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Infiltration through three contrasting biological soil crusts in patterned landscapes in the Negev, Israel

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Abstract

We examined the role of soil crusts in infiltration processes in three contrasting environments in the Northern, Central, and Central-Western Negev, Israel. The removal of a thin cyanobacterial-dominant crust from a sandy dune at Nizzana in the Central-Western Negev and of a well-developed lichen-dominant and a cyanobacterial-dominant crust from a loess-covered hillslope at Sayeret Shaked in the Northern Negev resulted in three to fivefold increases in sorptivity and steady-state infiltration under both ponding and tension. The removal of a depositional crust colonised by cyanobacteria from a loess floodplain at Sede Zin in the Central Negev resulted in an increased infiltration under tension, but had no significant effect under ponding. We attribute the lack of effect under ponding to exposure of surface silts to water, which resulted in the clogging of matrix pores and surface sealing. The removal of the crusts in all three landscapes influences resource flows, particularly the redistribution of runoff water, which is essential for the maintenance of desert soil surface patterning. It would also have marked effects on germination, establishment and survival of vascular plants and soil biota, leading ultimately to desertification. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Soil crusting; Soil patterning; Infiltration; Negev Desert; Vegetation patchiness; Desertification; Microbiotic crust; Microphytic crust

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1. Introduction

In arid and semi-arid landscapes, soil crusts form a boundary between the biosphere and the atmosphere (West, 1990). Crusts vary markedly in morphology and genesis, and they can be either biological (or biogenic; West, 1990) or abiotic (Eldridge et al., 1995) and be dominated by the soil's mineral components. Biotic and abiotic crusts are often closely associated, and both are typically thin-layered. In dry environments, sealing and crusting surfaces play major roles in ecosystem processes, particularly in water and soil flows, and are therefore critical for landscape structure and function (Mücher et al., 1988; Eldridge et al.,1995; Zaady et al., 1997).

The landscape of Israel's Negev Desert is strongly patterned at a range of scales. At a landscape scale, the interaction of geology and soil leads to a redistribution of the runoff water from rocky, upper slopes, and its accumulation within deeper soils on the lower slopes (Yair and Danin, 1980; Weider et al., 1985). At a finer spatial scale, water is shed from nutrient-poor intershrub areas, and accumulates within shrub mounds enhancing the productivity of these patches (Garner and Steinberger, 1989; Schlesinger et al., 1990). Within this arid shrub-steppe, zones of resource shedding (source zones) are characterised by shallow, nutrient-poor substrates with low infiltration rates and sparse vegetation cover (Tongway and Ludwig, 1994). In contrast, the shrub mounds (sinks) have generally deeper, nutrient-enriched substrates that are high in biological activity and levels of favourable soil physical and chemical properties. Together, the concentration of resources such as water, nutrients and sediments into favourable, patchy microsites separated by nutrient-deprived patches leads to greater plant growth and biomass, and enhanced species diversity (Boeken and Shachak, 1994; Boeken et al., 1995).

Spatial heterogeneity in Negev Desert landscapes is characterised by a ''matrix'' (White and Pickett, 1985) of crusted soil with microphytic communities, and distinct patches of perennial vegetation, typically, shrubs on soil mounds with an associated herbaceous understorey. Both biological and physical soil crusts occur in the interspaces between shrub-covered mounds, and both tightly control the flow of water across the landscape and through the soil matrix. Water and nutrients shed from crusted patches accumulate in the shrub-dominated patches (Schlesinger et al., 1990). Through their influence on surface properties, and hence, on water movement, the biological and physical soil crusts play major roles in seedling emergence and establishment (Harper and Marble, 1988; Eldridge et al., 1995; Zaady et al., 1997). Crusts also influence erosion processes, and protect the soil against both the raindrop impact (Eldridge and Kinnell, 1997) and the erosive force of the wind (Williams et al., 1995; McKenna-Neuman et al., 1996).

