Geomorphology 195 (2013) 99–109

Contents lists available at SciVerse ScienceDirect

Geomorphology

journal homepage: www.elsevier.com/locate/geomorph

Geomorphic controls on biological soil crust distribution: A conceptual model from the Mojave Desert (USA)

Amanda J. Williams [a,b,*], Brenda J. Buck [a], Deborah A. Soukup [a], Douglas J. Merkler [c]

[a] Department of Geoscience, University of Nevada, Las Vegas, 4505 S. Maryland Parkway, Las Vegas, NV 89154-4010, USA
[b] School of Life Sciences, University of Nevada, Las Vegas, 4505 S. Maryland Parkway, Las Vegas, NV, 89154-4004, USA
[c] USDA-NRCS, 5820 South Pecos Rd., Bldg. A, Suite 400, Las Vegas, NV 89120, USA

ARTICLE INFO

Article history:
Received 30 November 2012
Received in revised form 17 April 2013
Accepted 18 April 2013
Available online 1 May 2013

Keywords:
Biological soil crust
Soil-geomorphology
Pedogenesis
Vesicular (Av) horizon
Ecology
Biogeomorphology

ABSTRACT

Biological soil crusts (BSCs) are bio-sedimentary features that play critical geomorphic and ecological roles in arid environments. Extensive mapping, surface characterization, GIS overlays, and statistical analyses explored relationships among BSCs, geomorphology, and soil characteristics in a portion of the Mojave Desert (USA). These results were used to develop a conceptual model that explains the spatial distribution of BSCs. In this model, geologic and geomorphic processes control the ratio of fine sand to rocks, which constrains the development of three surface cover types and biogeomorphic feedbacks across intermontane basins. (1) Cyanobacteria crusts grow where abundant fine sand and negligible rocks form saltating sand sheets. Cyanobacteria facilitate moderate sand sheet activity that reduces growth potential of mosses and lichens. (2) Extensive tall moss–lichen pinnacled crusts are favored on early to late Holocene surfaces composed of mixed rock and fine sand. Moss–lichen crusts induce a dust capture feedback mechanism that promotes further crust propagation and forms biologically-mediated vesicular (Av) horizons. The presence of thick biogenic vesicular horizons supports the interpretation that BSCs are long-lived surface features. (3) Low to moderate density moss–lichen crusts grow on early Holocene and older geomorphic surfaces that display high rock cover and negligible surficial fine sand. Desert pavement processes and abiotic vesicular horizon formation dominate these surfaces and minimize bioturbation potential. The biogeomorphic interactions that sustain these three surface cover trajectories support unique biological communities and soil conditions, thereby sustaining ecological stability. The proposed conceptual model helps predict BSC distribution within intermontane basins to identify biologically sensitive areas, set reference conditions for ecological restoration, and potentially enhance arid landscape models, as scientists address impacts of climate change and anthropogenic disturbances.

1. Introduction

Biological soil crusts (BSCs) are complex matrices of soil particles, cyanobacteria, lichens, mosses, algae, microfungi, and bacteria (Friedmann and Galun, 1974; Belnap and Gardner, 1993; Williams et al., 2012). BSCs provide crucial soil cover in arid and semi-arid landscapes. Biotic structures grow around surface sediments, fusing into a desert skin that mitigates erosion (McKenna Neuman et al., 1996) and provides ecosystem services including soil nutrient inputs (Kleiner and Harper, 1977; Evans and Belnap, 1999), regulation of soil moisture and temperature (Belnap, 1995, 2006), enhancement of landscape stability (Canton et al., 2003; Thomas and Dougill, 2007), and interactions with vascular plant communities (DeFalco et al., 2001; Escudero et al., 2007). The ecological impacts of BSCs are potentially enormous, as crusts can comprise up to 70 percent of the living soil cover in arid landscapes (Belnap, 1994), and commonly fill shrub interspaces, which are the exposed surfaces between vascular plants.

BSCs vary widely in biotic composition and surface morphology (Fig. 1). Smooth, early succession crusts are dominated by filamentous cyanobacteria (Fig. 1B) (Belnap, 2001). Once soils are stabilized, mosses and lichens colonize the surface with cyanobacteria to form short moss–lichen crusts with rolling surface morphologies and less than 2 cm of vertical relief (Fig. 1E) (Belnap, 2001; Williams et al., 2012). Eventually, tall moss–lichen pinnacled crusts develop, which display rougher surfaces and up to 5 cm of vertical relief (Fig. 1D) (Williams et al., 2012).

A number of models have been developed to predict the distribution of crust types throughout many of the world's arid and semi-arid regions (Eldridge and Greene, 1994; Kidron et al., 2000; Ponzetti and McCune, 2001; Belnap et al., 2006; Bowker et al., 2006; Thomas and Dougill, 2006; Bowker, 2007; Bowker and Belnap, 2008; Rivera-Aguilar

Abbreviations: BSCs, biological soil crusts; OHVs, off-highway vehicles; MRPP, multi-response permutation procedures.

* Corresponding author at: School of Life Sciences, University of Nevada, Las Vegas, 4505 S. Maryland Parkway, Las Vegas, NV, 89154-4004, USA. Tel.: +1 702 895 0809; fax: +1 702 895 3956.
E-mail address: mandy.williams@unlv.edu (A.J. Williams).

0169-555X/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.geomorph.2013.04.031

