for north-facing.
[b] Includes living and dead organisms.

addition, in order to examine our hypothesis that the moisture at the upper soil layers will follow the pattern found for the surface wetness duration with A < B < C < D < E, we calculated absolute and relative differences. We examined if the average absolute difference (B-A, C-B, D-C, E-D) or the relative difference ((B-A)/A, (C-B)/C, (D-C)/D, (E-D)/E) is higher than zero. Values that are lower than zero will imply that our assumption that the habitats show a consistent pattern is invalid while values higher than zero will support our hypothesis. We applied a *t*-test and the differences were regarded significant at $P < 0.05$.

3. Results

Both years had fundamental differences in their precipitation regime. While 1993/94 was a drought year with a total of only 46.9 mm, 1994/95 was exceptionally wet with a total of 172.0 mm (Table 2).

Daylight surface wetness duration showed substantial inter-annual differences. Daylight surface wetness duration ranged between 153 and 359 h in 1993/94; it ranged between 451 and 996 h in 1994/95 (Fig. 2a). Substantial differences, although much lower in range, also characterized the chlorophyll content of the crusts, ranging between 16.0 and 45.4 mg m^{-2} in 1993/94 and between 23.6 and 75.6 mg m^{-2} in 1994/95 (Fig. 2b). When the daylight surface wetness duration was plotted against the crust's chlorophyll content, high correlations were found with r^2 ranging between 0.96 and 0.97 (Fig. 3).

The data show high differences between both years, with available water content (AWC) being substantially higher during the wet year of 1994/95. At both years, AWC at the moss-dominated crust E was higher than that of the cyanobacterial crusts A–D. For the sake of a clear presentation, the soil profiles of only three crusts, crust, A, C and E are presented (Figs. 4 and 5). When the total AWC for the upper 30 cm of all surfaces was plotted, a gradual increase with A < B < C < D < E was evident (Fig. 6). This is clearly shown when the AWC for all sampling days was averaged (Fig. 7a) and the total duration for all crusted habitats (i.e., crust types) calculated (Fig. 7b). Both average available water content (AWC) and available water duration (AWD) increased with A < B < C < D < E.

All three variables examined, rain, year and crust type yielded significant relations with AWC (Table 3). Whereas no interaction existed between all three variables, year × rain interacted, explained by the fact that while 1993/94 was a drought year with predominantly <5 mm rains, 1994/95 was extremely wet (the wettest year in 25 years) with predominantly >5 mm events. As for the interaction between rain and crust, this was verified when

Table 2
Rain depth during 1993/94 (a) and 1994/95 (b).

Date 1993/94	Rain depth (mm)
a	
26–27.11	3.1
21–23.12	20.7
1–2.1	1.8
14–15.1	3.9
23–25.1	7.6
26–28.1	2.2
23.2	0.5
27–28.2	2.0
10.3	2.2
12.3	2.7
1.4	0.2
Total	46.9
Date 1994/95	
b	
8–10.10	2.3
12.10	0.5
2–6.11	56.1
14–17.11	7.7
20.11	0.2
22–25.11	14.9
27.11	0.4
29–30.11	2.7
2–6.12	33.0
17.12	2.7
19.12	1.2
4–5.2	30.0
6.2	0.9
8.2	5.1
15–16.2	2.7
22–23.2	10.1
26.3	0.5
2.4	1.0
Total	172.0

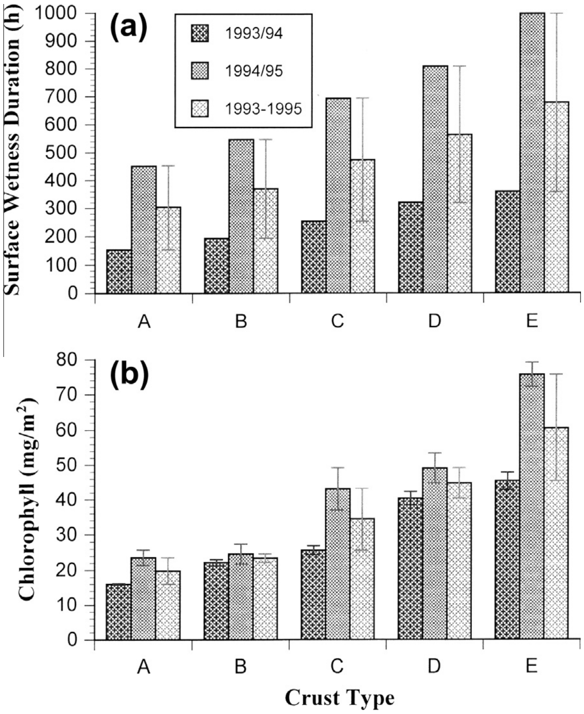

Fig. 2. Cumulative annual daylight surface wetness duration (a) and the crust's chlorophyll content (b) during 1993/94 and 1994/95 at the crusted habitats A–E. Bars represent one SE.