To understand more about the role of soil crusts in the movement of water in the Negev Desert, we measured the infiltration at three sites supporting crusts of markedly different type and morphology. The three crust types were: (i) a dune sand supporting an almost continuous thin cyanobacterial and moss crust, (ii) a predominantly physically (depositional) crusted loess soil sparsely colonised by cyanobacterial filaments, and (iii) a loamy hillslope soil supporting a well-developed crust colonised by cyanobacteria, lichens, and some mosses. The sites represented different landscapes in the Northern,

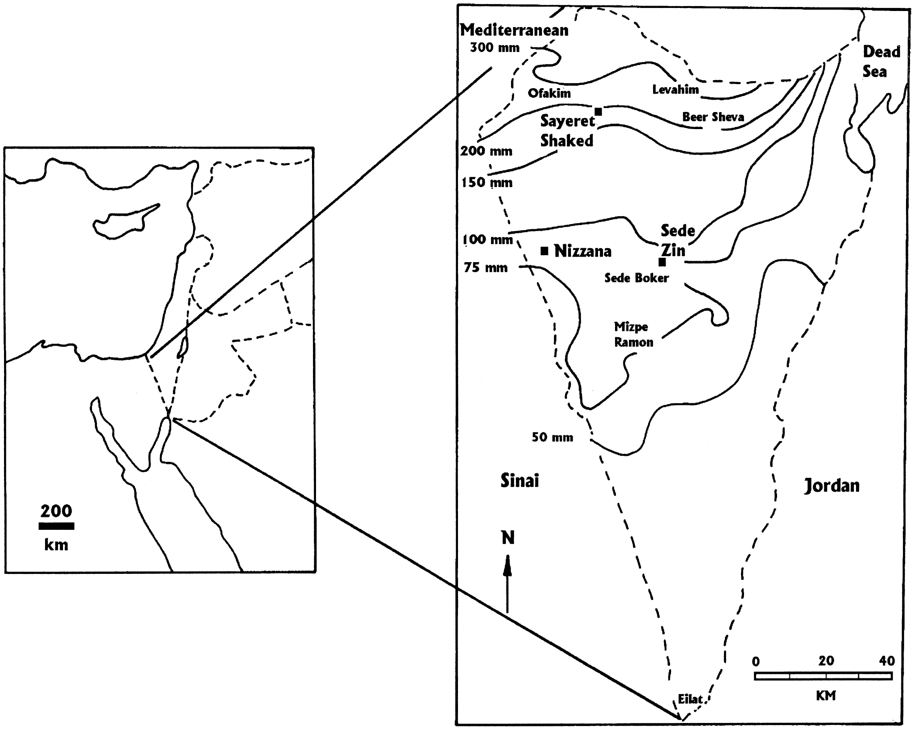

Fig. 1. Location of the study sites at Nizzana, Sayeret Shaked, and Sede Zin in the Negev and the rainfall isohyets (adapted from Offer et al., 1997).

Central, and Central-Western Negev (Fig. 1). At each site, we measured sorptivity, steady-state infiltration, and depth to wetting front under tension and ponding using disc permeameters. By comparing infiltration properties on intact surfaces with those on surfaces from which the crust had been removed, we examined the influence of crusts on water flow, and infer likely effects of crusts and their removal on ecological processes in landscapes characterised by a patchy distribution of resources.

2. Methods

2.1. Study areas

The Nizzana site (i) was located on the eastern extension of the Sinai continental sand fields at the station of the Arid Ecosystem Research Center of the Hebrew University of Jerusalem in the Central-Western Negev (30°75′N, 34°22′E). Average annual rainfall is 90 mm with predominantly low rainfall intensities, and daily falls of rain is < 5 mm (Yair, 1990). Rainfall is winter-dominant. The landscape comprises linear west–east trending sand dunes superimposed on a broad sand ridge (Tsoar and Moller, 1986). The Nizzana dune system comprises an area of sandy ridges with intervening playa surfaces dominated by silts and clays (Yair, 1990). The dunes are active, sharply crested sand ridges with steeply sloping flanks. Their soils consist of loosely consolidated sands, which are sparsely vegetated by *Retama raetam*, *Anabasis articulata*, *Artemesia herba-alba*, and *Thymelaea hirsuta* on the lower slopes and the grass *Stipagrostis* sp. on the crests. The lower flanks of the dunes are well vegetated, and covered by a contiguous, flexible biological crust (Yair, 1990). Sites for infiltration measurements had a north-facing aspect and an average slope of 22%.

