Desert crust morphology and its relations to microbiotic succession at Mt. Sedom, Israel

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The upper surface of alluvial terraces at Mt. Sedom, Israel are covered with a biogenic crust populated by filamentous cyanobacteria. The cyanobacteria expand when wet and shrink when dry, forming when time passes cracks in the soil surface in the form of polygons. These polygons are smaller than those formed by shrinking of the mineralogical component of the substratum. Continuing to grow and expand laterally the cyanobacteria cause upfolding of the polygon margins which in time become populated with cyanophilous lichens. The lateral growth accompanied by increasing trapping of airborne dust in the cracks of thalli of cyanophilous lichens leads to the development of microridges along the former upturned margins of cracks. Increasing water storage in the depressions of the surface with augmenting roughness ameliorates the moisture regime by decreasing water runoff from the soil surface.

Cyanobacteria of the early stages of colonization occur at the drought-latent stage below the surface of the flat soil and emerge phototactically when sufficiently wetted. Their fronds are green. The microbionts on the elevated terraces representing progressive, older stages of colonization are situated above the rugged-surfaced soil and have dark thalli or fronds. The number of microbiont species, chlorophyll a, and polysaccharide content of the crust increase from the young to the old terrace. Calcite content, compaction, and linear structure increase too. All these quantitative changes lead us to regard the different stands as parts of microbiotic succession. We recommend the use of the micro-geomorphological structures as age indicators which are correlated here with the relative time sequence system of alluvial terraces in other places, even if they are not in such an obvious chronosequence.

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Keywords: alluvial terraces; microbiotic succession; desert; cyanobacteria; calcite crusts
Introduction

Most studies of microbiotic succession are related to recovery of the crust from disturbance by human activity (West, 1990). In a previous study (Danin & Barbour, 1982) one aspect of succession of cryptogams and phananogams in the Dead Sea area was studied. The authors discuss how local disturbance of soil conditions by channels erosion or by bioturbation leads to salinization of the otherwise leached soil. Consequently, a few components of the crust die, resulting in removal of the top 10 cm of soil and to the processes of secondary succession. Primary succession of the cyanobacteria populating the microbiotic crust at Mt. Sedom, in the Dead Sea rift valley, was studied by Dor & Danin (1996). They studied five alluvial terraces of different relative age of a short wadi on the flat top of that mountain. Such a system is a well known tool in geomorphological research (Lobeck, 1939, pp. 238–241). That study showed that during the time sequence of terrace formation the number of species, chlorophyll a, and polysaccharide content of the soil crust increase.

The present study deals with the same ecosystem of Mt. Sedom and considers mineralogical, micromorphological and microtopography changes with time along with changes in the microbiotic components of each terrace.

Location and environment

The study site was at co-ordinates 35°22’50” E, 31°04’45” N, at an elevation of 240 m below sea level. It is a short wadi which cuts through a local small drainage basin of about 500 m². This wadi has five alluvial terraces along its active channel, marked 1 the youngest, to 5 the oldest (Fig. 1). Mean annual rainfall is 70 mm and mean annual temperature is 25°C (Rosenan & Gilead, 1985). The substratum at this locality is of the lacustrine Lisan Formation, made of alternating aragonite or fine detritus.

Figure 1. A system of a small wadi with five old alluvial terraces at Mt. Sedom.
varves. Locally, thin beds of gypsum, halite and dolomite also occur (Zak, 1967; Begin et al., 1974).

Due to pedogenetic processes the soils developed from the Lisan formation in Mt. Sedom are often rich in salts (Yaalon, 1963; Danin, 1976; Danin & Barbour, 1982). Vegetation cover in the study area is rather scanty, with trees and shrubs restricted to dry watercourses and to sites with a high water-table. Annual plants, which grow out of the wadis, were not seen in the study site even during a rainy year. Irrespective of the phanerogam cover, most of the area is covered by a thin microbiotic crust (sensu St. Clair & Johansen, 1993; Danin, 1996) that is composed of communities of cyanobacteria and cyanophilous lichens (Dor & Danin, 1996).