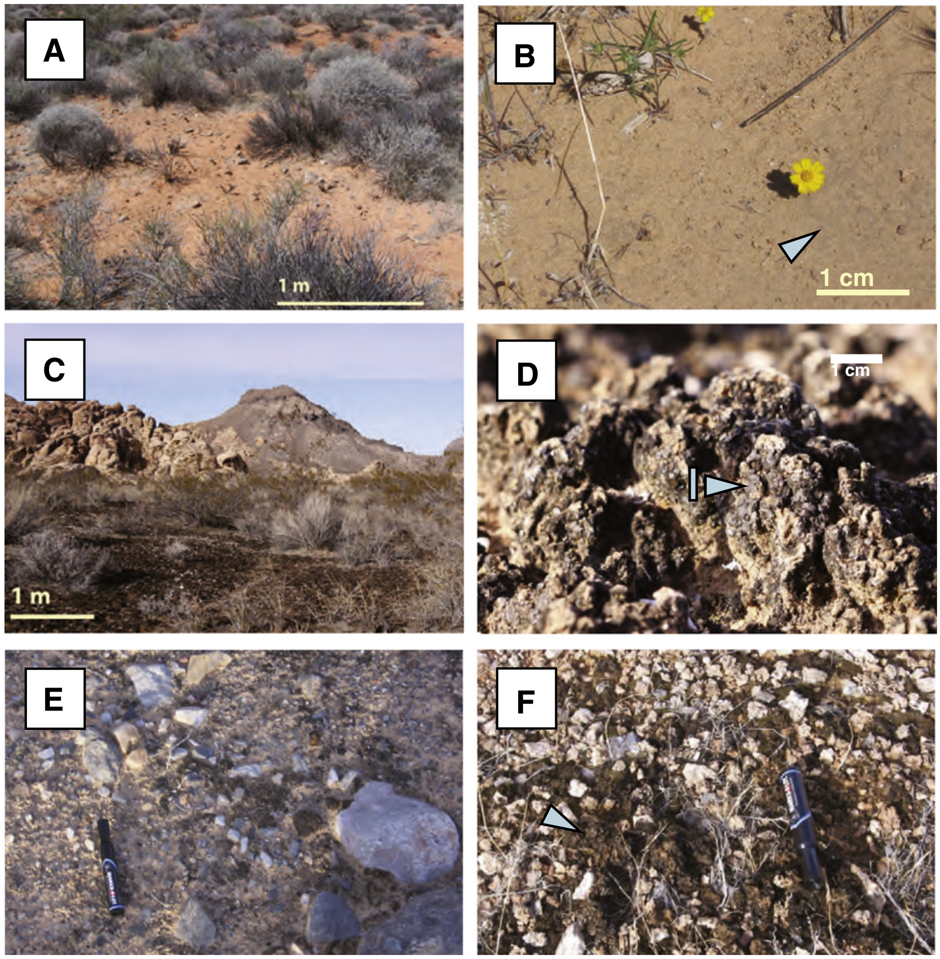


Fig. 1. (A) High density cyanobacteria-bare crusts (BSC map unit CB.1). (B) Cyanobacteria crusts display slightly darkened surfaces (arrow). (C) High density, tall moss–lichen pinnacled crusts (BSC map unit ML.1). (D) Squamulose lichens (l) dominate a tall pinnacle. (E) Moderate density, short moss–lichen crusts (BSC map unit CB.2, marker for scale). (F) Scattered, moderate density tall moss–lichen pinnacled crusts (BSC map unit S.2, marker for scale). See Tables 1and S2 for BSC map unit descriptions. (Images adapted from Williams et al., 2012.)

et al., 2009). To date, however, no predictive models exist for Mojave Desert crusts, and only a few studies from any environment have considered the interaction of BSCs with geomorphic or physical soil-forming processes that could strongly influence crust establishment and propagation (Brostoff, 2002; Thomas and Dougill, 2007; Wang et al., 2007; Bowker and Belnap, 2008; Lazaro et al., 2008; Li et al., 2010). For example, surface stability (Bowker and Belnap, 2008; Rivera-Aguilar et al., 2009), topography (Lazaro et al., 2008; Li et al., 2010), rock cover (Kaltenecker et al., 1999; Quade, 2001), soil texture and mineralogy (Bowker and Belnap, 2008; Rivera-Aguilar et al., 2009), and hydrological dynamics (Kidron et al., 2000; Bowker et al., 2010) are key factors influencing BSC distribution and species composition. These factors commonly vary as a function of soil-geomorphology, particularly within the intermontane basins of the Mojave Desert (Peterson, 1981; Young et al., 2004; Soil Survey Staff, 2007; Robins et al., 2009).

The objectives of this study were (1) to investigate the relationships among geomorphology, soil characteristics, and BSC distribution in the Mojave Desert; (2) to understand the landscape feedback mechanisms that control geomorphic stability, pedogenesis, and BSC development within the region; and (3) to use soil-geomorphic relationships to predict BSC distribution for land management applications.

2. Background and geologic setting

The study site lies within the Hidden Valley Area of Critical Environmental Concern, inside the Muddy Mountains Wilderness in the Mojave Desert of southern Nevada, USA (Fig. 2) at 36°20′N and 114°42′W. The area is ideal for studying BSC-soil-geomorphic interactions as the valley contains well-developed and variable BSCs, numerous geomorphic surfaces, and common Mojave Desert soil types and plant communities (Soil Survey Staff, 2007). Mean annual temperature is 27 °C, and mean annual precipitation is 114 mm (Gorelow and Skrbac, 2005). Precipitation is greatest from January to March when average highs range from 14 to 21 °C, but precipitation also occurs from July to August, when average highs are 39–40 °C (Gorelow and Skrbac, 2005).

Hidden Valley is a semi-enclosed basin that displays typical intermontane basin geomorphology (Peterson, 1981). The valley lies at 1000 m elevation and is surrounded by mountains comprised of carbonate and sandstone bedrock that rise up to 1642 m. These mountains formed during Sevier-age thrusting when Paleozoic carbonates were thrust eastward over younger Jurassic Aztec Sandstone along the Muddy Mountain Thrust Fault (Beard et al., 2007). Erosion of the upper plate of the thrust created a structural window that now exposes the underlying sandstone bedrock across the valley floor.

Off-highway vehicles (OHVs) have been prohibited since the area was designated a Federal Wilderness in 2002. Hidden Valley was previously grazed, but the trampling effects of livestock on the area's BSCs are unknown. Despite apparent disturbance to the area, Hidden Valley's crusts have remained relatively pristine compared to other Mojave Desert locations. As Hidden Valley becomes increasingly popular to sightseers in the Las Vegas metropolitan area, off-trail foot traffic and illegal OHV use are becoming significant management concerns.

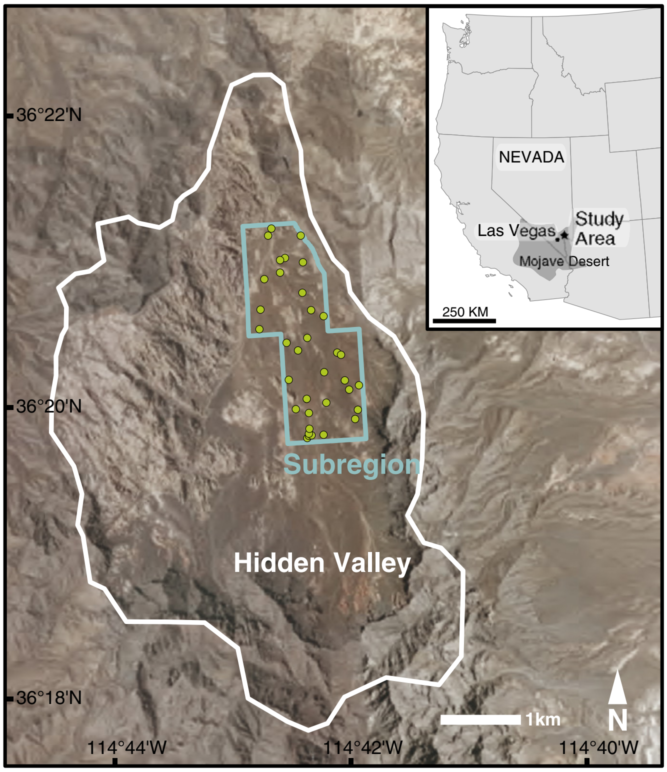


Fig. 2. The study area lies within the Hidden Valley portion (white) of the Muddy Mountains Wilderness Area, Nevada, U.S.A. Sampling locations (green), geomorphic mapping, and detailed site characterization were completed within the 2.8 km^2 sub-region (aqua).

3. Methods

3.1. Mapping

Two original maps were created to delineate (1) BSCs and (2) geomorphology within the study area. First, base imagery was examined for differences in surface tones, which became the initial polygon lines of the two maps. Base imagery data used for the BSC and geomorphic maps were Quickbird® panchromatic/multispectral satellite imagery and NAIP aerial photos, respectively. Extensive field reconnaissance verified line accuracy and classified individual polygons. Map units were digitized in ESRI ArcGIS 9.3 Desktop and Manifold GIS at a scale of 1:6500. The BSC map delineated interspace cover by the three crust morphological types (Fig. 1) throughout the Hidden Valley basin. The geomorphic map, covering a 2.8 km^2 sub-region of the valley, delineated distinct geomorphic surfaces defined according to depositional environment and relative age.