The second site (ii) was at Sayeret Shaked Park near Beer Sheva in the Northern Negev (31°17′N, 34°37′E). Average annual rainfall is approximately 200 mm, most of which fall between November and March. The loess soil is approximately 1-m thick, contains 14% clay, 27% silt, 59% sand, and small amounts of soluble salts and has low electrical conductivity levels (<0.4 mmhos cm^{-2}; Teomim, 1990). Infiltration was measured on a south-facing slope of ca. 15%. The soil surface supported a biological crust of bacteria, cyanobacteria, algae, mosses, lichens, and scattered mounds of aeolian accretion with patches of *Noaea mucronata* and *Atractylis serratuloides* (Feinbrun-Dothan and Danin, 1991).

Site (iii) was located on a loess floodplain at Sede Zin near Sede Boker, approximately 50 km south of Beer Sheva in the Central Negev Desert (30°84′N, 34°78′E). The average annual rainfall is about 100 mm. The soils are deep, often >10 m, and are rich in silt and clay, though particle size analyses are unavailable. Crusts commonly develop after the rainfall, which is generally winter-dominant, with a thin cyanobacteria film forming on the silt surface a few days after the rainfall (Zaady et al., 1997). At the time of measurement, there was $<10\%$ vegetation cover over most of the area, and the sparsely vegetated plains were dominated by the shrub *Hammada scoparia* at an average spacing of 2–3 m, and scattered shrubs of *Reaumuria negevensis* and *A. articulata* (Luria and Noy-Meir, 1979/80; Danin, 1983).

2.2. Measurement of soil hydrological properties

During October and November 1997, we assessed infiltration by measuring sorptivity (mm h$^{-0.5}$) and steady-state infiltration (mm h^{-1}) with disc permeameters at supply potentials of -40 mm (tension) and $+10$ mm (ponded; Perroux and White, 1988). The sorptivity stage of infiltration occurs when the soil is initially dry and water flow is dominated by the soil's capillarity properties. Steady-state infiltration, which occurs once the flow rate is constant, is governed by capillarity, gravity, the size of the disc, and the potential at which the water is supplied (CSIRO, 1988). Sites with a homogeneous cover of $>75\%$ crust were selected for the determination of infiltration. This was necessary as previous research in Australia (Eldridge, 1993) has indicated relationships between infiltration and the proportion of the soil covered by crusts. Infiltration (ponded and tension) was measured at five-paired crusted and scalped locations at each of the three sites. At the scalped sites, the upper surface of the soil representing the area of maximum biological activity was carefully removed using a wide bladed scraper.

The permeameter at -40 mm supply potential was placed on a thin bed of sand to provide a uniform contact with the soil surface. The ponded ($+10$ mm) permeameter was placed on a steel ring of 220 mm internal diameter, which was gently pressed into the soil to a depth of about 7–10 mm, and sealed along the outside edge to prevent the leakage of water. We ran the permeameters for approximately 30 min, by which time steady-state had been achieved. At each supply potential, sorptivity was calculated according to the method of Cook and Broeren (1994) and steady-state infiltration according to White (1988). The depth of water penetration at the cessation of infiltration measurements was assessed by pushing a probe into the soil. These depths were standardised by calculating the depth per litre of the infiltrated water as the infiltration measurements differed in the amount of water they received.

2.3. Soil dispersion and slaking

The degree of dispersion and slaking was measured on soils from Sede Zin and Sayeret Shaked using a modification of the Emerson aggregate test (McKenzie and Jacquier, 1997). Nizzana crust samples were not tested because most samples disintegrated on transport back to the laboratory at Sede Boker. Five-replicate samples of the crust from each soil were tested by placing a small aggregate (2–10 mm diameter) into 600 ml of distilled water and ranking the degree of dispersion and slaking after 2 min and 2 h, respectively. Similar sized aggregates, taken from a bolus used to determine texture in the field, were similarly treated, and the resulting dispersion and slaking noted at the same time periods. These tests enabled us to separate differences in dispersion and slaking potential of aggregates stabilised by soil biota (cyanobacterial filaments, lichen rhizines, and moss protonema) from those related to soil physical forces.