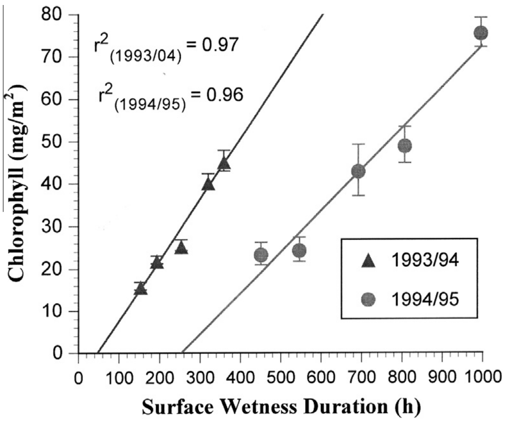

Fig. 3. The relationship between daylight surface wetness duration and chlorophyll content. Bars represent one SE.

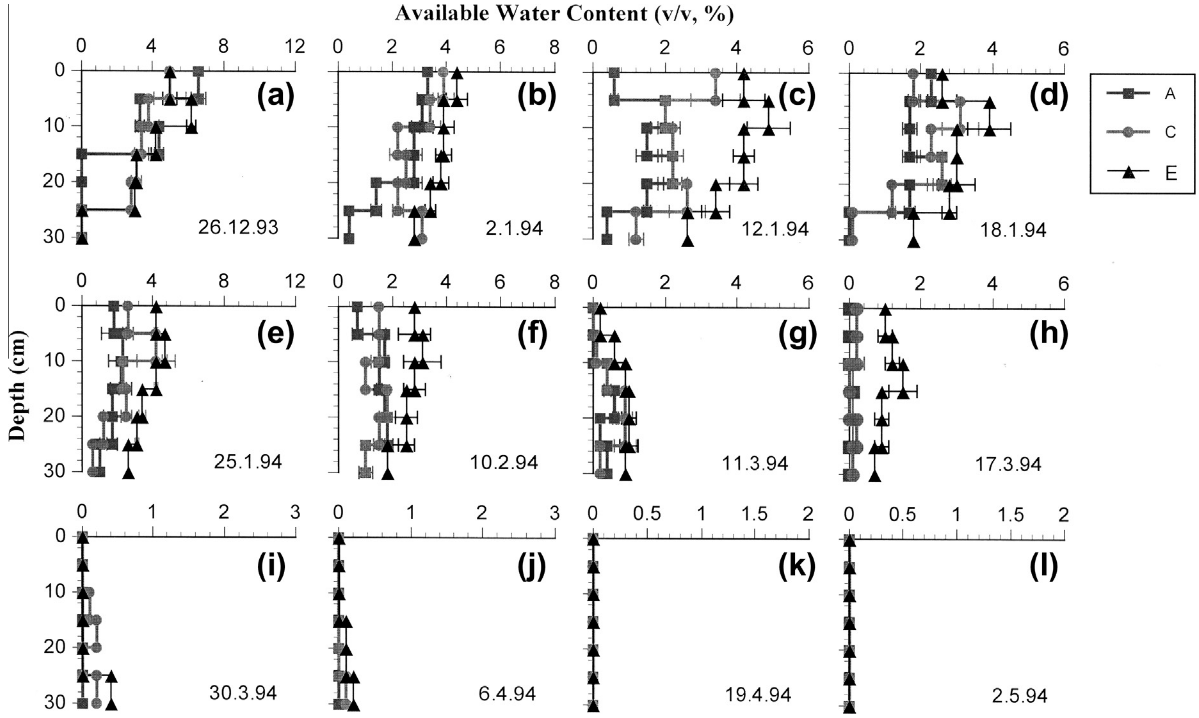

Fig. 4. Available water content at soil profiles of selected crust types (crusts A, C, E) during periodic sampling of 1993/94. Bars represent one SE.