3.2. Site characterization

During June 2007 and January–February 2008, surface characterization and sampling were completed within thirty-six 12 m-diameter circular plots that were randomly selected from the 2.8 km^2 sub-region of Hidden Valley (Fig. 2). At least three locations were chosen from each BSC unit, which corresponded to one or more geomorphic units. Line intercept data, point count data, and additional site observations were collected from each plot. Line intercepts were established along two perpendicular transects that bisected each plot. Vascular plant canopies were recorded along these transects to the nearest cm. Point data, collected with a 25 × 25 cm square grid with 25 evenly spaced points (Belnap et al., 2001), were used to quantify interspace surface cover. The grid was randomly tossed within the boundaries of each plot, and a minimum of 150 grid points were collected. Points were recorded as one of the following: cyanobacteria crust, moss, *Collema*, *Placidium*, *Peltula*, bare soil, limestone clast, sandstone clast, petrocalcic clast, exotic grass litter, or non-grass plant litter. Additional site observations included hillslope position, slope complexity, and morphology of surface clasts.

Geomorphic surface units were further assessed with respect to depositional environment, topography, and relative age as determined by cross-cutting relationships (Christenson and Purcell, 1985; Bull, 1991). Soil profile descriptions (Schoeneberger et al., 2002) were completed for each geomorphic map unit but were limited to arroyo exposures and erosional outcrops because of wilderness area restrictions. Because of logistical constraints, no absolute age dating of the geomorphic surfaces by isotopic, cosmogenic, or luminescence methods was completed. Ages were instead estimated using landform type (Peterson, 1981), soil surface morphology, desert pavement development (McFadden et al., 1987; Wells et al., 1987), and stage of pedogenic carbonate accumulation (Gile et al., 1966; Bachman and Machette, 1977; Machette, 1985) and correlated to other local and regional soil-geomorphic investigations (Sowers et al., 1989; Bull, 1991; Harden et al., 1991; Reheis et al., 1992; Peterson et al., 1995; Bell et al., 1998; Bell and Ramelli, 1999; Brock and Buck, 2005; Page et al., 2005; Brock and Buck, 2009; House et al., 2010). Geomorphic units were named according to conventional alphanumeric nomenclature (House et al., 2010).

Within each plot, a composite soil sample from ≥6 random locations was collected from the upper 0–3 cm of soil interspaces using a flat, stainless steel scoop. The composite samples were transported in plastic bags to the UNLV Environmental Soil Analysis Laboratory (ESAL), where they were air-dried, sieved to 2 mm, and analyzed for texture using the Malvern Mastersizer 2000 grain size analyzer (Malvern Instruments Ltd., Malvern, UK). To verify the accuracy of the Mastersizer particle size data, five samples were analyzed by the hydrometer and pipette methods (Dane and Topp, 2002; Burt, 2004). Particle size distributions from these three methods yielded similar results, which validated the use of Mastersizer data for soil texture interpretations. Additionally, laser diffraction has been shown to be an exceptionally accurate method for particle size analyses (e.g. Goossens, 2008). No effort was made to remove BSC material from the mineral soil because micromorphological investigations have shown that clay and silt-sized particles adhere to microbial structures (Williams et al., 2012), and techniques used to eliminate organic tissues can dissolve soluble minerals, which are an important component of the mineral fabric in arid soils (Buck et al., 2011). Therefore, the removal of soluble minerals and organic materials would likely create greater errors in grain size analyses than leaving these materials intact.

3.3. Spatial and statistical analyses

The geomorphic map was overlain with the BSC map to determine percent overlap between map units (House, 2005). First, the two maps were merged using the "Clip with Intersect" tool in ESRI ArcGIS 9.3 Desktop. Overlay data were exported into a digital spreadsheet and percent compositions of map unit areas were calculated.

Multi-response permutation procedures (MRPP) tested differences in soil surface cover among BSC map units and geomorphic map units using Sørensen (Bray–Curtis) distance measures (PC-ORD, MjM Software Design). Similar to MANOVA, MRPP tests for compositional differences among groups but requires no distributional assumptions (McCune and Grace, 2002). Groups having less than 2 plots were removed from the analyses.

Kruskal–Wallis H Tests with post-hoc Mann–Whitney U Tests were used as a non-parametric alternative to ANOVAs to test differences in surface cover and soil texture among 4 geomorphic groups. Units were grouped according to similar characteristics as follows: (1) early to late Holocene Qay$_1$ and Qay$_2$ inset fans (2) Qea sand sheets, (3) Pleistocene Qai inset fans, and (4) earliest to early Pleistocene

Qao_1 and Qao_2 erosional fan remnants (nomenclature from House et al., 2010). In addition, non-parametric Spearman's rank order correlations, or rho values, were used to quantify relationships among surface cover types and texture. All univariate and bivariate analyses were calculated at the 0.05 significance level.

4. Results

4.1. Mapping and characterization

The BSC map was comprised of three primary map unit classes, including high density cyanobacteria-bare units (CB), high density tall moss–lichen units (ML), and scattered tall moss–lichen units (S) (Table 1, Table S1). (Note: the cyanobacteria-bare designation is used because crusts formed by filamentous cyanobacteria commonly occur in conjunction with bare soil.) Primary map unit classes were further divided into 10 sub-classes that varied as a function of mean interspace cover by crust organisms and microtopography (Table 1, Table S1). In these units, *Microcoleus* was the dominant cyanobacterium, while component moss and lichen taxa included *Syntrichia caninervis*, *Bryum*, *Pterygoneurum*, *Collema*, *Placidium*, *Psora decipiens*, and *Peltula*. In addition to distinct differences in biotic composition (Table 1), BSC units varied with respect to rock cover and soil surface characteristics (Table S1).

The geomorphic map included 12 units (Figs. 3, 4, Table S2), with estimated ages ranging from recent Holocene to earliest Pleistocene. Clasts were primarily composed of locally-derived outcrops of limestone, and to a lesser extent, sandstone. Eolian fine sand was also largely derived from the nearby outcrops of Aztec Sandstone and commonly incorporated into gravelly alluvium. Geomorphic units varied with respect to profile particle size distribution, bar-and-swale morphology, carbonate morphological stage (Gile et al., 1966; Bachman and Machette, 1977; Machette, 1985), interspace rock cover or desert pavement morphology, and vesicular (Av) horizon thickness (Figs. 3, 4). Colluvium, Qc, was highly variable within the field area and not thoroughly characterized due to a lack of soil profile exposures. The 12 geomorphic units corresponded to eight soil types, including four USDA Official Soil Series (Williams, 2011a). See BSC and geomorphic maps in Figs. S1 and S2 and detailed unit descriptions in Tables S1 and S2.

4.2. GIS and statistical analyses

GIS overlays between the three BSC map unit classes and the three primary groups of geomorphic surfaces revealed important relationships between geomorphic position and BSC distribution (Table 2). The cyanobacteria-bare BSC unit CB.1 overlapped 66% with Qea deep Holocene sand sheets. BSC units ML.1 and ML.2, which displayed high density tall moss–lichen crusts, overlapped 57–59% with early to late Holocene alluvial surfaces Qay_1–Qay_2. Scattered low to moderate density tall moss–lichen crusts (BSC units S.1, S.2, S.3), which commonly occurred with some form of desert pavement, overlapped 63–87% with Pleistocene Qao–Qai alluvial surfaces. Despite these patterns, BSC map units displayed some complicated overlapping relationships with geomorphic surfaces (Williams, 2011a). For example, while ML.1 and ML.2 primarily occurred along early to late Holocene surfaces, these BSC units comprised only 25–33% of the total area those surfaces. Early to latest Holocene alluvial surfaces, Qay_1–Qay_2–Qay_3, also displayed 13–37% cover by cyanobacteria-bare units CB.1 and CB.2. Moss–lichen units ML.1 and ML.2 overlapped 12–37% with Qea Holocene sand sheets.