2.4. Statistical analyses

Differences in sorptivity, steady-state infiltration, and depth to wetting front were compared using one-way ANOVA (Minitab, 1994) after testing for homogeneity of variance (Bartlett's test). Results in the text are expressed as mean ± standard error of the mean (SEM). Differences in infiltration parameters between the three sites were examined using a Generalised Linear Model with ''sites'' random and levels of ''crust'' fixed. The two-way ANOVA was performed on $\log_{10}$ transformed data in order to stabilise the error variance from each of the individual one-way ANOVAs.

3. Results

3.1. Crust type and morphology

Crust composition and morphology differed markedly between the three sites. The thin crust at Nizzana, up to 2 mm thick, was separated from the subcrust by a dense network of cyanobacterial filaments (Yair, 1990). Typically, the Nizzana crust is rich in organic matter (1.2% by weight) and fine material, comprising approximately 80% silt + clay (Yair, 1990), and was dominated by cyanobacteria and green algae of the genera *Microcoleus, Calothrix, Nostoc, Schizothrix, Scytonema, Chroococcidiopsis,* and *Phormidium* (Lange et al., 1992; Danin, 1996). Mosses, such as *Aloina bifrons,* *Crossidium* sp., *Bryum* sp., and *Pterygoneurum subsessile* occurred in areas of silt and clay accumulation, particularly under shrubs at sites with a northerly aspect.

The depositional crust at Sede Zin showed clear evidence of vesicular development, indicating restricted fluid diffusivity (C. Valentin, personal communication, 1999). This crust was probably formed through the processes of raindrop impact and deposition. In the dry state, the crust was composed of large silty platelets of mean (± standard deviation) dimensions of 69.0 (± 15.7) mm long by 48.1 (± 10.3) mm wide. These platelets, which were approximately 1.5–3 mm thick with upturned margins, were separated by inter-platelet cracks and fissures of about 1.5–2.0 mm wide. When wetted, the margins gradually coalesced, forming a contiguous silty–clay skin with little or no microrelief. Initial examination of the crusts indicated clearly defined zones of sorting of fine-grained particles, typical of depositional crusts (Bresson and Valentin, 1994). At the time of infiltration measurements, cyanobacterial filaments were present in the surface 0.5 mm. These crusts support cyanobacteria such as *N. muscorum*, *M. chtonoplastes*, and *M. vaginatus*, and green algae such as *Protosiphon cinamoneus* and *P. gravilii* (Friedmann and Galun, 1974). The activity of cyanobacteria and algae is apparent after wetting (Zaady et al., 1997).

The crust at Sayeret Shaked was relatively thick (10–30 mm), containing fungal hyphae, cyanobacterial filaments, and moss protonema extending to depths of ca. 30 mm. The thickness of the crust suggests that it was probable polyphasic (C. Valentin, personal communication, 1999). In the unvegetated shrub interspaces (microphytic patches; Zaady and Shachak, 1994), the surface of the crust was dominated mainly by cyanobacteria, including *M. vaginatus* and *N. punctiforme*, mosses, crustose, and squamulose lichens. Common mosses included *C. crossinerv* var. *laevipilum*, *A. bifrons*, *Bryum* sp., and *Ephemerum* sp. Crustose lichens were dominated by *Collema tenax* var *vulgare*.

3.2. Slaking and dispersion

Crusts occurring on intact aggregates from Sayeret Shaked were strongly resistant to slaking. However, crusts at Sede Zin completely slaked after 2 min, leaving only a small core of fine material. When the slaking test was repeated for both soils using remoulded crust, the Sayeret Shaked soils displayed a similar degree of slaking, suggesting that biotic elements (i.e., filaments and hyphae) contribute to the inherent stability of the aggregates. Crusts from both surfaces were non-dispersive.

3.3. Infiltration parameters across sites

Given the marked differences in soil physical properties, such as texture between Nizzana (predominantly coarse sands), and Sayeret Shaked and Sede Zin (clay loams and silts, respectively), we expected major differences in infiltration, at least between the two broad groups. For both crusted and scalped surfaces, sorptivity and steady-state infiltation were significantly greater at Nizzana compared with Sayeret Shaked and Sede Zin, which were not significantly different from each other. However, differences in sorptivity and steady-state infiltration were significant only under tension ($F_{2,2} = 19.39$,

$P = 0.049$ for sorptivity under tension and $F_{2,2} = 60.69$, $P = 0.016$ for steady-state infiltration under tension).

