# Biological Soil Crusts in the Mojave Desert, USA: Micromorphology and Pedogenesis

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# Biological Soil Crusts in the Mojave Desert, USA: Micromorphology and Pedogenesis

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Biological soil crusts (BSCs) are bio-sedimentary complexes that play critical ecological roles in arid landscapes; however, the interactions between component biota and sediments are poorly understood. A detailed micromorphological investigation of BSC development and crust microstructure in the Muddy Mountains Wilderness Area, Nevada, examined features in thin section using petrographic microscopy, light microscopy, scanning electron microscopy, and energy dispersive x-ray spectroscopy. The >1800 microscopic observations were linked to crust macroscale features and soil geomorphology. Complex bio-sedimentary structures of BSCs reflect a dynamic genetic history and diverse formative processes, including: (i) stabilization and authigenic mineral precipitation; (ii) wetting–drying and expansion–contraction; (iii) dust capture; (iv) microscale mass wasting; and (v) vesicular (Av) horizon formation. A new conceptual model for hot deserts illustrates how these processes co-develop with BSC succession, during countless wet–dry cycles, to build up pinnacle microtopography while simultaneously forming Av horizons in the bio-rich and bio-poor zones. Complex surficial and internal bio-sedimentary structures, which vary as a function of crust morphology, trap surface water for uptake by crust organisms, while dust influx provides a source of nutrients. These phenomena influence landscape-scale water dynamics and biogeochemical cycling, increasing the availability of soil resources during times of biotic stress. Biological soil crusts uniquely facilitate the accumulation, morphology, and ecosystem function of dust and should, therefore, be considered critical agents in arid pedogenesis and landscape development.

Abbreviations: BSC, biological soil crust; EPS, extracellular polymeric secretions; XPL, cross-polarized light.

Biological soil crusts are complex matrices of cyanobacteria, mosses, lichens, bacteria, algae, and fungi that fuse around soil particles to create a living, protective membrane in arid soils (Eldridge and Greene, 1994). Biological soil crusts control the movement of water, gases, and solutes across soil surfaces (Belnap et al., 2003) and prevent desertification by impacting particle detachment and transport (McKenna Neuman et al., 1996; Miralles-Mellado et al., 2011), water and energy balances (Belnap, 2006), soil fertility (Kleiner and Harper, 1977; Evans and Belnap, 1999), and plant community establishment (Li et al., 2005; Escudero et al., 2007). Biological soil crusts are extremely fragile and sensitive to physical impacts such as off-road vehicles, hiking, and grazing, making them excellent indicators of disturbance (Belnap, 1998).

Biological soil crust development follows a natural succession (Belnap, 2001), beginning with the development of smooth cyanobacterial-algal crusts and, under favorable conditions, is followed by formation of short moss-lichen crusts and eventually tall moss-lichen pinnacled crusts (Fig. 1). Estimated rates of crust formation, or recovery after disturbance, range from 10s to 1000s of years depending on climate, soil texture, and geomorphic stability as well as metabolic adaptations and
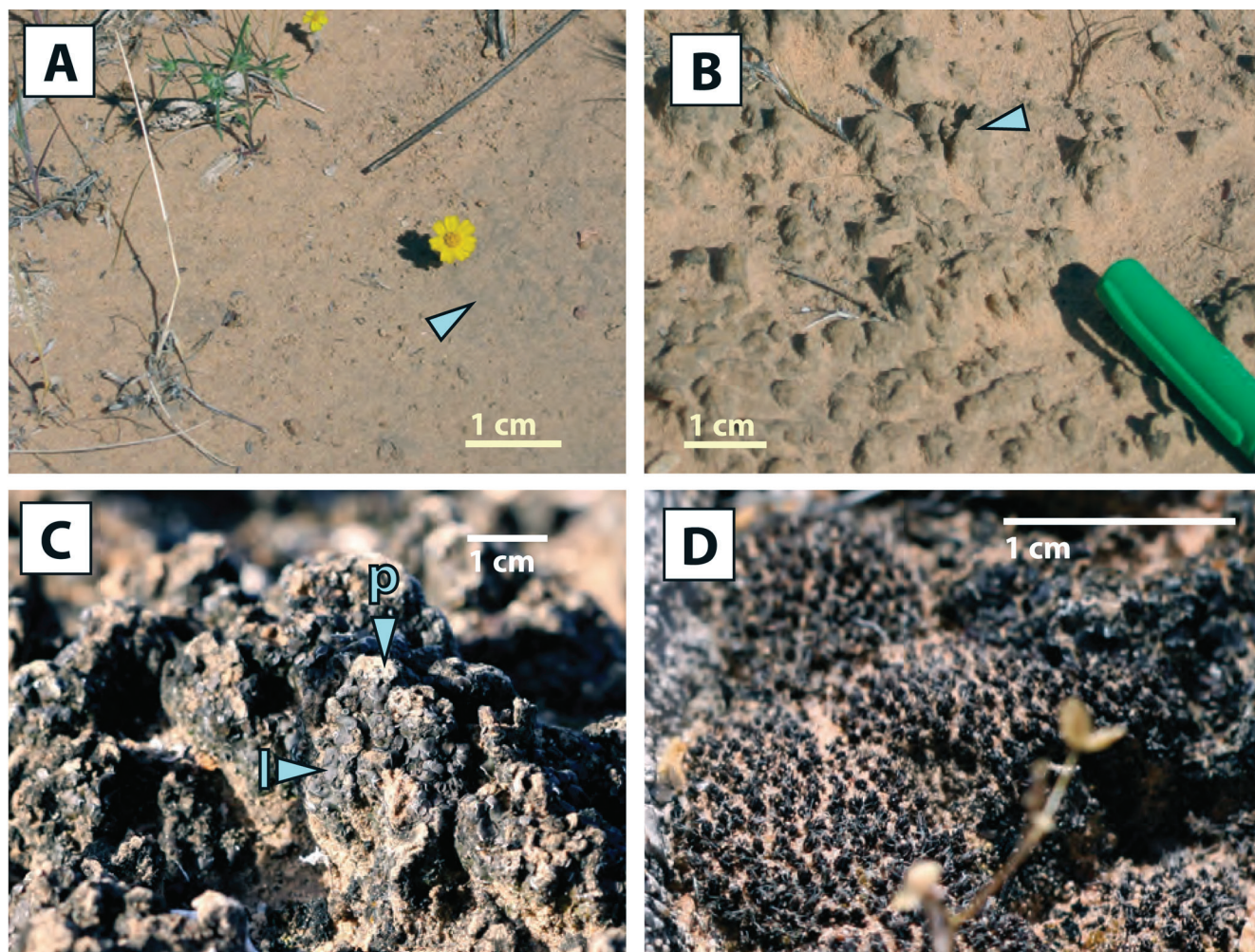
Fig. 1. (A) Cyanobacteria crusts display slightly darkened surfaces (arrow) and (B) knob features (arrow; marker for scale); (C) tall, pinnacled crusts with extensive lichens (l) have summits cemented in authigenic mineral precipitates (p); and (D) short, moss-dominated crusts accumulate eolian sand grains.

reproductive strategies of the component organisms (Belnap and Warren, 2002; Thomas and Dougill, 2007; Kidron et al., 2008; Williams et al., 2008; Langhans et al., 2010). Previous studies have identified recovery times of individual species but not restoration of bio-sedimentary features. Despite the conspicuous surface microtopography of moss-lichen pinnacles (Fig. 1C), few have critically analyzed their internal structure (e.g., Campbell, 1979; Danin and Ganor, 1991; Belnap, 2001; Miralles-Mellado et al., 2011) or the genesis of their unique morphology in hot, arid deserts. These microfeatures potentially control distributions of soil water, nutrients, and energy and should, therefore, be investigated to maximize restoration efforts and to understand their role in pedogenesis and landscape development.