Results from MRPP indicated that BSC and geomorphic map units effectively differentiated between different types of soil interspace cover. MRPP results are reported as association values (A) of 0 to 1, where $A > 0.3$ is considered to be high for ecological data sets (McCune and Grace, 2002). BSC units yielded $A = 0.52$ ($p < .00001$), while geomorphic units had $A = 0.35$ ($p < .00001$).

Kruskal–Wallis H Tests indicated several statistically significant differences ($p \leq .05$) in interspace characteristics among geomorphic surface groups. Cover by mosses, *Collema* lichens, *Placidium* lichens, and total mosses–lichens were significantly elevated along early to late Holocene Qay_1–Qay_2 surfaces. Total rock cover was elevated along Pleistocene Qai surfaces. Petrocalcic clast cover and total rock cover were elevated along earliest to early Pleistocene Qao_1–Qao_2 erosional fan remnants. Total percent sand was elevated in early to late Holocene Qay_1–Qay_2 inset fans and Qea sand sheets, while percent clay and percent silt were elevated in the Pleistocene Qai surfaces.

Non-parametric correlation coefficients indicated strong, statistically significant relationships among soil interspace characteristics (Table S3). In general, moss and lichen taxa were positively correlated to one another and negatively correlated to bare soil and rock cover. Soil texture was strongly associated with surface cover types. *Placidium* lichens were negatively correlated to percent fine sand and positively correlated to percent silt and percent very fine sand, while mosses were negatively related to percent clay content. Rock cover was positively correlated to percent silt but negatively to most sand fractions and bare soil. Bare soil cover was negatively correlated with percent silt and percent very fine sand, and positively correlated to other sand fractions.

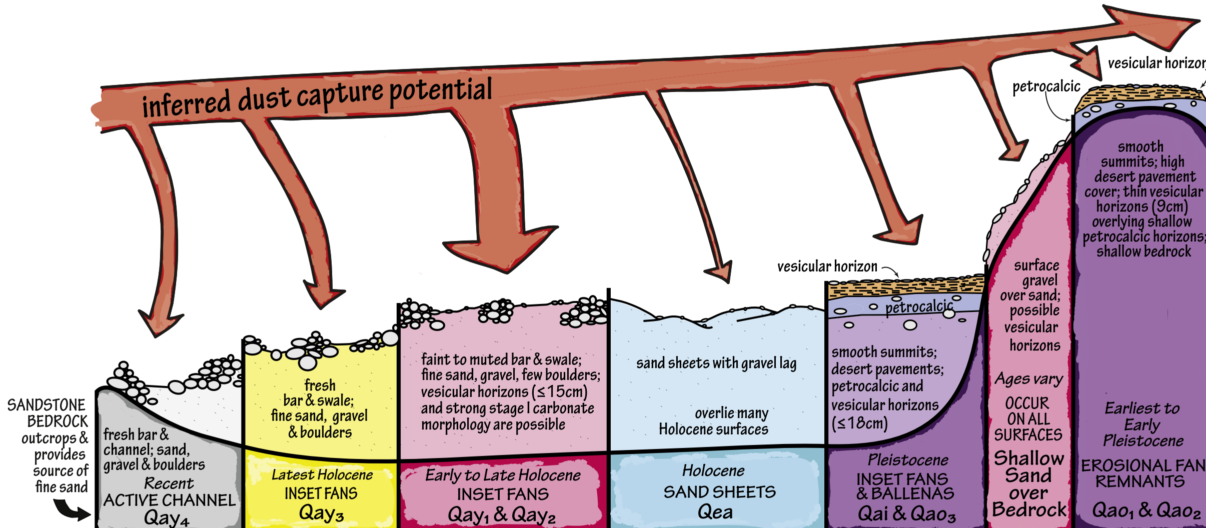
5. Interpretations and discussion

5.1. Conceptual models of BSCs and soil-geomorphic factors

The data from this study were used to develop a conceptual model for BSC development and distribution across Mojave Desert landscapes. The data show a strong correlation between individual geomorphic surfaces and BSC characteristics (Table 2). Detailed examination of geomorphic surface characteristics and soil profile morphology suggest that the underlying commonality among crust types is the relative particle size distribution of the soil profile (Fig. 3). As we propose in our model and describe below, the ratio of fine sand to rocks controls

Table 1
Surface cover summary of BSC map units.

BSC map units	Mean interspace cover		
	Moss–lichen	Cyanobacteria-bare	Rock
CB.1: High density cyanobacteria-bare crusts	2%	68%	18%
CB.2: High density cyanobacteria-bare crusts, low to moderate density short moss–lichen crusts	10%	64%	20%
CB.3: Variable density cyanobacteria-bare crusts, variable density short moss–lichen crusts	9%	45%	46%
ML.1: High density tall moss–lichen pinnacled crusts, moderate density cyanobacteria-bare crusts	52%	26%	10%
ML.2: Moderately-high density tall moss–lichen pinnacled crusts, low to moderate density cyanobacteria-bare crusts	42%	11%	26%
ML.3: High density tall moss–lichen pinnacled crusts, low to moderate density cyanobacteria-bare crusts	51%	15%	27%
S.1: Scattered, moderate density tall moss–lichen pinnacled crusts, low to moderate density cyanobacteria-bare crusts	16%	17%	57%
S.2: Scattered, moderate density tall moss–lichen pinnacled crusts, moderate density cyanobacteria-bare crusts	16%	29%	36%
S.3: Scattered, low to moderate density tall moss–lichen pinnacled crusts, low to moderate density cyanobacteria-bare crusts	13%	11%	72%
S.4: Scattered, low density tall moss–lichen pinnacled crusts, low density cyanobacteria-bare crusts	8%	6%	83%



Mean Interspace Surface Cover	No Crusts No Desert Pavement	46% Gravel 45% Cyanobacteria-Bare 9% Short Moss-Lichen	43% Tall Moss-Lichen 18% Cyanobacteria-Bare 22% Desert Pavement	48% Cyanobacteria-Bare 30% Gravel Lag 10% Short Moss-Lichen	42-63% Desert Pavement 17-23% Moss-Lichen 17-22% Cyanobacteria -Bare	Moss-Lichen or Cyano-bacteria	60% Desert Pavement 23% Moss-Lichen 14% Cyanobacteria -Bare
Stability	Very Low Stability	Low Stability	Moderate to High Stability	Low Stability	High Stability	Variable Stability	High Stability
Roughness	High Surface Roughness	High Surface Roughness	High Surface Roughness	Low Surface Roughness	Low Surface Roughness	Moderate Surface Roughness	Low Surface Roughness
Profile Particle Size	Fine Sand or Mixed Fine Sand & Gravel	Fine Sand or Mixed Fine Sand & Gravel	Mixed Fine Sand & Gravel	Fine Sand	Loam or Mixed Loam & Gravel	Fine Sand or Mixed Sand & Gravel	Loam or Mixed Loam & Gravel

Fig. 3. Surface and profile characteristics of geomorphic units. Shading represents the dominance of cyanobacteria crusts (blue), short moss–lichen crusts (yellow), tall moss–lichen crusts (pink) and desert pavement with scattered moss–lichen crusts (purple). Dust capture potential (proportional to width of red arrows) is inferred from relative surface roughness and stability.

the stability, surface roughness, and morphology of fine-grained matrices of arid soil surfaces, thereby constraining the development of (1) cyanobacteria crusts, (2) tall moss–lichen pinnacled crusts, and (3) desert pavements with scattered BSCs (Fig. 5). The data further suggest geomorphic processes determine relative elevation and proximity to sand sources, regulating the fine sand-to-rock ratio and surface cover types across intermontane basins (Fig. 6). While geological processes determine sand influx, our model illustrates how biogeomorphic interactions drive feedback mechanisms that sustain surface cover trajectories.