3.4. *Influence of crust removal on infiltration parameters*

3.4.1. *Sorptivity*

At Nizzana, sorptivity under tension was significantly greater on the scalped plots (mean ± SEM = 295.5 ± 21.5 mm $h^{-0.5}$) than on the crusted plots (46.0 ± 2.9 mm $h^{-0.5}$; $F_{1,8} = 132.3$, $P < 0.001$; Fig. 2a). Under ponded (+10 mm) conditions, sorptivity was again greater on the scalped plots (652.4 ± 96.4 mm $h^{-0.5}$) than on the crusted plots (180.1 ± 49.6 mm $h^{-0.5}$; $F_{1,8} = 18.98$, $P = 0.002$; Fig. 2b). At Sayeret Shaked, sorptivity under both tension and ponded conditions was significantly greater on the scalped plots than on the crusted plots ($F_{1,8} = 94.7$, $P < 0.001$, and $F_{1,8} = 25.3$, $P < 0.001$ for tension and ponded conditions, respectively; Fig. 2a and b). At Sede Zin, there was a fourfold increase in sorptivity under tension on the scalped surfaces than on the crusted surfaces ($F_{1,8} = 83.3$, $P < 0.001$; Fig. 2a). Under ponded conditions, however, the small increase in sorptivity on the crusted plots was not significant, because of the high spatial variability in sorptivity across the site ($F_{1,8} = 2.7$, $P = 0.136$; Fig. 2b).

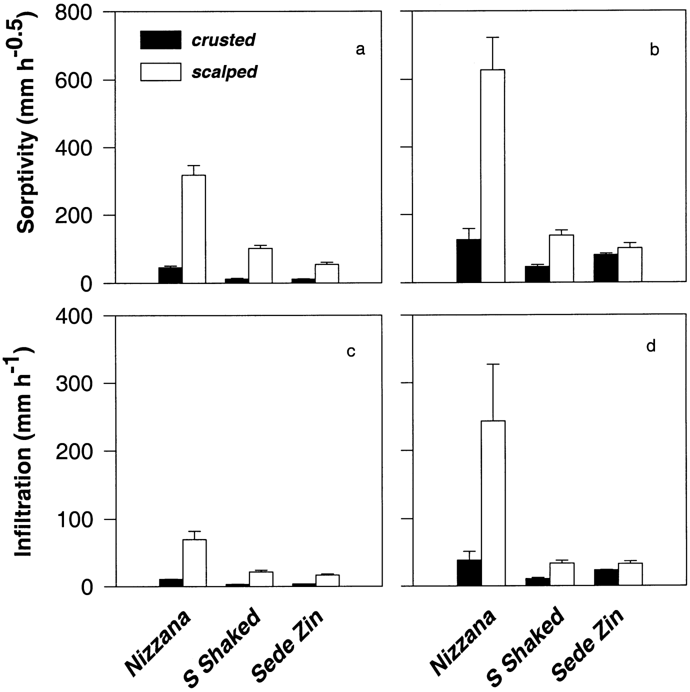

Fig. 2. Sorptivity (mm $h^{-0.5}$) for crusted and scalped soils under (a) −40 mm tension and (b) +10 mm ponding, and steady-state infiltration (mm h^{-1}) for crusted and scalped soils under (c) −40 mm tension and (d) +10 mm ponding. The bars indicate the standard errors of the means.