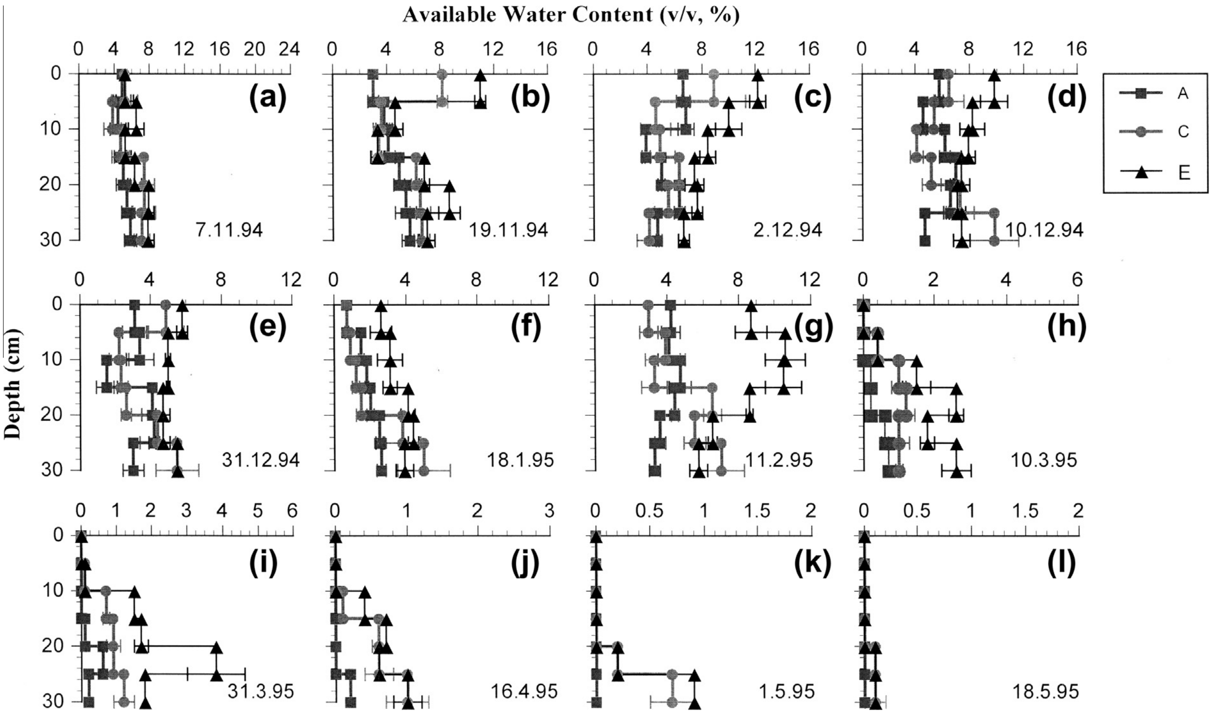

Fig. 5. Available water content at soil profiles of selected crust types (crusts A, C, E) during periodic sampling of 1994/95. Bars represent one SE.

a two-way ANOVA coupled with a post hoc test (using Tukey) was executed, with year and crust as independent variables. Whereas year was significant for <5 mm and >5 mm rains, crust was significant only for >5 mm rains. This was explained by high standard deviation during <5 mm rains (up to 128% of average in comparison to up to 42% of average for rains >5 mm) resulting from the sampling time, with relatively high AWC close to the event and very low AWC a few days following the event.

The important role of the crust was however evident when the relative and absolute differences between adjacent crusts were calculated. Significant relations with all values being higher than zero were obtained (Table 4). The data validated our initial hypothesis that the moisture content of the crusted habitats will follow the pattern A < B < C < D < E.

When AWC at 0–30 cm was compared to the daylight surface AWD, high annual correlations (with $r^2 = 0.96$) were obtained

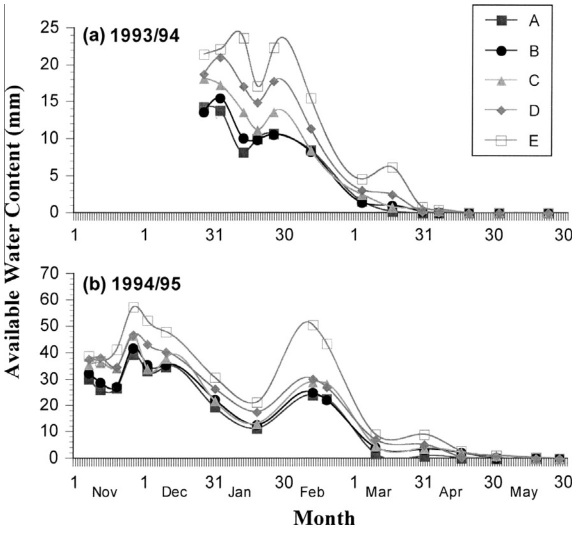

Fig. 6. Available water content at all crust types (crusts A–E) at the 0–30 cm soil profiles during 1993/94 and 1994/95.