5.2. Cyanobacterial trajectories and feedbacks

Extensive sand sheets composed of fine sand provide ideal substrates for growth and propagation of terrestrial filamentous cyanobacteria. Studies from terrestrial and marine siliciclastic systems indicate fine sands are the optimal size for filamentous cyanobacteria growth (Bowker and Belnap, 2008) and motility (Noffke et al., 2002). Previous studies have also suggested that surfaces of fine sand, such as sand sheets or dunes, favor filamentous cyanobacteria propagation (McKenna Neuman et al., 1996; Kidron et al., 2000; Belnap, 2001; Wang et al., 2007; Bowker and Belnap, 2008). Therefore, understanding the thickness and spatial distribution of fine sand sheets or dunes is critical to predicting cyanobacteria growth across the landscape.

Geological and geomorphic processes control where fine sands occur, and thus, where cyanobacteria are most extensive. The Mojave Desert is a weathering-limited environment (Bull, 1991), in which the dominant bedrock types, limestone, dolomite, and various volcanic rocks, weather into gravel or boulders. Fine sands are uncommon and primarily found in sand sheets derived from sandstone bedrock or from arroyos and playa margins (Fig. 6) (Peterson, 1981; Soil Survey Staff, 2007; House et al., 2010). Sand blown up out of these active arroyos or playa margins most commonly accumulates as sheets on nearby young, topographically low, geomorphic surfaces. Consequently, older, elevated surfaces generally receive significantly less sand input; however, localized exceptions can occur under specific circumstances (see Tek unit in House et al., 2010). In this study, 66% of the cyanobacteria-bare unit (CB.1) occurred along Holocene sand sheets (Qea), which were found in active arroyos and/or near sandstone bedrock outcrops and covered many low-lying, early Holocene and younger alluvial surfaces (Fig. 3, Table 2). The Mojave Desert's deficiency in fine sand contrasts with the Colorado Plateau Desert, which has abundant sandstone bedrock and widespread sand sheets. These observations may further explain the ubiquity of BSCs within southern Utah and northern Arizona (USA) (e.g., Bowker and Belnap, 2008) as compared to other arid regions that receive less fine sand input and display fewer soil crusts.

A positive feedback exists between cyanobacteria and active or saltating sand. Filamentous cyanobacteria are motile and capable of moving to reclaim soil surfaces after burial by a thin layer of sand (Belnap and Gardner, 1993; Garcia-Pichel and Pringault, 2001). If sand sheet activity is high, however, cyanobacteria may become too deeply buried to reach the soil surface. Here, we define sand sheet activity as the saltation and transport of sand, which leads to deflation of sand in some areas and deposition of sand grains in other locations. Our observations suggest moderately stable fine sands are optimal for filamentous cyanobacteria propagation, similar to observations in marine siliciclastic environments (Noffke et al., 2002). In these conditions, cyanobacteria bind sand grains (Belnap and Gardner, 1993; Issa et al., 1999) and form surface crusts through fine-grained dust accretion and facilitation of calcium carbonate precipitation (Campbell, 1979; McKenna Neuman and Maxwell, 2002; Williams et al., 2012). While cyanobacteria stabilize sand sheets sufficiently for their own growth, they permit moderate sand saltation, which is generally too

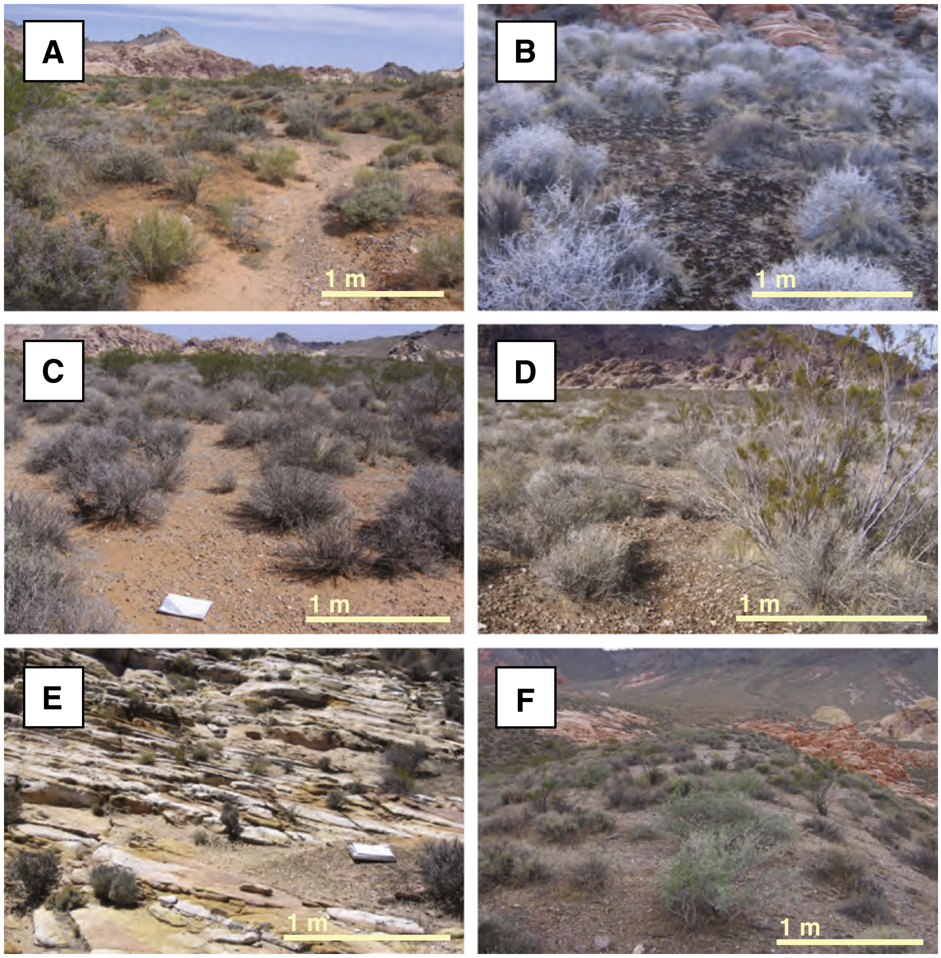


Fig. 4. (A) Latest Holocene inset fan (Qay3). (B) Early to mid-Holocene inset fan (Qay1). (C) Holocene sand sheet (Qea). (D) Early Pleistocene ballena (Qao3). (E) Shallow sand over bedrock. (F) Early Pleistocene erosional fan remnant (Qao2) (nomenclature from House et al., 2010).

unstable for moss–lichen crust or desert pavement development. These biogeomorphic interactions create a self-enhancing feedback that favors cyanobacteria propagation and facilitates persistence of sand sheet activity in the absence of climate change or other extrinsic perturbations.