**Sampling and methods**

**Sampling**

Terraces 1 to 5 and the surface of the channel bed were sampled at 0–4 cm depth. In addition, surfaces 2 and 5 were sampled at about 10 cm and 15 cm depths each. Their surface microtopography was photographed.

**Quantitative morphology**

A study of crack and polygon formation was carried out on the microbiotic crust in the vicinity of the catchment area described above. Six squares were sampled of each type and for each total area (in cm²) and the number of polygons were measured. Since we are interested in the ratio of one variable (the number of polygons) to the other variable (the area), we employed ratio estimate techniques (Cochran, 1977) to estimate the ratios and their standard errors. t-test (for unequal variances) was used to compare the two ratios estimates.

In order to quantify the observations on expansion of the cyanobacterial crust when wetted, the following procedure was used. A crust similar to that of terrace 1 (Fig. 2)

![Figure 2](image-url) The first terrace: note the crust divided by shrinking cracks into flat polygons, and the somewhat upturned margins of several polygons.
was collected for analysing crust expansion and contraction following wetting or desiccation. Water-saturated 2-mm thick crust following more than 2 h of wetting was cut into 40 pieces, each with at least one side 10 mm long. After desiccating for 15 h on glass the former 10-mm long side was measured under a dissecting microscope.

Taxonomy

Samples of the entire crust from a square of $10 \times 10$ cm$^2$ were placed in Petri dishes, wetted with distilled water and incubated under fluorescent illumination of 95 E m$^{-2}$ s$^{-1}$ at 22°C. After 1 week small subsamples of the greening crusts were examined under a microscope and the cyanobacteria identified according to classical taxonomic literature (e.g. Frémy, 1929; Geitler, 1932; Desikachary, 1959).

Chlorophyll a and polysaccharide analysis

Chlorophyll a content was measured in $2 \times 2$ cm duplicate subsamples of the various crusts incubated for 1 week. The crusts were crushed in a mortar and extracted in boiling methanol for approximately 2 min. After centrifugation, optical density was measured at 665 nm (Cary 1 E Spectrophotometer) and the mean chlorophyll a content per square cm was calculated according to Vollenweider (1969).

Polysaccharide concentration was determined according to the sulfuric acid-anthrone method (Brink et al., 1960). Duplicate pieces of $4 \times 4$ cm of the crust samples were incubated as above, then crushed and extracted for 24 h in hot sulfuric acid. After addition of anthrone solution to the hydrolyzate, optical density was measured at 625 nm and mean concentrations were calculated by comparison with corresponding glucose standards that had been similarly treated.

Petrographic, mineralogical and chemical analyses

Several crust samples were impregnated by epoxy resin. Thin sections of the impregnated samples were examined and photographed under a polarizing microscope.

Bulk mineralogical compositions were determined by X-ray diffraction (XRD) using a Phillips diffractometer (PW 1730/1710; CuK$_\alpha$ radiation). Scanning electron microscope (SEM) analysis was carried out on carbon- or gold-coated natural samples using a Jeol JSM-840 microscope equipped with a LINK energy dispersive X-ray spectrometer.

Results

Crust microtopographic changes

No biogenic crust was detected in the active channel. The youngest terrace displays flat surface, fissured into polygons the margins of which are somewhat elevated (Fig. 2). The elevated polygon margins are seen also in terrace 2 where they form wider and more rounded micro-ridges (Fig. 3). The beginnings of microbiont aggregates over the entire polygon area are distinguishable by rounded elevated crust face (right side of Fig. 3). In the higher and thus older terrace 3 (Fig. 4), the microtopography is highly rugged, polygon elevated margins are still prominent but the microbiont aggregates fill up much of the polygon. centre at the lower right and upper left sides of the photo. The
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sharp morphological transition between the latter two terraces is displayed in Fig 5. It is hard to see the microridge and thus polygon-derived topography in terraces 4 and 5 (Fig. 6). The prevailing microtopographic elements in these terraces are elevated 'hills' or 'ridges' which are built up of microbiont aggregates with inorganic material of the soil crust.