To better understand the structure, function, and genetic history of tall moss-lichen pinnacled crusts in hot environments, we completed a micromorphological investigation of the biotic and mineral components of several BSC types from Hidden Valley, Muddy Mountains Wilderness Area, in the Mojave Desert of southern Nevada (Fig. 2). This work provides insight into BSCs' role in dust accretion and pedogenesis and identifies crust microstructures that potentially influence soil resource allocation and water dynamics.

## MATERIALS AND METHODS

The Hidden Valley portion of the Muddy Mountains Wilderness Area in Nevada is an ideal natural laboratory to investigate BSC microstructure. This semi-enclosed basin contains a variety of BSC types that inhabit a diverse sequence of geomorphic surfaces and soils formed from mixed limestone and sandstone parent materials. The study area lies within the northern reaches of the Mojave Desert at approximately 1000-m elevation, where mean annual temperatures are 27°C and mean annual precipitation is 114 mm (Gorelow and Skrbac, 2005). Most precipitation falls from January to March, when average highs range from 14 to 21°C, while some rainfall occurs in July and August, when average highs range from 39 to 40°C (Gorelow and Skrbac, 2005). Given its proximity to the Las Vegas, NV, metropolitan area and its designation as a wilderness area, the valley is of critical concern to the Bureau of Land Management.

In June 2009, 70 BSC samples were collected, which included (i) tall, moss-lichen pinnacled crusts and (ii) cyanobacteria crusts, which were collected adjacent to (iii) short moss-lichen crusts (Williams, 2011, p. 10–103). Crust surfaces and cross-sections were examined for macroscopic features, such as pores, cracks, voids, microscopic surface relief, pedogenic structure,

and soil aggregation. Ten randomly distributed sites were sampled, including eolian and alluvial surfaces that ranged in age from recent Holocene to Pleistocene. Corresponding soil profiles and surfaces were described and characterized in two companion studies (Williams, 2011, p. 104–350).

Twenty-eight select BSC specimens were immersed in Spurr low-viscosity embedding medium and placed in a vacuum desiccator for 4 to 6 h under increasing pressure (1.03–4.14 MPa) and subsequently in an oven at 70°C for 16 h. Embedded samples were cut into 39 vertically oriented billets using a rock saw equipped with a diamond ISOMET wafering blade and an oil-based lubricant to prevent salt dissolution. Billets were ground into thin sections in lubricating oil (National Petrographic Service). Initially, thin sections were imaged under a digital flatbed scanner. Micromorphological features were then characterized at 4×, 10×, and 20× magnification under a Nikon Eclipse LV100POL polarized light microscope and under a light microscope at 0.8× to 3.2×. Microscopic photos were taken using digital still cameras. Lastly, thin sections were sputter coated in Au for 30 s with a Cressington 108 Auto Sputter and examined and imaged in the University of Nevada, Las Vegas Electron Microanalysis and Imaging Laboratory using a JEOL-5600 scanning electron microscope (SEM). The SEM observations were taken under the backscatter electron detector at 35 to 5000× magnifications with working distances of 15 to 20 mm, at 15 to 20 kV, and at spot sizes of 30 to 40. Elemental compositions were verified using an attached Oxford INCA energy dispersive x-ray spectroscopy (EDS) system at 270× to 5000× magnifications with working distances of 15 to 20 mm, at 15 to 20 kV, and at spot sizes of 30 to 40. In all cases in which authigenic precipitates were suspected, SEM-EDS was used to verify the mineralogy and potential origin. A total of >1800 microscopic observations were recorded and subsequently summarized in tabulate form.

## RESULTS

The three BSC morphotypes, with distinct species compositions, were characterized by unique surficial and internal micromorphological features (Fig. 3). All BSC types contained two macroscale zones: the upper, bio-rich zone that was highly cohesive and the lower, noncohesive bio-poor zone. The bio-rich zone varied from 0.50 to 22 mm thick and was capped by biological structures. The bio-poor zone was primarily composed of poorly consolidated and pedologically unstructured sand. In cross-section, the bio-rich and bio-poor zones were commonly separated by a linear void (Fig. 3).

The BSCs were composed of complex matrices of grains, voids and cracks, authigenic minerals, biological filaments, squamulose lichens, vascular plant roots, gelatinous lichens, and
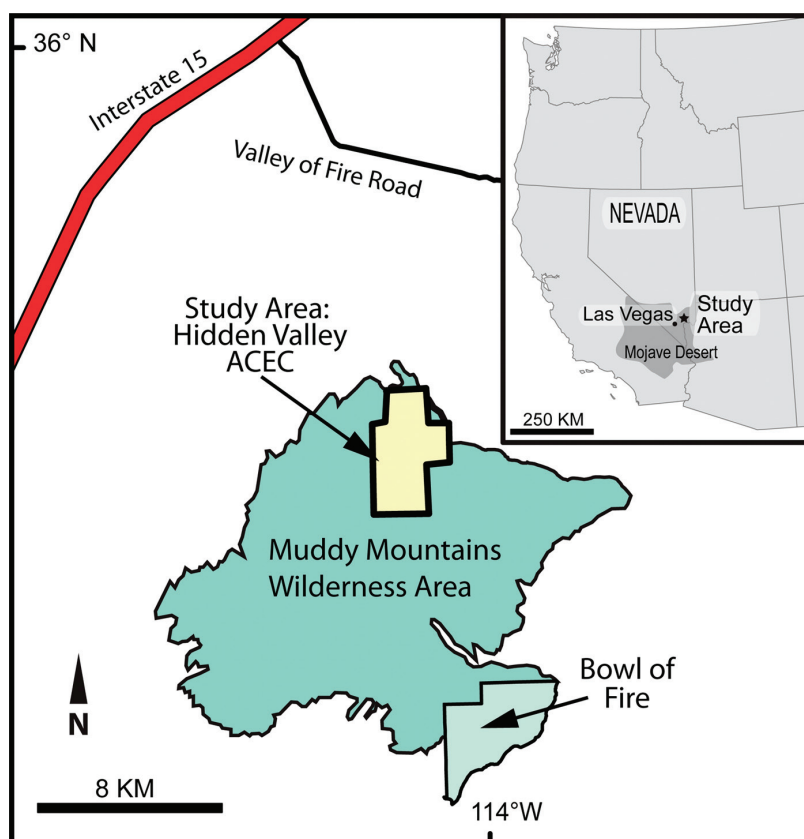