5.3. Moss–lichen trajectories and feedbacks

Mosses and lichens are relatively non-motile and require stable, fine-grained substrates for initial colonization (McKenna Neuman et al., 1996; Belnap, 2001). Crust propagation is further enhanced in areas where high surface roughness increases moss–lichen dust accretion potential. Geomorphic stability, in this case sand sheet activity, varies with climate and surface age. Sandy soils of cooler or wetter deserts, such as the Colorado Plateau, have lower sand sheet activity than hot deserts like the Mojave because increased water availability reduces sand saltation and supports greater vascular plant cover and higher cyanobacteria biomass (Belnap et al., 2007). Therefore, stabilized sand sheets of the Colorado Plateau commonly support extensive moss and lichen growth (e.g., Bowker and Belnap, 2008). While cyanobacteria also augment stability of fine-grained surfaces in the dry Mojave Desert, a climatic or textural change is commonly needed to adequately stabilize sand-dominated surfaces, so that mosses and lichens can initiate colonization. Under current Mojave Desert climatic conditions, surfaces of mixed rock and fine sand provide the optimal balance of stability, fine-grained surface availability, and surface roughness for moss and lichen propagation (Fig. 5). In this study, these characteristics were best expressed on early to late Holocene inset fans (Qay_1–Qay_2), which contained 57–59% of the extensive tall moss–lichen map units ML.1 and ML.2 (Fig. 3, Table 2). Along these surfaces, cyanobacteria stabilize the fine sands that infill gravel clasts, while rock fragments limit sand saltation such that mosses and lichens can colonize exposed fine-grained substrates. Rock fragments embedded in the soil profile provide effective stability, whereas non-embedded gravel lags can shift with raindrop impact (Herrick et al., 2010) and sand saltation, permitting continued sand sheet activity (Buck et al., 2002). Our observations suggest that, at our study site, ≥35% rock fragments by volume within the upper decimeters of the soil profile provides the optimal mix of embedded rocks and fine sand for extensive

Table 2
Summary of GIS overlay.

Crust cover	Dominant geomorphic surface (% Overlap)
Cyanobacteria-bare crusts BSC map unit CB.1	Qea (66%) *Deep Holocene sand sheets*
High density tall moss–lichen crusts BSC map units ML.1 & ML.2	Qay_1 & Qay_2 (57–59%) *Alluvium (Early to Late Holocene)*
Scattered low to moderate density tall moss–lichen crusts ("desert pavement") BSC map units *S.1, S.2, & S.3	Qai_3 & Older (63–87%) *Alluvium (Pleistocene)*

* Units S.1, S.2, and S.3 commonly included "desert pavement" or pavement-like rock cover.

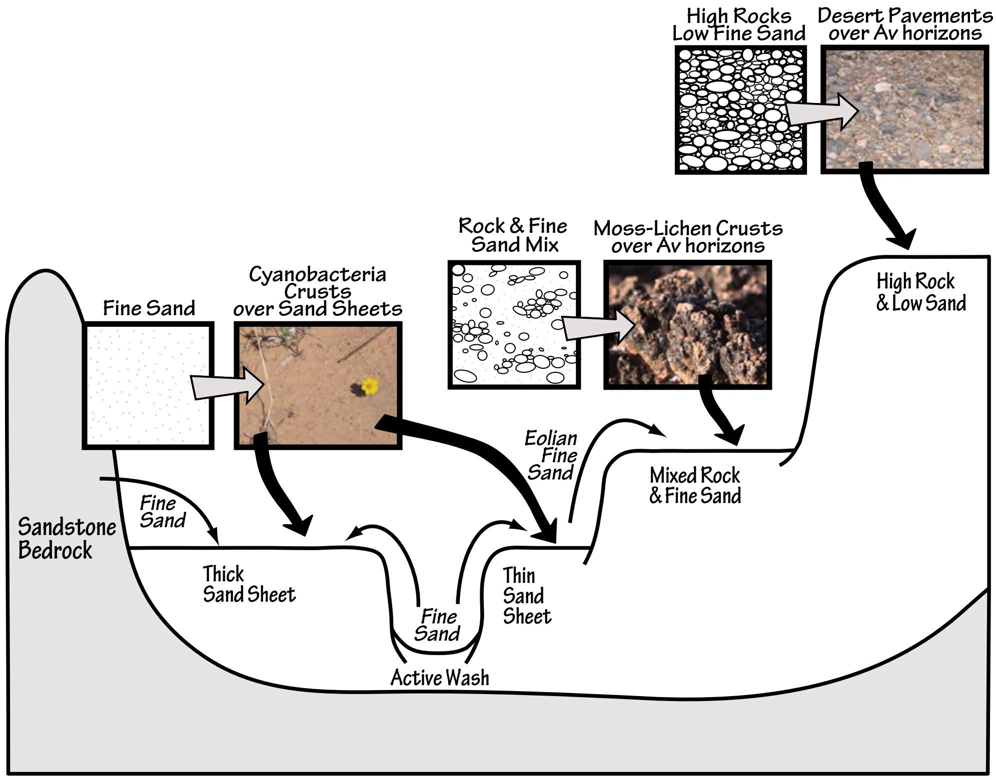


Fig. 5. Geomorphic processes and proximity to sand sources control soil profile particle size, which ultimately determines surface cover trajectories. Geomorphic surfaces adjacent to sandstone bedrock outcrops or active washes receive high influx of fine sand, forming sand sheets that facilitate colonization of cyanobacteria crusts. Stable surfaces that lie 1–2 m topographically higher than adjacent sand sheets, receive a moderate amount of fine sand, which produces profiles composed of fine sand and ≥35% rock fragments. These surfaces of mixed rock and fine sand lead to moss–lichen pinnacled crust development over biologically-mediated vesicular horizons. Older surfaces, which lie several meters above sand sheets, receive a negligible amount of fine sand, forming gravel-dominated surfaces that lead to desert pavement formation over loamy vesicular horizons.

moss–lichen propagation (Williams, 2011a). Embedded rocks from abandoned gravel bars, as found along younger surfaces that retain their bar and swale morphology, increase surface roughness, which helps capture dust (McFadden et al., 1986; Wells et al., 1987). Accreted dust provides new fine-grained substrates for mosses and lichens (Williams et al., 2012).

At a landscape scale, early to late Holocene surfaces composed of mixed rock and fine sand represent the most likely areas where

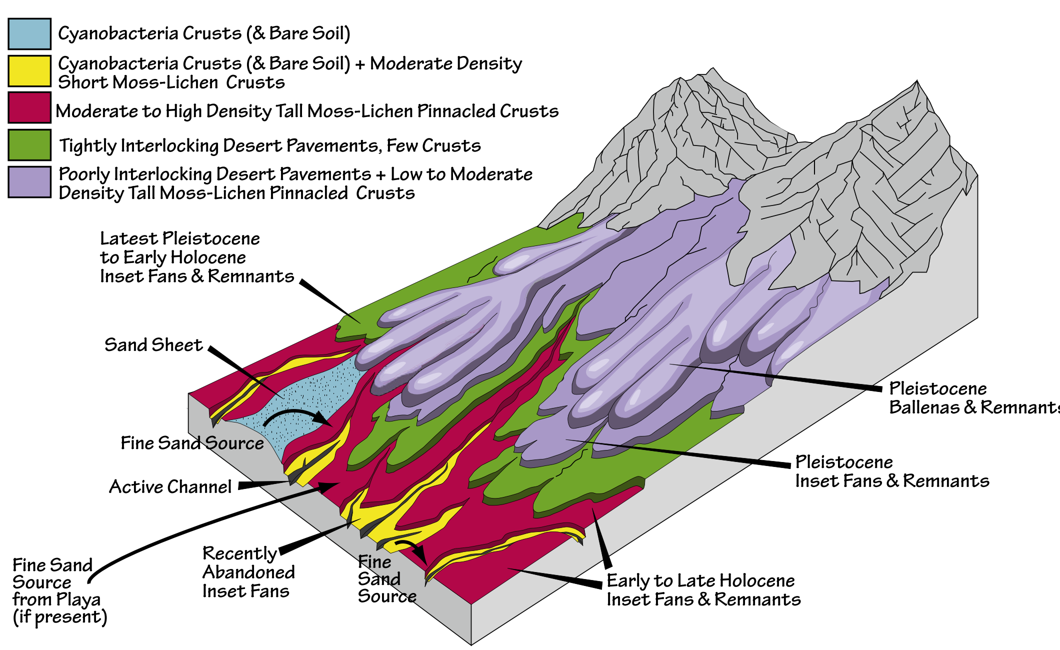


Fig. 6. Geomorphic surfaces predict interspace cover by BSCs and desert pavements. Fine sand sources include sand sheets, active channels, and alluvial flats or playas (not shown). Block model adapted after Peterson (1981).