Figure 3. The second terrace: polygons with more intensive growth into 'microridges' of the microbiotic crust in the microsites where the upturned margins of the polygons of the previous stage were located.

Figure 4. The third terrace with further growth in the 'microridges' and spaces among them
Polygon formation

We claim that in soil with a cyanobacterial crust the number of polygons per unit area is larger than in soil without any crust. Figures 7 and 8 display a site where most of the area is covered by microbiotic crust. The upper right corner is devoid of such a crust and has only the edaphic system of cracks and polygons. An edaphic fissure has right angle at the fissure shoulders with the canyon-like depression and thus differs from the cyanobacteria-induced crust cracks of Figs 2–4. This system, displayed by thick lines in Fig. 8, continues to the area with the microbiotic crust, and has an average polygon density of 192 per m². The polygon system associated with the microbiotic crust has an average polygon density of 3580 per m².

Figure 5. A close-up of terraces 2 and 3 and the step between them.

Figure 6. The fifth terrace with high surface complexity and hardly recognized hills, some of which were once ‘micro-ridges.’
The results of our measurements of the ratio between polygon number and area for soil without microbiotic crust are:

Sample size \((N) = 6\)

\[\text{Ratio} = 1.927 \pm 0.125/100 \text{ cm}^2\] (estimate \pm SE)

The results for polygons formed in soil with microbiotic crust:

Sample size \((N) = 6\)

\[\text{Ratio} = 8.497 \pm 0.969/100 \text{ cm}^2\] (estimate \pm SE)

\[t = 6.721\] (with approximately five degrees of freedom), and the \(p\) value is smaller than 0.001.

We thus conclude that the number of polygons per unit area is larger in soil with microbiotic crust than in soil without crust, and this result is statistically highly significant.

Expansion and contraction of the crust

The 10-mm long wet squares became 9.5 mm in 28 cases, 9.3 mm in three, 9 mm in five, and 10 remained 10 mm long. Thus average length became shorter in a highly significant way \((t_{59} = 12.55; p < 0.001)\). This crust is composed of a very dense network of filaments of *Microcoleus vaginatus* as the dominant component, which is involved with the significant contraction of the wet crust when dried.

**Figure 7.** A site in the Dead Sea Valley where most of the area is covered by microbiotic crust at a development stage similar to that of terrace 2. The upper right corner is devoid of such a crust and has only the edaphic system of cracks and polygons.
Species composition

No micro-organisms were detected in the superficial sediment of the wadi bottom. On the first terrace traces of *Schizotrix freisii* were found (Table 1). The number of species present in the crust increased as the terraces were higher, and thus older. *Schizotrix freisii* and *Microcoleus vaginatus* were invisible as long as the soil was dry and emerged within a few hours after wetting, forming a sparse blue-green network of filamentous fronds. At the highest terrace dark and compact aggregates of *Nostoc, Chlorogloea*, and a species of the cyanophilous lichen *Collema*, formed a prominent black crust on the soil surface.

![Figure 8. A drawing of the crack systems of Fig. 7. Thick lines represent the system of clay contraction-induced cracks; thin lines represent the system of microbiotic crust-induced cracks. A double thick line marks the boundary of the area with microbiotic crust.](image)

<table>
<thead>
<tr>
<th>Micro-organism</th>
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<th>2</th>
<th>3</th>
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<td><em>Collema</em> sp.</td>
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Table 1. Cyanobacteria and lichens listed in the order of appearance in the desert crust of alluvial terraces (0–5) at Mt. Sedom (after Dor & Danin, 1996)
MICROHABITAT SUCCESSION ON DESERT CRUST

Chlorophyll $a$ and polysaccharide concentrations

The concentrations of chlorophyll $a$ and polysaccharides in the crust samples increase with the terrace age. Concentrations of chlorophyll $a$ and of polysaccharide in terrace 5 were three- and six-fold greater, respectively, than in terrace 1 (Fig. 9).

Mineralogical composition

The clay fraction (2 $\mu$m) of the crusts was determined to consist of illite/smectite phases, kaolinite, illite, and palygorskite, in order of abundance.