Table 1

Depth to penetration of infiltrated water (mm l^{-1}) at three sites under -40 mm tension and under $+10$ mm ponding for crusted and scalped treatments. For a specific level of tension, different superscript letters within a row indicate a significant effect of crusts on the depth to water penetration ($P < 0.05$). SEM is the standard error of the mean

	-40 mm				$+10$ mm			
	Crusted		Scalped		Crusted		Scalped	
	mean	SEM	mean	SEM	mean	SEM	mean	SEM
Nizzana	95.7^a	1.6	34.1^b	2.7	54.2^a	6.7	25.9^b	12.1
Sayeret Shaked	282.1^a	19.1	124.2^b	3.9	186.4^a	12.7	108.1^b	4.5
Sede Zin	102.7^a	2.1	54.9^b	1.6	40.3^a	1.3	43.9^a	7.1

3.4.2. Steady-state infiltration

At Nizzana, steady-state infiltration (mm h^{-1}) was significantly greater on the scalped surfaces than on the crusted surfaces under both tension ($F_{1,8} = 87.5$, $P < 0.001$; Fig. 2c) and ponded conditions ($F_{1,8} = 14.4$, $P = 0.005$; Fig. 2d). At Sayeret Shaked, steady-state infiltration was again significantly greater on the scalped than on the crusted plots ($F_{1,8} = 35.4$ and $F_{1,8} = 31.2$; $P < 0.001$ for tension and ponded conditions, respectively; Fig. 2c and d). At Sede Zin, there was an almost fivefold increase in steady-state infiltration when the crust was removed compared to an intact crust, but this occurred only under tension ($F_{1,8} = 67.9$, $P < 0.001$; Fig. 2c). As with sorptivity under ponded conditions, there was a small and insignificant ($F_{1,8} = 4.53$, $P = 0.066$) increase in steady-state infiltration on the scalped plots (Fig. 2d).

3.4.3. Depth to penetration of water

As infiltration was significantly greater on the scalped surfaces, it was not surprising that water penetrated significantly further into the soil profile beneath the scalped plots at all three sites (Table 1). For example, at Nizzana, infiltrated water reached deeper into the soil profile on the scalped plots than on the crusted plots under both tension ($F_{1,33} = 333.04$, $P < 0.001$) and ponding ($F_{1,33} = 124.80$, $P < 0.001$). However, all plots received different volumes of infiltrated water, and when this depth to penetration was adjusted for the volume of applied water, mean depth per litre of applied water was generally 2–3 times greater on the crusted plots than on the scalped plots (Table 1). This trend was consistent at all sites except under ponded conditions at Sede Zin, where there was almost no difference between the scalped and crusted plots ($P = 0.627$; Table 1).

4. Discussion

Water movement is the critical process in semi-arid and arid landscapes characterised by a patchy distribution of essential resources (Schlesinger et al., 1990; Tongway and Ludwig, 1994). Some areas (source or runoff zones) respond rapidly to rainfall by shedding water, directing runoff to adjoining patches which absorb water (sink zones). The result is a sequence of fertile patches with greater soil moisture than they would normally receive through natural rainfall. Given the importance of water flow in the formation and maintenance of patchy landscapes, it follows that the factors influencing the amount and distribution of runoff and infiltration ultimately affect the patterning phenomenon itself. As water availability and landscape patchiness are essential components of these landscapes, a proper evaluation of the relationships between rainfall and runoff is crucial to understanding how water is distributed throughout the landscape (Yair, 1987).

Water flow within the landscape is related to the biotic and abiotic features of individual source and sink patches. Infiltration is influenced by soil surface characteristics such as microtopography, cracking, surface sealing and crusting, soil physical properties such as bulk density, organic matter and particle size distribution, and the characteristics of the vegetation such as plant biomass and cover. Biological crusts are an integral part of the soil surface providing an intimate connection between the biosphere and the atmosphere, and hence, playing a major role in the flow and redistribution of rainfall and runoff (West, 1990; Yair, 1990; Eldridge and Greene, 1994).

4.1. Role of crusts in infiltration and water flow

In our study, the removal of soil crust had a significant effect on sorptivity and steady-state infiltration. As expected, the highest infiltration rates occurred on the sand dunes, and the lowest rates occurred on the loess plain. Removal of the soil crust at both Nizzana and Sayeret Shaked resulted in a three to fivefold increase in sorptivity and steady-state infiltration under both ponding and tension (Fig. 2).

Although the removal of the crust increased sorptivity and infiltration under tension at Sede Zin, there was no significant effect under ponding (Fig. 2). This can be attributed to the physico-chemical nature of the loess soils at Sede Zin. Together with low levels of organic matter and high silt contents, loess soils are highly susceptible to physical crusting (Bouza et al., 1993). Vesicles in and immediately below the crust are often observed in sieved structural, erosional, and deposition crusts (C. Valentin, personal communication, 1999).