**Fig. 2. The study area, the Hidden Valley Area of Critical Environmental Concern (ACEC), lies within the Muddy Mountains Wilderness Area, Nevada.**

mosses (Fig. 4 and 5). Grain size, orientation, and compaction varied with biological and sedimentary factors but ranged from clay to medium sand with few coarse sand grains (Fig. 4A). Void morphologies included the following: irregular, linear voids up to 5 mm wide; irregular interior voids up to 24 by 36 mm with smooth margins of compacted clays, silts, and very fine sands that commonly contained photosynthetic tissues that appeared to be blocked from light (Fig. 4D and 5F); vesicular pores from 0.1 to 0.8 mm in diameter (Fig. 4B and 4C); and horizontal to vertical 0.5- to 1-mm-wide linear voids that commonly aligned parallel to all biological structures or penetrated the bio-rich zone. Authigenic minerals occurred at or near the surface of all crust types lying directly along or near biological structures or exudates (Fig. 5A and 5B). Almost exclusively authigenic $CaCO_3$ (with or without trace Mg) occurred as densely cemented zones or was finely disseminated within biological exudates and tissues. Biological filaments penetrated the entire bio-rich zone (Fig. 4A and 4F). Cyanobacterial and fungal filaments occurred as 3-μm-wide bare strands or as bundles up to 200 μm wide and 800 μm long (Fig. 5A). Bundles were sheathed in extracellular polymeric secretions (EPS) and coated in clay- to sand-sized grains or mineral precipitates. Squamulose lichen thalli, such as *Placidium lacinulatum* and *Placidium squamulosum*, formed irregular plates known as squamules at the soil surface and were anchored by root-like rhizine structures (Fig. 5C and 5E). *Collema* was the dominant gelatinous lichen, whose dehydrated thalli commonly displayed an irregular, tree-like form in cross-section (Fig.
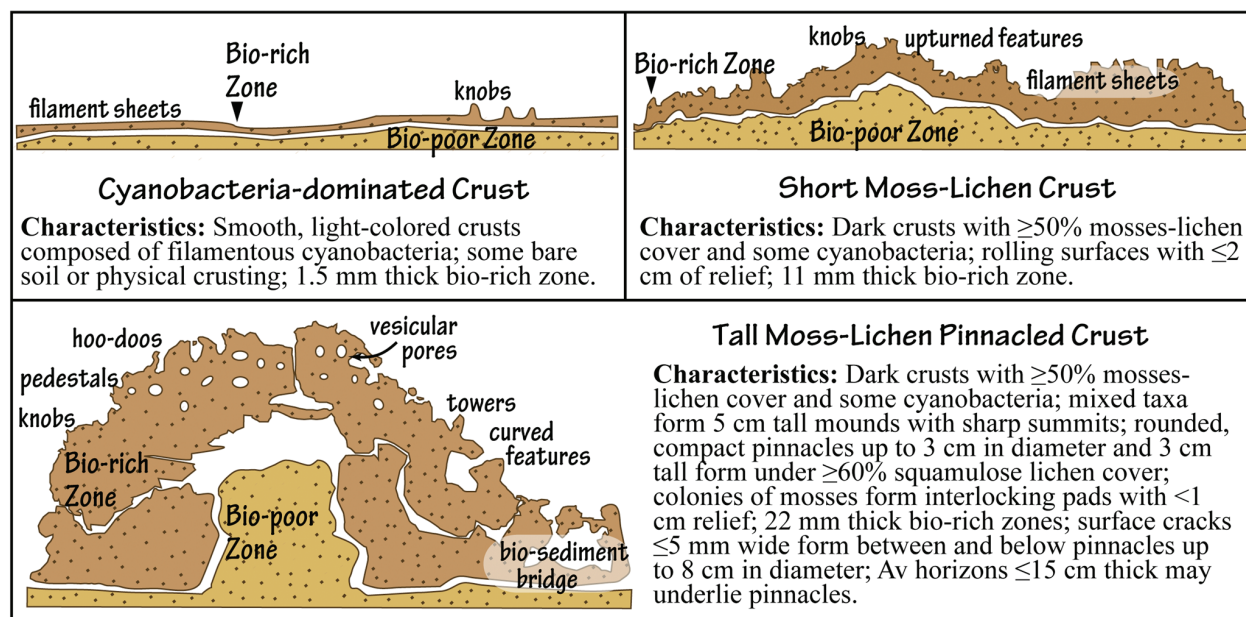
**Cyanobacteria-dominated Crust**
**Characteristics:** Smooth, light-colored crusts composed of filamentous cyanobacteria; some bare soil or physical crusting; 1.5 mm thick bio-rich zone.

**Short Moss-Lichen Crust**
**Characteristics:** Dark crusts with ≥50% mosses-lichen cover and some cyanobacteria; rolling surfaces with ≤2 cm of relief; 11 mm thick bio-rich zone.

**Tall Moss-Lichen Pinnacled Crust**
**Characteristics:** Dark crusts with ≥50% mosses-lichen cover and some cyanobacteria; mixed taxa form 5 cm tall mounds with sharp summits; rounded, compact pinnacles up to 3 cm in diameter and 3 cm tall form under ≥60% squamulose lichen cover; colonies of mosses form interlocking pads with <1 cm relief; 22 mm thick bio-rich zones; surface cracks ≤5 mm wide form between and below pinnacles up to 8 cm in diameter; Av horizons ≤15 cm thick may underlie pinnacles.

**Fig. 3. Three biological soil crust morphotypes display distinct bio-sedimentary structures and surface morphologies.**

4E). Vascular plant roots were uncommon features that occurred in large interior voids near the base of pinnacle mounds. Short mosses, such as *Bryum* and *Pterygoneurum*, commonly occurred as discrete individuals within pinnacles, whereas tall mosses, such as *Syntrichia* (Fig. 5D) grew as distinct pads within short moss-lichen crusts or adjacent to tall moss-lichen crusts. (For more detail, see Williams, 2011, p. 10–103.)

Bio-sedimentary structures included unique features composed of soil aggregates and biological components (Table 1). Nine distinct morphological features were observed in this study: (i) filament sheets (Fig. 4A), (ii) filament knobs (Fig. 4F), (iii) upturned or curled features (Fig. 5C), (iv) rafts, (v) pedestals (Fig. 5E), (vi) towers (Fig. 5C and 5F), (vii) micro hoo-doos and sharp protrusions, (viii) curved features (Fig. 5F), and (ix) bio-sediment bridges (Fig. 4D and 5F). The unique characteristics of each feature were tied to associated biota and varied with crust type. Soil surface texture, which included the bio-rich zone and the upper 1 cm of the underlying bio-poor zone, ranged from fine sand to fine sandy loam. Texture was not tied to specific bio-sedimentary structures but varied among geomorphic surfaces and corresponding BSC types (Williams, 2011, p. 104–219).