extensive, tall moss–lichen pinnacled crusts can be found, but the presence of these surfaces does not guarantee extensive moss–lichen cover. Because these surfaces lie low in the landscape near sand sources, sand influx may be too high, effectively preventing extensive moss and lichen growth. In fact, while the most extensive moss–lichen crusts (ML.1 and ML.2) in this study occurred along early to late Holocene surfaces, extensive moss–lichen map units comprised only 25–33% of the total surface area of these landforms. Therefore, this proposed landscape model of BSC distribution (Fig. 6) should be calibrated for local fine sand influx. If an area lacks sandstone bedrock, most surficial fine sand will be confined to active channels, recently abandoned inset fans, fan skirts, alluvial flats, and playa margins. Where sandstone bedrock is absent, only localized portions of early to late Holocene surfaces that receive sufficient fine sand would support development of extensive tall moss–lichen pinnacled BSCs. The majority of these surfaces would instead contain minimal BSCs and display some degree of desert pavement development (House et al., 2010). In addition, episodic flooding could prevent development of extensive tall moss–lichen pinnacles, allowing only cyanobacteria and patchy colonies of short moss–lichen crusts to form along recently abandoned inset fans (Figs. 3, 6) (House et al., 2010).

After colonizing a surface, mosses and lichens capture dust, creating a positive feedback mechanism that enhances propagation of tall moss–lichen pinnacles and formation of biogenic vesicular horizons. Mosses and lichens incrementally accrete dust at the soil surface to form pinnacle topography, transforming short moss–lichen crusts into tall moss–lichen pinnacled crusts (Williams et al., 2012). BSC bio-structures and surface dust accumulation lead to surface sealing that prevents erosion (Campbell et al., 1989; McKenna Neuman et al., 1996) and over many wetting and drying cycles support vesicular pore formation within the bio-rich zone (Danin et al., 1998; Williams et al., 2012). Dust may also accumulate below pinnacle mounds to form mineral vesicular (Av) horizons in the bio-poor zone (Williams et al., 2012). Fine-grained dust enhances water-holding capacity of the surface soils (Danin and Ganor, 1991; Simonson, 1995), while dust-related microstructures, such as surface seals, bio-rich vesicular pores, capillary discontinuities, and mineral vesicular (Av) horizons, help maintain water near the soil surface for uptake by crust organisms (Williams et al., 2012). Captured dust also provides a potential source of nutrients for crust biota (Simonson, 1995; Reynolds et al., 2006; Williams, 2011b). Surface roughness associated with moss–lichen pinnacles may decrease runoff, provide new substrates for BSC colonization, and enhance dust capture potential (McFadden et al., 1986; Wells et al., 1987; Li et al., 2010; Williams et al., 2012). Overall, the compounding impacts of moss–lichen dust capture feedbacks greatly increase soil water, nutrient, and surface area availability, which further promote BSC propagation (Williams et al., 2012).

The thickness of biologically-mediated mineral vesicular (Av) horizons below extensive moss–lichen crusts (Williams et al., 2012) reflects prolonged stability and dust accretion. Studies from a variety of deserts have attempted to estimate dust accretion by BSCs, but results largely vary as a function of regional climate, crust composition, and dust influx. A study from the Negev Desert estimated dust accumulation rates of live cyanobacteria crusts to be 277 g/m^2/year, which the authors calculated to be roughly 0.31 mm/year (Zaady and Offer, 2010). If the same dust accretion rate was applied to this study, the 15 cm-thick vesicular (Av) horizon found below moss–lichen pinnacled crusts along early to mid-Holocene surfaces (Fig. 3) would require 484 years to accumulate. Another study from the Negev estimated that moss–lichen interspaces accreted dust at a rate of 0.13 g/m^2/year (Shachak and Lovett, 1998), which would take roughly 1 million years to accumulate a 15 cm horizon, far exceeding its early to mid-Holocene surface age. If modern average dust influx rates from the Mojave Desert are used at 14 g/m^2/year (Reheis, 2006), it would take over 9500 years to accumulate a dust-rich horizon of 15 cm. All of these calculations may poorly estimate moss–lichen dust accretion along these early to mid-Holocene surfaces, as several factors are not considered. (1) Sand availability is high at this study site and may comprise a significant volume of the vesicular (Av) horizon, accelerating dust accretion. For example, the fine, medium and coarse sand fractions collectively comprise 39% of the upper 3 cm of soil from this horizon. (2) Macro-porosity associated with vesicular pore formation, BSC microstructures (Williams et al., 2012), and bioturbation (Eghbal and Southard, 1993) may decrease horizon density, thereby increasing horizon thickness relative to that expected from deposition rates calculations. (3) The high surface roughness of early to mid-Holocene surfaces and tall moss–lichen pinnacled crusts may enhance local dust accretion rates (McFadden et al., 1986). (4) Mojave Desert dust accretion rates are based on modern measurements, under a variety of environmental conditions, from 1984 to 1999 (Reheis, 2006). This was a period of increased anthropogenic activity and may not reflect the historical dust influx associated with climates and conditions over the past 100s to 1000s of years. (5) Finally, we currently have poor constraint on the disturbance history of the field area or the rates at which BSC-associated porosity and bio-sedimentary features formed. Nevertheless, a 15 cm-thick biologically-mediated vesicular (Av) horizon suggests that moss–lichen crusts are long-lived surface features, which required sustained stability for copious dust accretion and formation of intricate bio-sedimentary structures (Williams et al., 2012). Dust accretion feedbacks associated with moss–lichen crusts lead to surficial soil characteristics dissimilar to those of desert pavements and non-biogenic vesicular (Av) horizons.