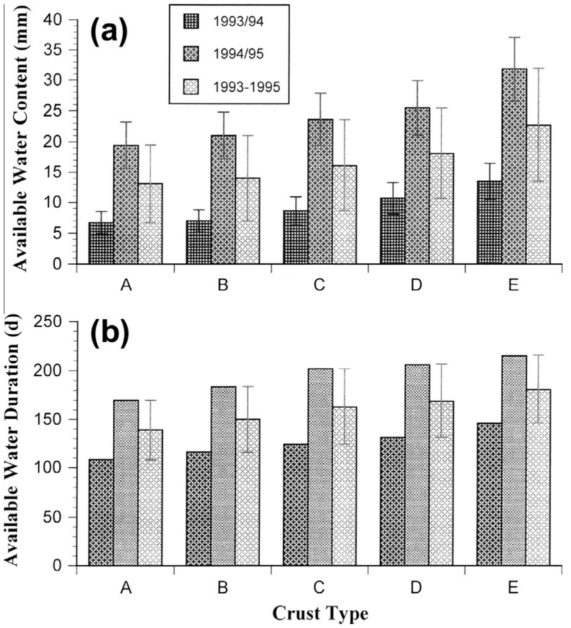

Fig. 7. Average available water content (a) and available water duration (b) during 1993/94 and 1994/95 at the upper 30 cm of the crusted habitats A–E. Bars represent one SE.

Table 3
Three-way ANOVA for available water content (mm) in relation to rain (above and below 5 mm), year, and crust type for 1993/94 and 1994/95.

Source of variation	SS	*df*	*F*	*P*-value
Year	6987.6	1	167.06	<0.001
Rain	19387.8	1	463.53	<0.001
Crust	2583.6	4	15.44	<0.001
Year × rain	3871.5	1	92.56	<0.001
Year × crust	86.8	4	0.52	0.722
Rain × crust	470.2	4	2.81	0.027
Year × rain × crust	47.2	4	0.28	0.889
Error	8783.5	210		
Total	132968.1	230		

Table 4
A comparison of the absolute (a) and relative (b) differences in the moisture content of adjacent crusted habitats.

Crust	N	Mean	St. Dev	Sig.
a. Absolute differences				
1993/94				
B-A	9	0.617	0.544	0.009
C-B	9	1.783	1.565	0.009
D-C	9	2.233	1.700	0.004
E-D	9	2.944	1.990	0.002
1994/95				
B-A	14	1.919	0.890	0.000
C-B	14	2.654	2.386	0.001
D-C	14	1.946	1.460	0.000
E-D	14	5.886	6.117	0.003
b. Relative differences				
1993/94				
B-A/B	9	0.209	0.268	0.048
C-B/C	9	0.259	1.565	0.005
D-C/D	9	0.194	0.073	0.000
E-D/E	9	0.232	0.164	0.003
1994/95				
B-A/B	14	0.260	0.302	0.009
C-B/C	14	0.143	0.151	0.004
D-C/D	14	0.126	0.111	0.001
E-D/E	14	0.192	0.124	0.000

(Fig. 8a). High, although lower correlations with $r^2 = 0.85$ (for 1993/94) and 0.88 (for 1994/95) were obtained with the daylight surface AWD (Fig. 8b). As expected following the high correlations between the chlorophyll content of the crust and the daylight surface AWD, high correlations (with $r^2 = 0.96$ for 1993/94 and $r^2 = 0.93$ for 1994/95) were also obtained between the chlorophyll content and AWC (Fig. 8c). Lower correlations (with $r^2 = 0.78$ for 1993/94 and $r^2 = 0.84$ for 1994/95) were obtained between the chlorophyll content and the daylight surface AWD (Fig. 8d).

4. Discussion

The interrelationship between the available water content of the upper 30 cm of the soil, daylight surface wetness duration and the chlorophyll content of the crust imply that any additional water or impediment of evaporation are expected to affect these three variables. It is therefore argued that topography and slope location may dictate the surface and subsurface moisture content of the habitat and hence the chlorophyll content of the crust. This will be shown for two years which represent extreme precipitation scenarios, 1993/94 and 1994/95.

While 1993/94 was a drought year with 46.9 mm, which is about half the long-term mean of 95 mm, 1994/95 was extremely wet, with 172.0 mm, i.e., approximately twice the long-term mean. The precipitation during 1994/95 stemmed mainly from an extremely large-scale Red Sea Trough (RST) event. The RST event, which only rarely affects the western Negev (Kidron and Pick, 2000), fell during November 2–6, 1994 and impacted the entire country. It brought 56.1 mm of precipitation to NRS.