## DISCUSSION
## Conceptual Model of Biological Soil Crust Morphology and Biogenic Av (Vesicular) Horizons

We propose a new conceptual model to explain how the succession of crust organisms builds up moss-lichen pinnacle microtopography through dust accretion and surface sealing, while simultaneously forming vesicular pores and mineral vesicular (Av) horizons. The Av terminology used here was first presented by Springer (1958) to describe fine-grained surface soil horizons containing vesicular porosity (see also McFadden et al., 1987; Turk and Graham 2011). Under suitable conditions, BSC suc-

cession proceeds from cyanobacteria crusts to tall moss-lichen pinnacled crusts overlying mineral Av horizons (Fig. 6). Through this succession, component organisms change, organic and mineral substrates accumulate, microtopographic relief increases, and intricate bio-sedimentary structures develop as formative processes become more complex. Stabilization dominates early crust formation. Expansion–contraction (caused by wetting–drying), microscale mass wasting, and magnified dust capture become increasingly important in later crust formation.

## Stabilization Processes

Smooth cyanobacteria crusts initiate the succession through stabilization and erosion mitigation processes, such as trapping and binding, surface sealing, and authigenic mineral precipitation. Terrestrial filamentous cyanobacteria form the basic building blocks of biological soil crust structure in a similar fashion as cyanobacteria dominate the formation of marine microbially induced sedimentary structures (Noffke et al., 2001). Cyanobacteria first inhabit and weave around fine sands and then form a thickened layer of finer grains by trapping atmospheric silt, clay, and very fine sand in their sticky sheaths (Campbell, 1979; Belnap and Gardner, 1993). After subsequent burial by sand, cyanobacteria move toward sunlight to reclaim the surface, restarting the process (Garcia-Pichel and Pringault, 2001; Thomas and Dougill, 2007). Trapping and binding cycles form alternating layers of fine and coarse sediment (Fig. 4A and 4F). Similar to stromatolites, homogenous distributions of cyanobacteria form smooth sheets (Fig. 4A), while heterogeneous distributions result in protruding knobs with filament tufts (Fig. 4F) (Grotzinger and Knoll, 1999; Noffke et al., 2001). Authigenic mineral precipitates form as EPS is mineralized (Campbell, 1979; Braissant et al., 2003), which further cements grains. Erosion mitigation continues throughout the succession
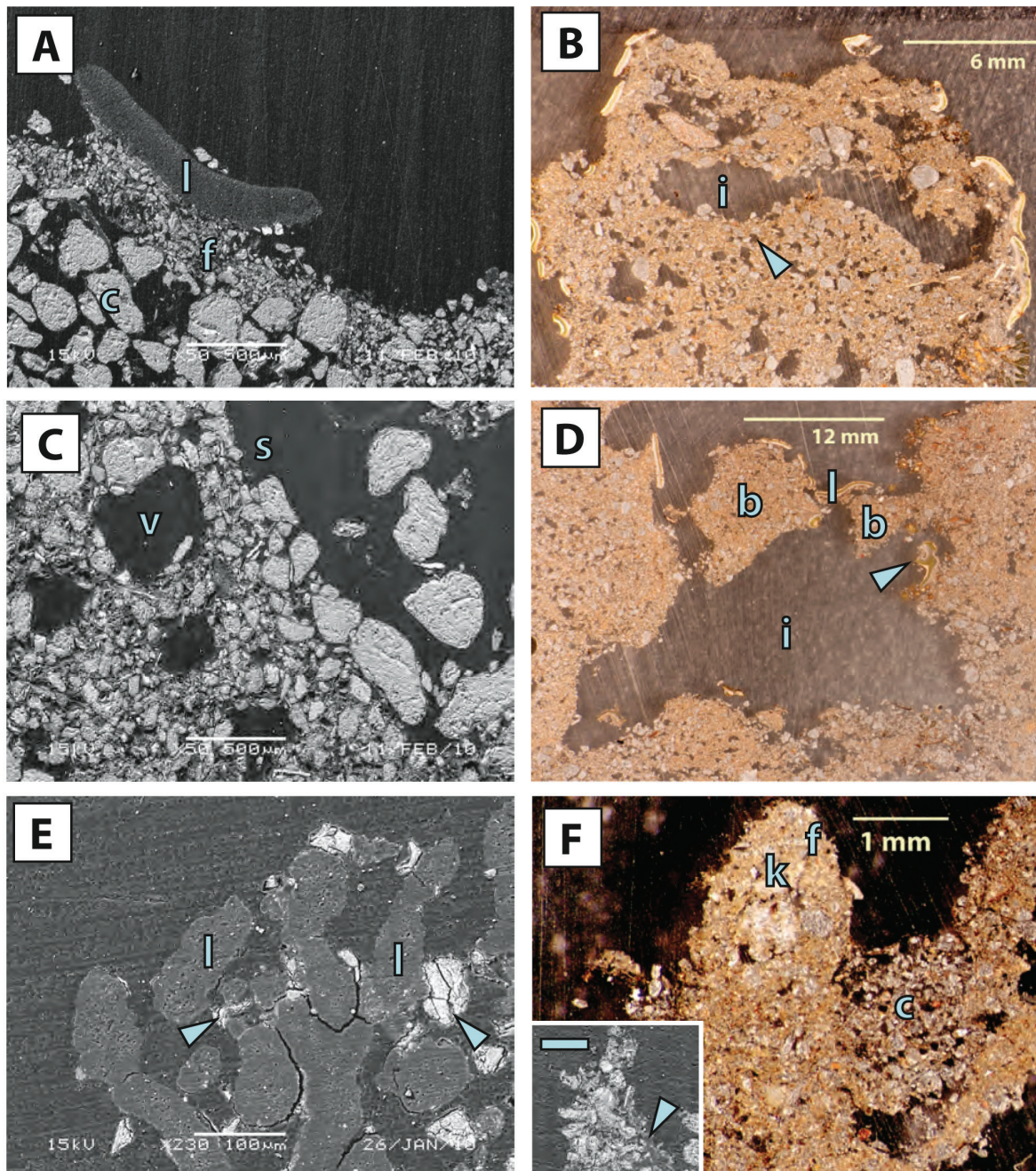
**Fig. 4. (A)** A lichen (l) with a layer of fines (f), including clays, silts, and very fine sands, and a mesh of filaments overlie coarse, unconsolidated sands (c) (backscatter electron detector [BES], scale 0.5 mm); **(B)** pinnacles contain irregular (i) or vesicular voids (arrow) (light microscope image); **(C)** vesicular pores (v) occur near the surface (s) of the bio-rich zone (BES, scale 0.5 mm); **(D)** sediment bridges (b) overlie an irregular void (i) with lichens (arrow) blocked from sunlight (light microscope image); **(E)** a gelatinous lichen (l), probably *Collema*, traps grains (arrows) (BES, scale 0.1 mm); **(F)** a knob (k) composed of fine grains (f) and filaments, with coarse, unconsolidated grains (c) infilling an adjacent depression (light microscope image) and a tuft (inset) of filaments (arrow), grains, and precipitates forming along the knob summit (BES, scale 0.05 mm). Images are oriented vertically.