All samples contain calcite, dolomite and quartz as the major minerals, together with minor quantities of feldspars, aragonite and clays. Gypsum is highly variable (Table 2). Aragonite is contributed exclusively by the parent rock of the Lisan Formation, whereas all other minerals originate from both airborne dust and the parent rock. Calcite content variability is apparently related to crust development. Its content rises from 10–15% in the surface of terraces 0 and 1 to 20, 35, and 40% in the crust of terraces 2, 3, and 5, respectively, and from 10% at 10 cm and 15 cm depth to 25% at the surface of terrace 2.

SEM observation showed that the predominant mineralogical component of the crust (terrace 3) is calcic ‘needles’ of $7 \times 0.4$ $\mu$m dimensions (Fig. 10). The needles are either separate or bound into bundles. Detrital grains of quartz, feldspars, clays and calcite are abundant. Dolomite often exhibits aggregates of euhedral crystals, indicating its origin from the dolomite bed at the top of the Lisan sequence here. The mineral grains of all types are bounded or coated by organic mass or distinct filaments. The uppermost crust and the layer below are enriched by calcic needles or organic filaments, respectively. This relative enrichment in needles is in accord with the equivalent increase in calcite content as analysed by XRD (samples 3–0 and 3–0.5,
Table 2) while aragonite content remains very low. This observation enables the identification of the needles as made of calcite and not of aragonite. SEM observations of samples from terrace 2 profile at depths 0, 10, and 15 cm showed abundance of the calcic needles but low aragonite content (Table 1) in all three samples. The needles are calcite polymorphs after the original parent rock aragonite. This transformation rapidly occurs in contact with fresh water (Katz et al., 1977).

The calcite-rich crust of terrace 3 exhibits microridges on its surface made of solid material. A close examination of these ridges by SEM reveals its microstructure: parallel plates within organic mass, apparently made of the polysaccharides (Fig. 11).

**Table 2.** Mineralogical composition (%) of terraces sediments and of representative parent rock (p.r., Lisan Fm.). The results are semi-quantitative, rounded to the nearest 5% to make up a total of 100 ± 5%. Accuracy is estimated as ±20% for results >20% and ±40% for results <20%. The first digit of the sample number depicts the terrace number and the second digit the depth in cm (0-0 = the top part of the crust, 0-3 = crust at 3 mm depth)

<table>
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<tr>
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<th>Calcite</th>
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<th>Quartz</th>
<th>Gypsum</th>
<th>Aragonite</th>
<th>Feldspars</th>
<th>Clays</th>
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![Figure 10](image)  
**Figure 10.** Scanning electron micrograph of the surface of terrace 4 displaying the densely packed calcite crystals.
The EDS analysis of separate plates from disaggregated ridges gives only Ca and points to these plates as the main source for calcium enrichment in the mature crusts.

Micromorphology of the crust

The increase in the degree of development of the biogenic crusts with time is expressed by its micromorphological characteristics. The studied thin sections from terraces 2–5 display an increase in the laminar structure of the crusts and its compactness (Fig. 12). Recycled old crust particles with laminated structure are incorporated into the current crust of the oldest terrace.

Discussion and conclusions

Successional processes in the microbiotic synusia of the vegetation are hardly discussed in the literature. West's (1990) review of microbiotic crust (naming it 'microphytic') shows that only a few studies deal with crust recovery after human destruction of natural systems. The processes of microtopographic succession observed in alluvial terraces at Mt. Sedom represent a clear geomorphic sequence where the temporal vector is expressed by spatial changes. Although critical opinions of ecologists oppose replacing time by spatial phenomena (e.g. Armesto et al., 1991), alluvial terraces and fan surfaces are well known to form chronosequences and therefore are used for relative dating (Birkeland, 1984; Bull, 1991). In our study area the biotic changes, along the temporal vector indicated by wadi terraces, include an increase in chlorophyll a and polysaccharide concentrations, and an increase in the number of species.