The surface of the Sede Zin soil rapidly slaked, and we attribute this to the high proportion of silt in the crust. On contact with water, soil structure declines rapidly, ultimately restricting infiltration. Our observations suggest that where the immediate surface crust (< 500 μm thick) remains intact, ponded infiltration remains relatively high (23 mm h^{-1}). Removal of the crust under ponded infiltration, however, exposes the matrix of surface silts and clays to water, resulting in the reorganisation of soil minerals, clogging of matrix pores (Danin, 1983), and the development of a surface seal (Valentin, 1991; Bresson and Valentin, 1994). Although infiltration increased to 33 mm h^{-1}, it is likely that subsequent infiltration would be less because of the structural rearrangement. Under tension, however, the negative pressure on the soil surface is probably sufficient to maintain the structural integrity of the matrix pores (B.W. Murphy, personal communication, 1997) preventing the throttling of infiltration.

Although the genesis of the Sede Zin crusts is predominantly physico-chemical, they are readily invaded, and hence, stabilised by cyanobacteria (Zaady et al., 1997). Our slaking and dispersion measurements using crushed aggregates in which the cyanobacterial bonds were destroyed demonstrated that cyanobacteria contributed very little to the stability of aggregates. This is supported by the previous researches of Eldridge (1993) and Williams et al. (1995) suggesting a commonality of this trait with Australia and North America where cyanobacterial crusts are common. However, the thin upper layer of the soil (~ 500 μm thick) seemed to be more stable than the underlying soil (500–2000 μm thick). The sheath material of the aquatic cyanobacterial is known to co-flocculate clay particles (Bar-Or and Shilo, 1988). Also, cell-bound extracellular polysaccharidic flocculants are known to bind onto cyanobacterial filaments, leading to benthic cyanobacterial mats, and similar mechanisms may be involved in terrestrial species (Danin, 1996).

4.2. Effects of crusts on ecosystem processes

Crust removal can influence ecosystem processes such as infiltration, erosion, and the development of physical soil crusts. This influence can have a major impact on ecological processes such as the germination and establishment of vascular plants (Harper and Marble, 1988; West, 1990; Eldridge and Greene, 1994; Danin, 1996; Zaady et al., 1997). Given the manner in which crusts redistribute water in all three landscapes, what are the consequences of crust removal on ecosystem processes?

Despite the gentle slopes ($< 2\%$) at the Sede Zin site, there is a considerable redistribution of runoff from the intershrub to the shrub patches, resulting from the combination of soil physical properties and the nature of the vegetation in the intershrub patches. A combination of (i) densely packed silty clays in the soil matrix, (ii) subsequent formation of a raindrop-impacted structural crust, and (iii) paucity of the macropores in the intershrub zone, restricts infiltration to predominantly matrix flow, and thus, retards it in the intershrub patches. As loess soils are high in silt and clay, less than half of their stored moisture is available for vascular plant growth (Danin, 1983). This results in a sparse, ephemeral-dominant vegetation between the shrubs (Luria and Noy-Meir, 1979/80) providing little resistance to runoff, and further accentuating the differences in water availability between shrub and intershrub patches. Lower levels of infiltration in the intershrub patches, coupled with high evaporation and naturally high levels of soluble salts in the soil profile, may also exacerbate soil salinization (Yair, 1994).

At Nizzana, soil crusts on the dunes have a marked impact on how and when water is redistributed to the downslope areas of the dunes and to the playas. Cyanobacterial filaments in the crusts have the capacity to absorb relatively large amounts of rainfall by increasing their volume 10-fold (Wang et al., 1981). Once the crust becomes saturated, crusted surfaces can retain this moisture for much longer periods than non-crusted surfaces (Verrecchia et al,. 1995; Kidron and Yair, 1997). The effect of crusts on water shedding depends on the duration of rainfall as well as on the spatial distribution of the crusts. The time taken for crusts to reach saturation is more critical than the actual amount of rainfall, so that short high intensity storms, which are common in the Negev (Yair 1990), may fail to produce runoff (Kidron and Yair, 1997). Under more prolonged rainfall events, which saturate the crusts, water will therefore be shed onto areas lower in the landscape. In the upper levels of the dunes, however, this redistribution is thought to be a local phenomenon, as crust cover and thickness decreases upslope (Kidron and Yair, 1997). A spatially variable crust at the dune–playa interface may be responsible for the considerable redistribution of runoff to the lower reaches of the dune and to the playa. Thus, the consequences of the crust removal depend on the spatial arrangement of crusts in the landscape and the prevailing climatic conditions.