(Fig. 6) as all crust organisms stabilize surfaces and sustain the accumulation of atmospheric dust.

## Dust Capture and Topographic Relief

Dust accretion is magnified through the succession as component biota change and microtopography increases (Fig. 6). Although previous geochemical data indicated potential dust signatures in BSC sediments (Reynolds et al., 2001; Beraldi-Campesi et al., 2009), our conceptual model comprehensively explains the mechanisms that lead to dust accumulation. Our results suggest that organism morphology controls the mechanism and amount of dust capture, which ultimately defines surface relief. Filamentous cyanobacteria of early succession crusts capture small volumes of dust (Fig. 4A) (Campbell, 1979; Belnap and Gardner, 1993), which produce relatively smooth surfaces (Fig. 1A and 1B). Mosses (Danin and Ganor, 1991) and lichens of short moss-lichen crusts enhance local dust capture, leading to greater fine-grained material accumulation and rolling surface
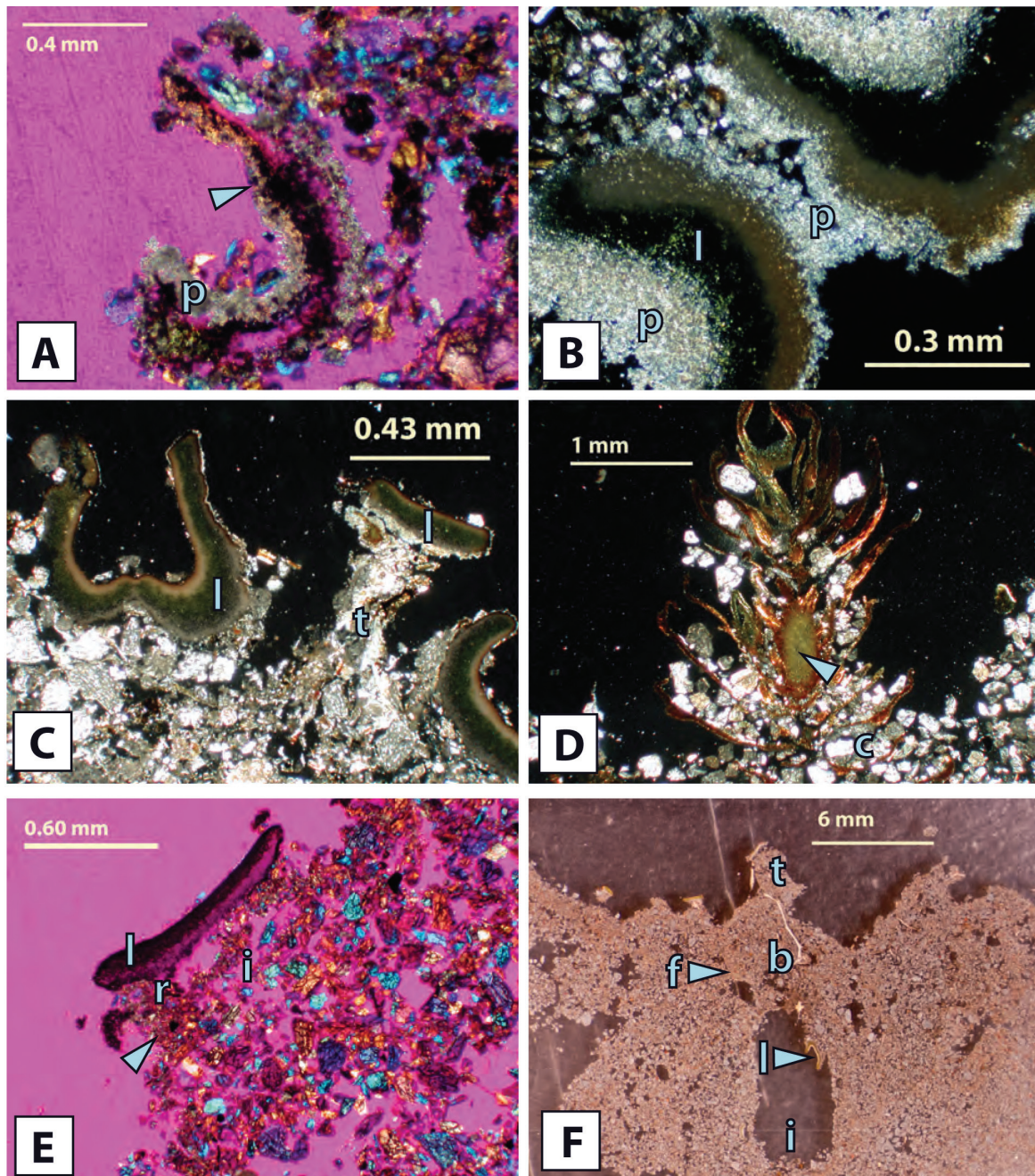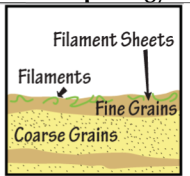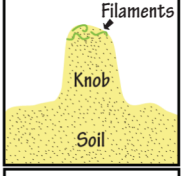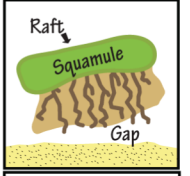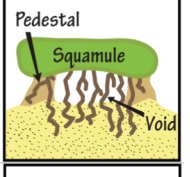
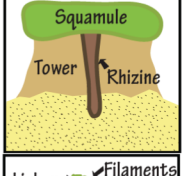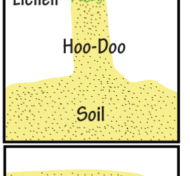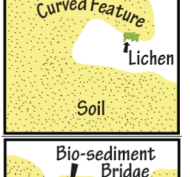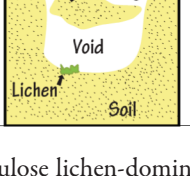Fig. 5. (A) Calcium carbonate precipitates (p) permeate cyanobacterial extracellular polymeric secretions (arrow) (cross-polarized light [XPL] image) and (B) cover lichen squamules (l) (petrographic image); (C) dry lichen squamules (l) detach from the soil and top a bio-sediment tower (t) (petrographic image); (D) coarse grains rest among "tall" moss leaves (arrow) (petrographic image); (E) a lichen squamule (l) with rhizoidal rhizines (r) tops a bio-sediment pedestal (arrow) with interior voids (i) (XPL image); (F) a tower (t) topped by a lichen squamule overlies a bio-sediment bridge (b) and a large, irregular void (i), composed of silt and clay grains, containing a lichen thallus (l); a fine-grained lamina lies along the left side of the sediment bridge (f) (light microscope image). Images are oriented vertically.

topography (Fig. 1D). Moss-lichen pinnacled crusts, up to 5 cm tall, have the greatest surface roughness and microtopography, which, in addition to the open cracks, collectively causes the highest degree of and potential for dust capture (Fig. 1C).