As far as surface wetness and soil moisture are concerned, faster desiccation characterized crust A. This is not surprising following the crust location at the south-facing slope and the interdune, both subjected to higher radiational load than the north-facing slope, as also found in the Tengger Desert in China (Li et al., 2010). The increase in the slope angle and subsequently the shading effect at the north-facing slope resulted in higher available water content and duration at crusts B–D. Located at the interface between the north-facing slope and the interdune and subsequently receiving extra water from runoff and subsurface flow (Kidron and Vonshak, 2012), crust E exhibited the highest AWC lasting for the longest duration.

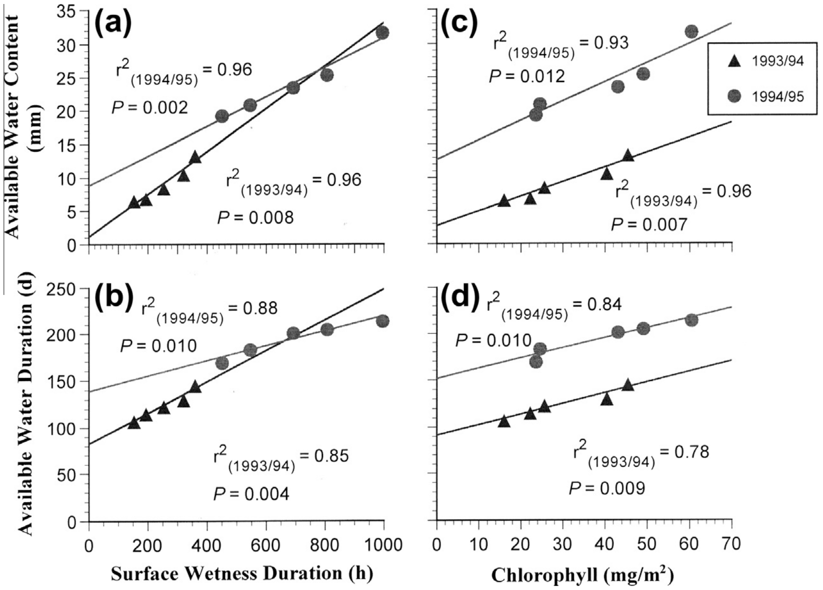

Fig. 8. The relationship between daylight surface wetness duration and the average available water content (a) and duration (b) at the upper 30 cm and the relationships between the chlorophyll content and the average available water content (c) and duration (d) at the upper 30 cm.

As all surfaces are impacted by evaporation, the high correlations between the daylight wetness duration of the crust, available water content and duration of the upper 30 cm is not surprising. Since daylight surface wetness duration determines the chlorophyll content of the crust (Kidron et al., 2009), significant correlations between the chlorophyll content of the crust and available water content and duration at the upper 30 cm are expected. It follows that surface wetness duration not only reflects crust activity and biomass but also available water content and duration at the upper soil layer.

The interrelationship between AWC of the upper 30 cm of the soil, daylight surface AWD and the chlorophyll content of the crust imply that any additional amount of water or hindrance of evaporation are expected to affect these three variables. And thus, as shown by the current data, topography and slope location may dictate the surface and subsurface moisture content of the habitat and hence the crust's chlorophyll content. With the increase in slope angle from ~5° to ~25° (from crust B to D; see Table 1) and therefore with increasing shading, higher subsurface AWC and AWD will characterize the north-facing slope. This results in turn in an increase in the chlorophyll content of the crust from 22.2 (crust B) to 40.4 (crust D) mg m^{-2} and from 24.6 (crust B) to 49.1 (crust D) mg m^{-2} during 1993/94 and 1994/95, respectively. Following the lower slope angles that characterize the footslope habitat of crust E, an increase in shading (which leads to lower evaporation) cannot be seen as the major contributing factor toward the increase in the chlorophyll content of crust E. Addition of water by runoff and especially by subsurface flow (Kidron et al., 2010) explains the increase in surface wetness duration, subsurface moisture content, and the higher chlorophyll content of crust E, highlighting the role of slope position in the habitat's water regime and subsequently in the biomass of crust E.

Both variables, addition of water and shading may also affect crust properties on a local scale. Fig. 9 shows periodic soil measurements that were carried out during the winter of 1993/94 at small (2–3 m diameter) depressions at the interdunes (ID-PON) in comparison to the adjacent interdunal surfaces (ID) in which runoff did not concentrate. Much higher moisture content characterized ID-PON. Subsequently, ID-PON was characterized by longer daylight surface wetness duration of 405 h in comparison to only 250 h of ID (Kidron and Vonshak, 2012). It was also characterized by a high-chlorophyll crust, reaching on average 59.8 (SD = 27.6) mg m^{-2} in comparison to only 16.7 (SD = 7.6) mg m^{-2} in ID.