Studies at Sayeret Shaked show that the microphytic patches are capable of redistributing 20–40% of applied rainfall to the macrophytic (shrub) patches (Shachak et al., unpublished data; Eldridge et al., unpublished data). The biomass of vascular plants is greater in the shrub patches (1.4 kg m^{-2}) than in the microphytic patches (0.06 kg m^{-2}). Species richness is also greater in the shrub patches (2.6 species, 10 cm^{-2}) than in the microphytic patches (1.6 10 cm^{-2}) (Shachak et al., 1998). Thus, the consequence of crust removal is to reduce the redistribution of runoff to the macrophytic patches, and thus, decrease patch productivity and species diversity.

4.3. Crust functioning in relation to patch dynamics

At all three sites, crusts were responsible for the substantial redistribution of water from the intershrub (microphytic) patches to the shrub (macrophytic) patches. Removal of the crust causes a breakdown in spatial organisation of patchiness. This results in reduced flows of vital resources, such as water, nitrogen, phosphorus, and seeds of vascular plants (Boeken et al., 1995; Zaady et al., 1998). Reduced patchiness means that annual rainfall alone (in the absence of runon) may be insufficient to sustain the growth of perennial shrubs such as *Noaea*, *Retama*, *Anabasis* and *Artemesia*. Reduced infiltration on the mounds would ultimately result in a change in vascular floristics from the one dominated by perennials to the one dominated by ephemerals. The consequences of this change is not easily known, but simulation experiments involving the destruction of *N. mucronata* shrub patches at Sayeret Shaked demonstrate that cyanobacterial crusts can develop and cover the mounds in 5–10 years (Zaady et al., unpublished data). The short-term consequences are a decrease in infiltration rates on the mounds through the death of the perennial shrubs, erosion around the mound base, reduced aeolian deposition on the mounds, and eventually, partial attrition of the mounds (Offer et al., 1997). Removal of the crust is therefore likely to influence germination, establishment and survival of vascular plants (Zaady et al., 1997), and even changes in invertebrate populations as a result of altered plant cover, further reducing the potential infiltration capacity of the mounds.

Given the structural and floristic complexity of the crust at Sayeret Shaked, recovery to full cover level may take many years once it has been removed. However, data from Nizzana suggest that recovery to full cover can occur within 1 year given suitable rainfall (G. Kidron, personal communication, 1997), and recovery at Sede Zin is likely to be more rapid. Destruction of the predominantly physical soil crust at Sede Zin is likely to lead to a decreased runoff and a reduction in productivity in the mounds, but only in the short term. After one or two rainfall and drying events, a new raindrop-impact structural crust is likely to form (Bresson and Valentin, 1994), and will probably be reinvaded by cyanobacteria (Zaady et al., 1997).

The combined effect of crust removal and shrub disappearance is a decrease in productivity and diversity of the vegetation, and ultimately, a breakdown in landscape function (Ludwig et al., 1997). Along with the other human-induced activities, such as trampling and overgrazing, this breakdown of function ultimately contributes to xerification (West, 1986), an unfortunate feature of many areas of the Middle East.

5. Conclusions

Our experiment revealed that crust removal resulted in marked increases in infiltration on soil crusts in the Negev Desert. Crust removal reduces the redistribution of runoff to shrub mounds, which support the highest plant diversity and productivity. Reduced infiltration into the shrub patches results in a decline in landscape function and changes in plant communities to the one dominated by short-lived species. Reduced runoff also results in the diminishing flows of vital resources such as nitrogen, phosphorus, organic matter, and the seeds of vascular plants, and will likely influence ecological processes such as germination and survival. Crusts are therefore essential to support a stable, productive shrubland, which cannot survive in the absence of runoff.

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