Filamentous cyanobacteria are the first colonizers of the new substratum exposed for colonization as the alluvial terrace was formed. Populating the entire surface, the cyanobacteria with their polysaccharide sheaths induce two opposing processes. They

Figure 11. Parallel plates being the main source for calcium enrichment in the mature crusts.
induce partial impermeability to water through the imbibition and swelling of their mucilaginous sheath. Sealing paths in the soil leads to the formation of vesicular layer in the soil (Evenari et al., 1974; Danin, 1976). The air trapped in the wet soil, as evidenced by the vesicular appearance, indicates the obstacle the crust represents for gases to escape from the soil during water infiltration. However, the formation of cracks through the swelling and shrinkage of the polysaccharides of their mucilaginous sheaths (Navarini et al., 1992) locally increases soil permeability in the cracks. This leads to the formation of opened paths for water in the relatively impermeable area where the cyanobacterial crust is continuous. The lateral growth of cyanobacteria in the crust leads to folding upward of the margins near the cracks and thus to increased leaching and aeration of the soil there. Once leached, this microsite becomes available for the establishment of additional cyanobacteria and cyanophilous lichens. The increasing complexity of the surface leads to higher water storage capacity in the depressions and to an amelioration in the moisture regime. Additional life-forms become established in the area with increasing complexity, thus leading to even better leaching, to higher biomass production, as indicated by the increase in chlorophyll a content, and to higher complexity in the nutrient regime.

When comparing the morphological characteristics of the species prevailing in the early and late stages of the succession it becomes evident that entirely different life strategies are displayed. Microcoleus and Schizothrix, which are flat network-forming filamentous cyanobacteria, dominate on the least stable, coarse grained first terrace. Among them the primary colonizer and soil stabilizer, Microcoleus vaginatus, shows prominent motility, which helps it to emerge above the covering sediment (I. Dor, unpublished data). These two organisms are end-edaphic (Friedmann & Galun, 1974). By contrast, the three genera thriving on the elevated microridges of the late stages of the succession, Colema, Nostoc and Chlorogloea, are ep-edaphic (Friedmann & Galun, 1974), and exhibit morphological convergence. Their thallus or frond aggregate is hard, gelatinous, resistant to rain and wind impact by swelling rapidly when wetted and preserving moisture for prolonged time. Another converging feature

![Figure 12. Thin sections of a crust from terrace 4. Note the laminar structure of the compact crust.](image-url)
of these three genera is their dark brown colour resulting from the thick, pigmented sheaths (cf. color plates in Dor & Danin, 1996), which obviously provide UV-photoprotection in this high-irradiation environment (Abeliovich & Shilo, 1972). Such colours are never seen in the end-edaphic colonizers Microcoleus and Schizothrix which emerge for a short time from the ground with their blue-green thallus only after an effective rain.

The higher diversity of organisms in the crust is evidently associated with different nutrition regimes (as reviewed widely by West, 1990). All the components of the crust function also as a trap for airborne dust (Danin et al., 1989; Danin & Ganor, 1991, 1997). The repeated trapping is the mechanism for creating a thin laminar crust, which is apparently the extreme and equivalent of better developed laminar calcrites in less arid climates (e.g. Vogt, 1984). The advanced stages of succession are not only richer in organisms, biomass, and polysaccharides but in biogenic calcite as well. This unusual platy form in intimate association with the polysaccharide sheaths of the calcite increases much the stability of the substratum. Calcite secretion by biogenic agents such as cyanobacteria or fungi has been reported from different environments and in various crystal forms (e.g. Boquet et al., 1973; Callot et al., 1985a, b; Wright, 1986; Phillips et al., 1987; Monget et al., 1991; Amit & Harrison, 1995; Jones, 1995). This pedogenic calcite production is a major contributor to the formation of surficial crusts.

In conclusion, the microbiotic succession leads to increasing microtopographic complexity. This induces better leaching of the soil and better moisture regime, thus enabling more kinds of organisms to grow in the site and increasing biomass production. The various impacts of the increasing number of organisms on the nutrient regime together with amelioration of the moisture regime induce the biotic positive feedback sequence. Stability of the crust increases to high levels as a result of calcite sedimentation at the surface.

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References