The size and type of biotic structures control the size of trapped dust particles as well as resulting sedimentary features. For example, the leaf structure of moss taxa controls the size of trapped grains: scattered, short mosses that grow in moss-lichen pinnacles accommodate the capture of finer material than the colonies of tall mosses (Fig. 1D and 5D) seen in short moss-li-

chen crusts (Williams, 2011, p. 10–103). Gelatinous lichens capture dust within cracks that form adjacent to their dehydrated thalli (Fig. 4E). The high shrink–swell potential of gelatinous lichens and incremental dust accretion cause soils to buckle and form sharp surface topographies (Williams, 2011, p. 10–103) as well as internal structures that resemble similar expansion–contraction features of Vertisols (Nordt et al., 2004). Squamulose lichens form another unique set of bio-sedimentary features. Through alternating wet–dry cycles, lichen squamules desiccate, shrink, and curl (Fig. 5C), then subsequently rehydrate, expand,

**Table 1. Summary of observed bio-sedimentary features.**

| Feature | Characteristics | Morphology |
|---|---|---|
| Filament sheets | horizontal strata of compacted clays, silts, and very fine sands among mesh of filaments that are probable cyanobacteria; strata are up to 250–300 µm thick and overlie layers of loose, unconsolidated fine to coarse sands; commonly contain authigenic minerals; occur in all crust types and are most pervasive in cyanobacteria-dominated crusts |  |
| Filament knobs | protrusions of clay, silt, and sand; 2 mm wide and up to 3.8 mm tall; summits are convex; short knobs contain 1.5- by 0.25-mm linear voids that align parallel with knob summits, 1 mm from the surface; many tall knobs contain poorly and well-developed vesicular pores; sharp protrusions of filaments coated in silt and clay commonly cap knobs; occur in all crust types and are most pervasive in cyanobacteria-dominated crusts |  |
| Upturned features | biological or bio-sedimentary structures partially detached from the soil surface; examples include lichen thalli, filaments, and filament sheets; biological structures commonly curl upward and downward in conjunction with attached grains; occur in all crust types |  |
| Rafts | lichen thalli completely separated from the soil surface; grains or precipitates are attached to or embedded within rhizines or exudates; form bio-sedimentary aggregates up to 1.1 mm thick and 2 mm long; occur in short moss-lichen crusts and tall moss-lichen pinnacled crusts |  |
| Pedestals | lichen squamules cap small sediment protrusions up to 0.75 mm tall; occur in conjunction with multiple-rhizine squamulose lichens such as *Placidium squamulosum*; contain clays and silts and commonly overlie coarser grains; commonly contain a 1.5-mm-diameter void with precipitate-coated rhizines up to 1.5 mm long; occur in tall moss-lichen pinnacled crusts |  |
| Towers | lichen squamules cap large, linear sediment protrusions up to 4.75 mm tall and 0.95 mm wide; *Placidium lacinulatum* lichen thalli have single, thick rhizines; towers contain sands but are dominated by silts and clays; rhizines commonly penetrate the entire length of the tower, running parallel with 0.1-mm-wide linear voids; occur in tall moss-lichen pinnacled crusts |  |
| Micro hoo-doos and sharp protrusions | gelatinous lichens and filaments top "hoo-doo-like" protrusions and sharp bio-sediment aggregates; grain sizes include mostly sand with some clay and silt; protrusions show no obvious stratification and are up to 1 mm wide and 6 mm tall; vertical margins are commonly concave; occur in tall moss-lichen pinnacled crusts |  |
| Curved features | thumb-like aggregates of grains and biostructures that form "U" or "L" shapes; up to 3.5 mm wide and 7 mm long; contain clay, silt, and sand; commonly occur in conjunction with sediment bridges and interior voids containing photosynthetic biostructures; occur in tall moss-lichen pinnacled crusts |  |
| Bio-sediment bridges | horizontal, linear soil aggregates that may or may not contain biotic structures; aggregates are up to 12 mm wide and 24 mm long; overlie interior voids as large as 24 mm by 36 mm; interior voids commonly contain photosynthetic biostructures; aggregates are comprised of sand, silt, and clay; occur in tall moss-lichen pinnacled crusts |  |

and flatten. In some cases, curling may cause lichen–sediment aggregates to detach, forming "rafts," which act as potential propagules that are deposited nearby or move long distances via wind currents (Wynn-Williams, 1990). If dehydrated lichen squamules remain attached during curling, dust incrementally accretes (Fig. 7) to form fine-grained towers (Fig. 5C and 5F; Table 1) and pedestals (Fig. 5E; Table 1). This dust capture mechanism facilitates radial expansion along squamulose lichen-dominated surfaces, which eventually produces rounded, compact pinnacle morphologies (Fig. 1C and 4B). Towers and pedestals also increase surface roughness for enhanced dust capture and create new, exposed substrates for colonization.
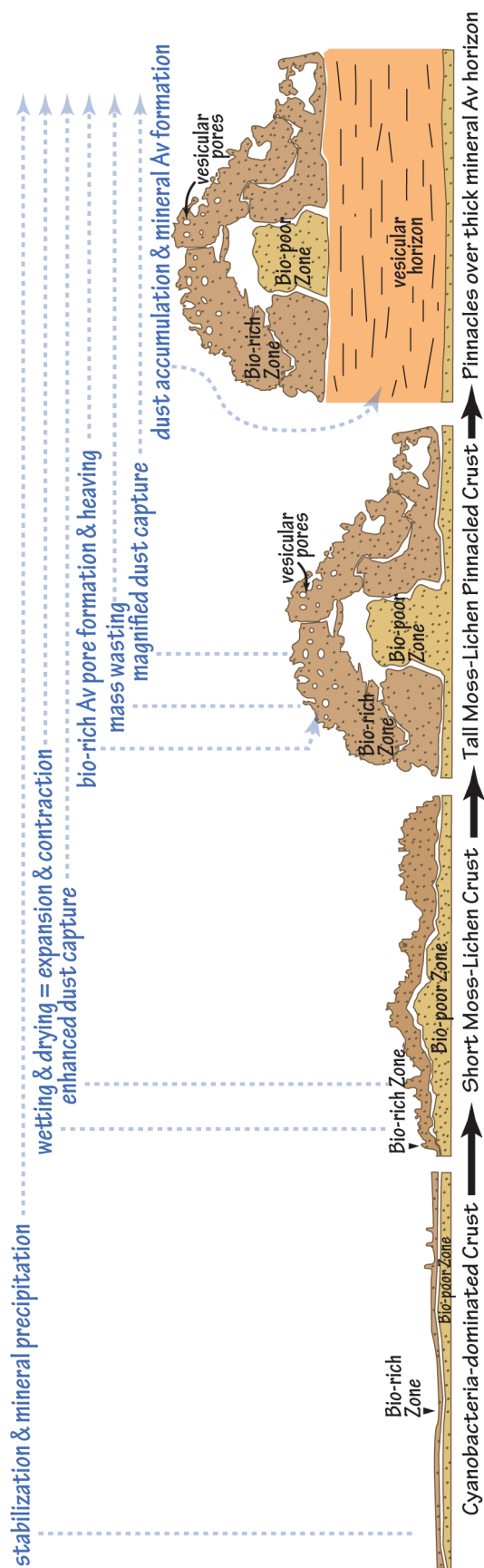
Fig. 6. Biological soil crust succession proceeds along geomorphically inactive fine-grained sediments. Processes (blue) co-develop with changes in species composition and surface morphology.