Similarly, local shading such as by shrubs resulted in higher daylight surface AWD and subsequently higher chlorophyll content of the under-canopy crusts (Kidron and Vonshak, 2012). Concomitantly, moisture content at the under-canopy was significantly higher than that of the adjacent sun-exposed habitats, lasting for ~1 month longer (Kidron, 2010), substantiating the link between subsurface AWC, AWD and the chlorophyll content of the crust also at a local scale.

The apparent link between daylight surface AWD and the subsurface AWC is supported by the relations between the average AWC at 0–10 cm and 10–30 cm soil. As can be seen in Fig. 10a, high correlations with $r^2 = 0.97$ (for 1993/94) and $r^2 = 0.92$ (for 1994/95) were found for the average AWC of both layers. High correlations with $r^2 = 0.94$ (for 1993/94) and $r^2 = 0.90$ (for 1994/95) were found between AWD at 0–10 cm and 0–30 cm (Fig. 10b). As for AWC, while during 1993/94 the amount of AWC at 0–10 cm and 0–30 cm was similar, it was approximately twice as high at 10–30 cm in comparison to 0–10 cm during 1994/95. This is explained by the fact that while very light rains mainly contributed water to the 0–10 cm layer during the drought year of 1993/94, high-depth rain events during 1994/95 contributed water also to the 10–30 cm layer. Consequently, AWD during 1994/95 was substantially longer. These and similar observations (Li et al., 2004) indicate that soil moisture at the upper 0–10 cm may serve as a good indicator also for the deeper 10–30 cm layer.

The data may have important implications regarding the relations between surface and subsurface wetness durations and between wetness duration at different depths. According to preliminary data (Kidron, unpub.), nighttime wetness duration is ≈1.3 times the daylight wetness duration. It implies that AWD at 0–30 cm is by a factor of 3–5 longer than at the surface. As for the AWD at depth, the data indicates that AWD at 0–30 cm for 1993/94 and 1994/95 range between 1 and 2 times that of 0–10 cm (Fig. 10b). Assuming that both these years can be taken to represent a year with near-average precipitation, AWD at 0–30 cm may thus be, on average ≈1.5 times that of 0–10 cm.

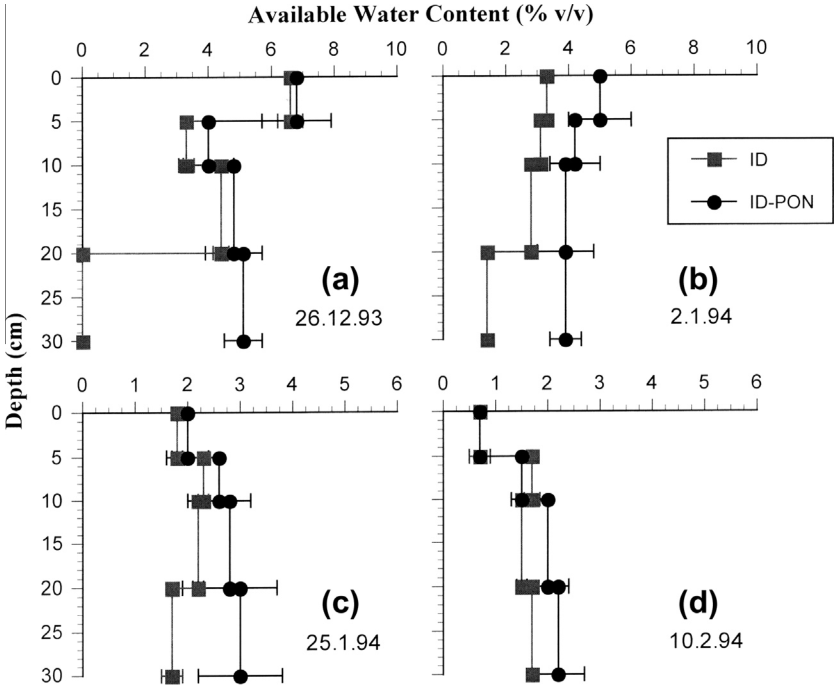

Fig. 9. Periodic measurements of the available water content at small depressions subjected to runoff addition (ID-PON) in comparison to adjacent habitats at the interdune (ID). Bars represent one SE.