## Processes Forming Topographic Relief

Several theories of crust topographic development have been proposed by previous researchers. Some suggested that crust microtopography in warm deserts forms as microbial-sediment sheets curl (Danin et al., 1998), which closely resembles the upturned features described here (Table 1). In cold environments, hoof traffic from native ungulates enhances topography (Csotonyi and Addicott, 2004). Others have hypothesized that frost heave and differential erosion produce most pinnacle topographic relief (Belnap, 2001). While frost heave may play a dominant role in cooler deserts, it has minimal influence on crust microtopography in hot deserts, like the Mojave, where soils rarely freeze. This study shows direct evidence that wetting and drying processes drive microtopographic change in Mojave Desert crusts through dust capture, mass wasting, expansion and contraction, and eventually Av horizon formation.

## Expansion–Contraction in the Bio-rich Zone and Microscale Mass Wasting

Alternating wetting and drying of the bio-rich zone causes repeated hydration expansion and desiccation contraction of the organic materials and dissolution and reprecipitation of soluble authigenic minerals. This process is more pronounced if there are clay minerals present to enhance cohesion and expansion–contraction. Repeated expansion–contraction further destabilizes aggregates to increase mass wasting processes and opens cracks that facilitate dust capture.

While pinnacle buildup requires prolonged landscape stability, accretionary processes lead to microscale instability and mass wasting that form complex pore space (Fig. 4B, 4D, and 5F). If accretionary aggregates such as towers become too tall, undercutting may destabilize the structure, which causes toppling and the formation of bio-sedimentary bridges (Williams, 2011, p. 10–103). These bridges commonly trap photosynthetic materials within interior voids (Fig. 4D and 5F), which suggests that they were once exposed at the soil surface. Differential erosion can also form micro hoo-doos (Table 1) (Bryan, 1925) and may augment the relief of accretionary knob structures. Wet–dry cycles cause alternating shrinking and heaving that together with subsequent gravitational settling produce curved structures (Table 1) that resemble creep features of hillslopes (Kirkby, 1967). Sloughing or collapse augment creep processes to close near-surface pores. Noncohesive aggregates of the bio-poor zone commonly collapse and detach from the cohesive bio-rich zone that is bound by biotic structures and cemented by associated authigenic minerals (Fig. 4B). Differential dissolution of soluble precipitates could also weaken aggregates and enhance mass wasting. These observations demonstrate that despite their net buildup of material, crusts are not static but undergo a turbulent life history that forms intricate internal voids.

## Vesicular Pore and Horizon Formation

A combination of organic structures, physical crusting, and cementing authigenic minerals in the bio-rich zone create a sur-

ficial seal that traps air and results in the formation of vesicular pores. Vesicular pores are a defining feature of Av soil horizons (Turk and Graham, 2011). These horizons are known to form in environments where eolian materials are added to the surface and a surficial seal or some other condition traps air (Evenari et al., 1974; Bunting, 1977). Vesicular horizons are common in arid environments with desert pavements (e.g., Peterson, 1980; McFadden et al., 1998; Anderson et al., 2002), salt crusts (Buck et al., 2011), and arctic and subarctic soils (Bunting, 1977). While previous studies have reported vesicular pores in association with BSCs (e.g., Danin et al., 1998; Marsh et al., 2006; Miralles-Mellado et al., 2011), our conceptual model describes how Av (vesicular) soil horizons develop during BSC succession. While these horizons were only observed in tall moss-lichen pinnacled crusts in this study, they could potentially form in earlier crust types given adequate fine-grained material and surface seals. Surfaces covered exclusively by mosses, however, do not display seals that block moisture flow (Eldridge and Rosentreter, 2003) and would presumably permit gas exchange, thus explaining the lack of bio-rich vesicular pores within moss-dominated crusts.

Thick Av horizons can form below tall pinnacle mounds because, during dry intervals, dust accumulates beneath the partially detached moss-lichen bio-rich zone (Fig. 7), similar to dust accretion below desert pavement clasts (McFadden et al., 1987; Anderson et al., 2002; Turk and Graham, 2011). Wetting and drying cycles cause ephemeral polygonal surface cracks to form around cohesive moss-lichen pinnacle mounds (Fig. 7) (Danin et al., 1998; Williams, 2011, p. 10–103), which act as entry points for dust. In these areas, surface rock cover is generally 20% or less, which is insufficient for thick, continuous dust layers (Goossens, 1995) to develop via desert pavement models (e.g., Anderson et al., 2002). Therefore, we propose a biologically mediated mechanism for mineral Av horizon formation, in which tall moss-lichen pinnacle mounds play a dominant role in dust accumulation and pedogenesis (Fig. 7). Mineral Av horizon accumulation below BSCs is a new step in the crust succession model that reflects prolonged surface stability (Fig. 6). The thickest Av horizon below pinnacle mounds was 15 cm thick, which, depending on local dust influx rates (e.g., Reheis, 2006), may require hundreds to thousands of years to form.
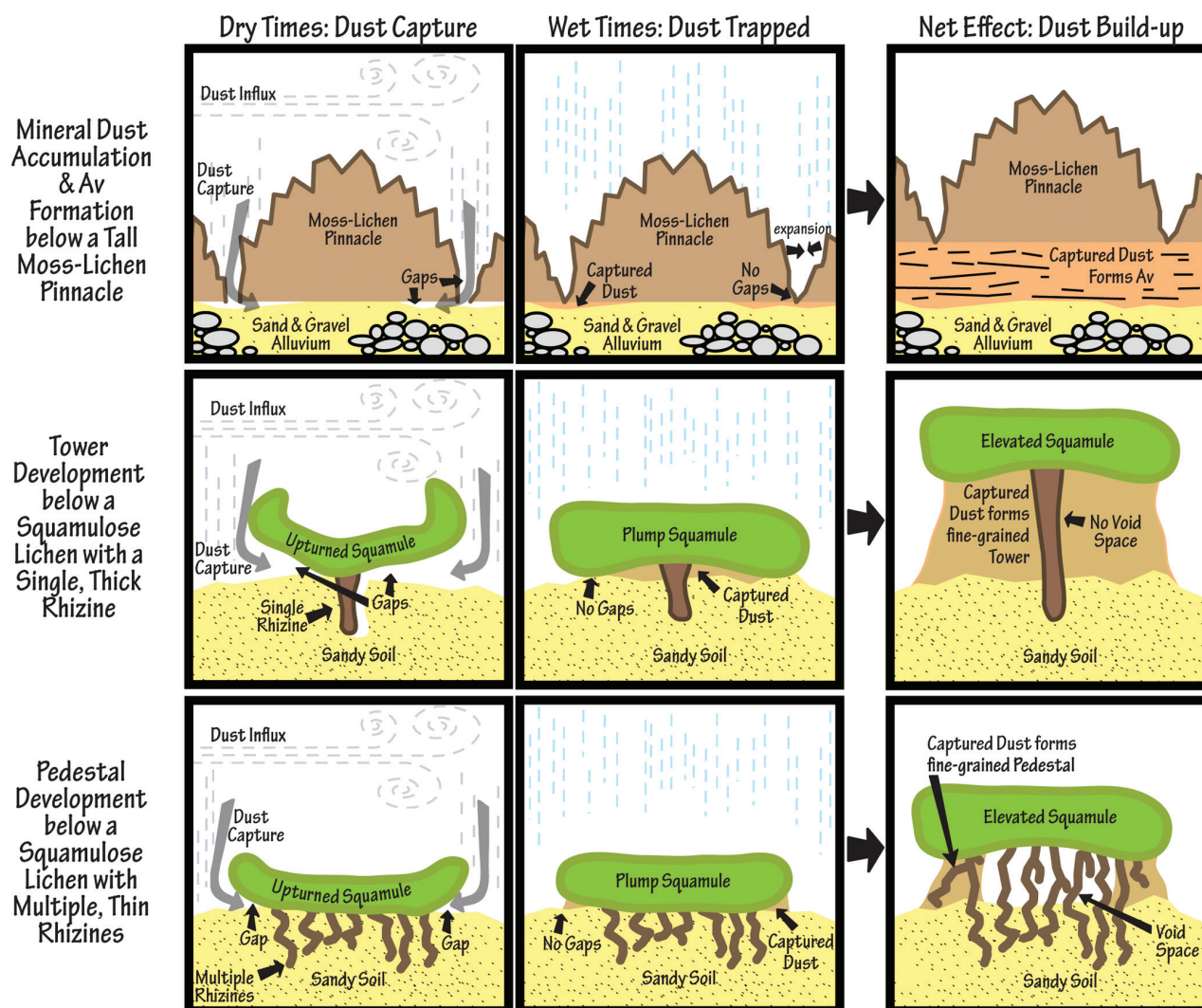


Fig. 7. Dust accretes during alternating wet–dry cycles. Bio-sedimentary features shrink and crack in dry times and subsequently expand on rehydration.

## Implications for Hydrology and Ecosystem Function

The microfeatures identified in this study help explain previous conflicting theories of BSC surface hydrology (Belnap, 2006). Some work has indicated that BSCs decrease infiltration and increase surface runoff (e.g., Eldridge et al., 2000; Yair, 1990), while others have suggested that crusts enhance infiltration and moisture availability (e.g., Eldridge and Rosentreter, 2003; Malam Issa et al., 2009). Our results show that surficial and internal structures vary as a function of BSC morphology and therefore could strongly influence water distribution before, during, and after precipitation events.

1. Many moss-lichen BSCs contain areas of dense, unconnected vesicular pores (Fig. 4B and 4C), which impede infiltration (e.g., Meadows et al., 2008) and could explain increased runoff and decreased infiltration rates associated with some moss-lichen BSCs (e.g., Eldridge et al., 2000).

2. Irregular macropores (Fig. 4B, 4D, and 5F) could enhance or decrease infiltration, depending on pore size and connectivity (Miralles-Mellado et al., 2011).

3. The irregular void space found between the bio-rich and bio-poor zones, especially where mineral Av horizons occur (Fig. 3), could potentially "perch" water, increasing surface moisture availability for crust organisms.

4. Surface crusting and pore clogging, as well as expansion caused during wetting, would decrease infiltration but provide surface seals for decreased evapotranspiration. Moreover, the increased dust-derived silt and clay content of the soil will increase the water-holding capacity.

5. Cracking along crust surfaces or between pinnacle mounds could increase infiltration locally (Danin et al., 1998), but these effects would vary as a function of rainfall timing, amount, and intensity (Meadows et al., 2008).

6. The rugose nature of BSC pinnacles potentially slows runoff (Fig. 1C), while smooth cyanobacterial crusts and associated surface seals may increase runoff (Fig. 1A) (Belnap, 2006; Kidron, 2007).

7. Laminae, formed by differences in particle size, compaction, or cementation (Fig. 4A, 4B, and 4F) would slow infiltration and induce horizontal overland flow.

The distribution of these surface features could control BSC impacts on water dynamics, with effects being highly localized and variable. Because most microstructures act to hold water near the soil surface, it is reasonable to suggest that BSCs can "engineer" bio-sedimentary structures, thus enhancing the availability of moisture in the upper millimeters of soil. This conceptual model for the genesis of these structures and their precise influence on hydrology should be tested experimentally and examined in other regions and geologic settings.

## CONCLUSIONS

Biological soil crusts should be considered crucial agents in arid pedogenesis and landscape development because they play unique roles in the accumulation, morphology, and ecosystem function of dust, thereby influencing nutrient influx, soil chemistry, surface microtopography, and Av horizon formation. Our new conceptual model from the Mojave Desert illustrates that BSC succession and buildup of moss-lichen pinnacle topography within this hot environment is not a static process but the result of a turbulent history driven by wet–dry cycles. Biological soil crust genetic processes, including (i) stabilization and authigenic mineral precipitation, (ii) wetting–drying and expansion–contraction, (iii) dust capture, and (iv) microscale mass wasting, simultaneously form biologically mediated Av horizons. Dust accumulation below moss-lichen pinnacled crusts volumetrically expands the fine-grained matrix of soil profiles, changing surface topography at the decimeter to meter scales (Williams, 2011, p. 104–219). Biological soil crust microfeatures, which vary as a function of crust morphology, enhance dust capture and form complex internal voids and vesicular pores (Fig. 6) that trap surface water for uptake by crust organisms. In turn, the resulting Av horizons of the bio-rich and bio-poor zones drive landscape-scale water distribution and subsurface soil processes (Turk and Graham, 2011). Increased water availability and nutrient influx enhance microbial activity and soil fertility, particularly within pinnacled crusts, which partially offsets nutrient disparities between shrub canopies and interspaces (Williams, 2011, p. 220–350). Therefore, moss-lichen crusts support ecosystem stability by supplementing soil resource availability during times of drought or biotic stress. Overall, these observations suggest that the restoration of BSCs and ecological function demands more than recolonization of crust organisms. Restoration also requires a process that reestablishes BSC bio-sedimentary structures and mineral dust-rich horizons, which probably occur on century to millennial time scales.

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