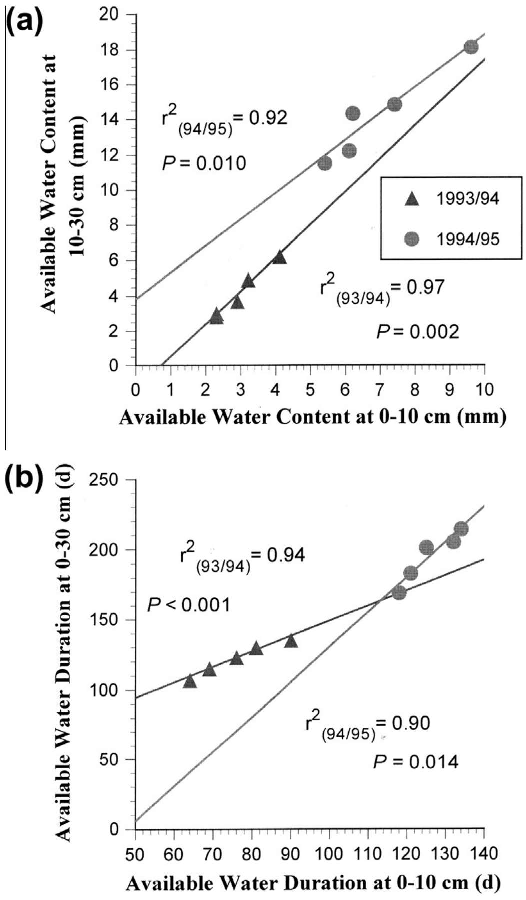

Fig. 10. The relationships between average available water content (a) and duration (b) at 0–10 cm and 10–30 cm during 1993/94 and 1994/95.

While biocrusts may reflect the subsurface moisture content, they may also affect, following their establishment, the water content of the underlying soil. As found for NRS, the dark-colored biocrusts decreased the surface albedo, subsequently increasing the evaporation rates of the underlying soil (Kidron and Tal, 2012). This is comparable to soil–plant interrelation. While on the one hand the plant biomass and type are determined by the moisture content of the soil (Stephenson, 1990; Lauenroth et al., 1993; Breshears and Barnes, 1999), once established, the plants affect in turn the soil moisture content, either directly (through water consumption) or indirectly (by shading or by promoting infiltration) (Breshears and Barnes, 1999; Baldocchi et al., 2000; Arora, 2002; Kidron and Gutschick, 2013). In parallel to plants, biocrusts also affect the soil moisture directly (through water consumption) or indirectly (through the change in surface albedo or by their effect on runoff/infiltration). Analogous to the soil–plant interaction, topographical-induced soil moisture (i.e., habitat location) serves as the major driver for crust establishment and growth while the effect of the crust on soil moisture content is secondary, falling short of the effect of the habitat location (aspect, slope angle and position).

The link between crust biomass (and type; see Kidron et al., 2010) and AWC and AWD at 0–30 cm highlights the importance of crust mapping for hydrologists. Since high-biomass crusts point to longer daylight surface AWD, and antecedent moisture promotes runoff generation (Kidron, 1999), crust mapping may point to areas which are either more likely to produce runoff or serve as runon zones. Crust mapping may also greatly assist pedologists as they may point at habitats with enhanced soil forming processes. Mapping is also relevant for ecologists and microbiologists. Considering the importance of moisture heterogeneity to the structure and function of arid ecosystems (Cantón et al., 2004), biocrust mapping facilitates a proxy estimation of the moisture content of the upper soil layer, paving the way for a greater understanding regarding ecosystem structure, function and productivity.

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References

Arora, V., 2002. Modeling vegetation as a dynamic component in soil-vegetation-atmosphere transfer schemes and hydrological models. Rev. Geophys. 40, 1006.

Baldocchi, D., Kelliher, F.M., Black, T.A., Jarvis, P., 2000. Climate and vegetation control on boreal zone energy exchange. Global Change Biol. 6, 69–83.

Breshears, D.D., Barnes, F.J., 1999. Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. Landscape Ecol. 14, 465–478.

Cantón, Y., Solé-Benet, A., Domingo, F., 2004. Temporal and spatial patterns of soil moisture in semiarid badlands of SE Spain. J. Hydrol. 285, 199–214.

Dan, J., Yaalon, D.H., Moshe, R., Nissim, S., 1982. Evolution of reg soils in southern Israel and Sinai. Geoderma 28, 173–202.

Evans, R.D., Lange, O.L., 2001. Biological soil crusts and ecosystem nitrogen and carbon dynamics. In: Belnap, J., Lange, O.L. (Eds.), Biological Soil Crusts: Structure, Function, and Management. Springer, Berlin, pp. 263–279.

Evenari, M., 1981. Ecology of the Negev Desert, a critical review of our knowledge. In: Shuval, H. (Ed.), Developments in Arid Zone Ecology and Environmental Quality. Balaban ISS, Philadelphia, pp. 1–33.

Hillel, D., Tadmor, N., 1962. Water regime and vegetation in central Negev Highlands of Israel. Ecology 43, 33–41.

Kidron, G.J., 1999. Differential water distribution over dune slopes as affected by slope position and microbiotic crust, Negev Desert. Israel. Hydrol. Process. 13, 1665–1682.

Kidron, G.J., 2001. Runoff-induced sediment yield from dune slopes in the Negev Desert, 2: texture, carbonate and organic matter. Earth Surf. Process. Landf. 26, 583–599.

Kidron, G.J., 2010. Under-canopy microclimate within sand dunes in the Negev Desert. J. Hydrol. 392, 201–210.

Kidron, G.J., Gutschick, V., 2013. Soil moisture correlates with shrub-grass association in the Chihuahuan Desert. Catena 107, 71–79.

Kidron, G.J., Pick, K., 2000. The limited role of localized convective storms in runoff production in the western Negev Desert. J. Hydrol. 229, 281–289.

Kidron, G.J., Tal, S.Y., 2012. The effect of biocrusts on evaporation from sand dunes in the Negev Desert. Geoderma 179–180, 104–112.

Kidron, G.J., Vonshak, A., 2012. The use of microbiotic crusts as biomarkers for ponding, subsurface flow and soil moisture content and duration. Geoderma 181–182, 56–64.

Kidron, G.J., Jones, T.L., Monger, H.C., Starinsky, A., 2002. Factors controlling Microbiotic Crusts: Negev and the Chihuahuan Desert. Semi Annual Report presented for IALC, May 2002.

Kidron, G.J., Vonshak, A., Abeliovich, A., 2008. Recovery rates of microbiotic crusts within a dune ecosystem in the Negev Desert. Geomorphology 100, 444–452.

Kidron, G.J., Vonshak, A., Abeliovich, A., 2009. Microbiotic crusts as biomarkers for surface stability and wetness duration in the Negev Desert. Earth Surf. Process. Landf. 34, 1594–1604.

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

Kidron, G.J., Barinova, S., Vonshak, A., 2012a. The effects of heavy winter rains and rare summer rains on biological soil crusts in the Negev Desert. Catena 95, 6–11.

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

Lange, O.L., Kidron, G.J., Büdel, B., Meyer, A., Kilian, E., Abeliovitch, A., 1992. Taxonomic composition and photosynthetic characteristics of the biological soil crusts covering sand dunes in the Western Negev Desert. Funct. Ecol. 6, 519–527.

Lauenroth, W.K., Urban, D.L., Coffin, D.P., Parton, W.J., Shugart, H.H., Kirchner, T.B., Smith, T.M., 1993. Modeling vegetation structure-ecosystem process interactions across sites and ecosystems. Ecol. Modell. 67, 49–80.

Li, X.R., Ma, F.Y., Xiao, H.L., Wang, X.P., Kim, K.C., 2004. Long-term effects of revegetation on soil water content of sand dunes in arid region of Northern China. J. Arid Environ. 57, 1–16.

Li, X.R., He, M.Z., Zerbe, S., Li, X.J., Liu, L.C., 2010. Micro-geomorphology determines community structure of biological soil crusts at small scales. Earth Surf. Process. Landf. 35, 932–940.

Mayland, H.F., McIntosh, T.H., 1966. Availability of biologically fixed nitrogen-15 to higher plants. Nature 209, 421–422.

Noy-Meir, I., 1973. Desert ecosystems: environment and producers. Ann. Rev. Ecol. Syst. 5, 25–51.

Rosenan, N., Gilad, M., 1985. Atlas of Israel. Meteorological Data, Sheet IV/2. Jerusalem (Israel), Carta.

Stephenson, N.L., 1990. Climatic control of vegetation distribution: the role of the water balance. Am. Nat. 135, 649–670.

Warsta, L., Karvonen, T., Koivusalo, H., Paasonen-Kivekäs, M., Taskinen, A., 2013. Simulation of water balance in a clayey, subsurface drained agricultural field with three-dimensional FLUSH model. J. Hydrol. 476, 395–409.

Wetzel, R.G., Westlake, D.F., 1969. Periphyton. In: Vollenweider, R.A. (Ed.), A Manual on Methods for Measuring Primary Production in Aquatic Environments. Blackwell, Oxford, pp. 33–40.

Wine, M.L., Zou, C.B., Bradford, J.A., Gunter, S.A., 2012. Runoff and sediment responses to grazing native and introduced species on highly erodible Southern Great Plains soil. J. Hydrol. 450–451, 336–341.

Yu, C., Gao, B., Muñoz-Carpena, R., 2012. Effect of dense vegetation on colloid transport and removal in surface runoff. J. Hydrol. 434–435, 1–6.