5.4. Pavement trajectories and feedbacks

Surfaces with high rock cover density lack fine-grained substrates for widespread BSC establishment. Instead, these surfaces are primarily dominated by the processes that initially form and eventually degrade desert pavements through time (Wells et al., 1987; McFadden et al., 1998; Hamerlynck et al., 2002; Young et al., 2004; Wood et al., 2005; Schafer et al., 2007). In this study, the early Holocene and older geomorphic surfaces are topographically removed from significant sources of eolian fine sand influx (Figs. 5, 6). High rock cover leads to the accumulation of dust below rock fragments and formation of desert pavements and abiotically-mediated vesicular (Av) horizons (McFadden et al., 1986, 1987; Goossens, 1995; Anderson et al., 2002). With time, clast shattering increases rock cover (McFadden et al., 2005) to form smooth, tightly interlocking pavements (Anderson et al., 2002; Wood et al., 2005) with few exposed fine-grained substrates for BSC colonization. Latest Pleistocene to early Holocene surfaces from nearby basins, such as the Ivanpah Valley (House et al., 2010) or other parts of the Mojave Desert (Bell et al., 1998; Bell and Ramelli, 1999), have smooth, tightly interlocking desert pavements that support sparse vascular plant cover (Hamerlynck et al., 2002) and negligible BSCs. These observations, along with negative relationships between rock cover and BSCs reported here, support the theory that areas with high surface rock densities provide poorly suited habitats for extensive BSC colonization (Kaltenecker et al., 1999; Quade, 2001). Moreover, tightly interlocking desert pavements with associated vesicular (Av) horizons decrease water availability, which minimizes growth potential of biotic communities (Hamerlynck et al., 2002; Wood et al., 2005; Meadows et al., 2008). Reduced bioturbation supports a feedback mechanism that promotes integrity of well-developed desert pavements (Wells et al., 1987; McFadden et al., 1998; Hamerlynck et al., 2002; Young et al., 2004; Wood et al., 2005; Schafer et al., 2007), which persist until they are destroyed by climate change (Quade, 2001), off-road-driving (Quade, 2001; Goossens and Buck, 2009), or incision caused by vesicular horizon-induced runoff (Wells and Dohrenwend, 1985; Wells et al., 1987).

Disturbance to interlocking desert pavements exposes fine-grain substrates and allows scattered moss and lichen colonization. In this study, these processes are observed along Pleistocene and older surfaces where disrupted surface rock fragments form poorly interlocking desert pavements (Figs. 3, 4) that provide exposed loamy substrates for initial BSC development. Once established at the surface, mosses and lichens accrete dust incrementally (Williams et al., 2012), forming scattered colonies of tall moss–lichen pinnacled crusts (Fig. 1F). Pleistocene and older alluvial surfaces contained 63–87% of areas with scattered tall moss–lichen pinnacles, which generally occurred with some form of disturbed desert pavement or high rock cover.

5.5. Land management implications

The proposed process-based models provide useful land management tools that can predict crust distribution as a function of geomorphic characteristics. While previous studies have shown strong ties between BSCs and geomorphology (Brostoff, 2002; Thomas and Dougill, 2007; Bowker and Belnap, 2008; Lazaro et al., 2008; Li et al., 2010), the data from this study indicate that in this portion of the Mojave desert, the most important controls of local BSC distribution are fine-grained substrate availability, stability, and inferred water holding capacity. These characteristics vary predictably as a function of surficial processes within intermontane basins and allow prediction of BSC growth potential along individual geomorphic surfaces (Fig. 6). Careful examination of the controls of the fine sand-to-rock ratio and how soil physical processes interact with locally-significant biotic processes (Monger and Bestelmeyer, 2006) would allow similar observations and predictions to be extended to other geomorphic and geologic settings. Such predictions of BSC distribution can help land managers set reference conditions and goals for ecological restoration and identify sensitive areas to protect from future disturbances.

This study also highlights the important role of dust accumulation in BSC development, restoration potential, and air quality. Our results along with data from companion studies (Williams, 2011b; Williams et al., 2012) suggest dust accretion by BSCs provides a source of nutrients, increases water availability, and provides new fine-grained substrates for propagation, allowing crust organisms to engineer their own favorable habitat. Active dust capture by BSCs could explain the apparent high fertility associated with moss–lichen crusts (Bowker et al., 2006; Beraldi-Campesi et al., 2009; Rivera-Aguilar et al., 2009). Therefore, fertilizer applications or micronutrient additions to BSCs may not be a sufficient trigger for moss–lichen crust development, as previously suggested (Bowker et al., 2005, 2006). Instead, land managers should recognize the importance of dust in the establishment, health, and continued propagation of moss–lichen crusts (Williams, 2011b; Williams et al., 2012). In fact, complete restoration of late succession crusts and ecological function likely requires re-establishment of biologically-mediated dust capture and reformation of biogenic vesicular (Av) horizons and BSC microfeatures (Williams et al., 2012), which may occur over 10s to 1000s of years. Because BSCs protect fragile fine-grained surfaces, physical disturbance to crusts should be avoided to prevent wind erosion that causes dust emissions and air pollution (Belnap, 1995; McKenna Neuman et al., 1996; Goossens and Buck, 2009), as well as loss of nutrient-rich and hydrologically-important surface soils (Simonson, 1995; Williams, 2011b; Williams et al., 2012).

6. Conclusions

A new conceptual model illustrates how self-enhancing geological and biological feedbacks constrain the stability, disturbance regime, dust-capture, and textural framework that ultimately control BSC distribution within the Mojave Desert. Geologic and geomorphic processes regulate the fine sand-to-rock ratio, which controls the development of three surface cover types and concomitant biogeomorphic feedbacks across intermontane basin landforms. (1) Cyanobacteria crusts dominate where abundant fine sand and negligible rocks form active sand sheets. Filamentous cyanobacteria support moderate sand saltation that minimizes moss and lichen colonization. (2) Tall moss–lichen pinnacled crusts are most extensive on stable surfaces composed of mixed rocks and fine sand. Younger inset surfaces near active arroyos or playas, such as early to late Holocene inset fans, are more likely to have increased fine sand deposition. These biogeomorphic conditions support a dust capture feedback that forms biologically-mediated vesicular horizons (Williams et al., 2012) and promotes extensive moss–lichen crust propagation. Thick biogenic vesicular horizons suggest moss–lichen pinnacles are long-lived surface features that may have developed over 10s to 1000s of years. (3) Scattered, low to moderate density moss–lichen crusts are favored on stable surfaces with high rock cover. Older surfaces that are farther away from active arroyos or playas are less likely to have fine sand deposition. Rock cover minimizes BSC colonization and supports desert pavement and abiotically-mediated vesicular horizon formation. Disruption of interlocking desert pavements creates micro-habitats for scattered, low density moss–lichen crust development.

BSC organisms and the plant communities they support are uniquely adapted to current hydrological patterns, stability conditions, and soil resource allocation under the three primary surface cover types, (1) cyanobacteria crusts, (2) moss–lichen crusts, and (3) desert pavements (Williams, 2011b). The perpetuation of the distinct biogeomorphic interactions that support these surface cover types promote geological and biological continuity, therein promoting ecological stability. While climate change and anthropogenic disturbances threaten these important feedbacks, a landscape perspective into BSC distribution and arid biogeomorphic processes provides a useful tool that may help mitigate and prevent future ecological disruption.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.geomorph.2013.04.031.

Acknowledgments

We sincerely appreciate the input, time, resources, and advice provided by Yuanxin Teng (UNLV Environmental Soil Analysis Laboratory), Mengesha Beyene, Scott Abella, John Brinda, Jayne Belnap, Ben Williams, Kyle House, Brett McLaurin, John Egelin, Seth Page, Henry Sun, Sarah Peterson, Bob Boyd, and Cathy Willey. Funding was provided by the Bureau of Land Management (task agreement FAA080005), UNLV Urban Sustainability Initiative Fellowship Program (DOE DE-FG02-08ER64709 and DOE DE-EE-0000716), NSF-Nevada EPSCor, SEPHAS Fellowship Program (NSF-EPSCor RING-TRUE III, grant no. 0447416), Farouk El-Baz Student Research Grant Program, Geological Society of America Student Grant Program, ExxonMobil Student Research Grant Program, UNLV Geoscience Scholarship Program, Bernada French Scholarship, and UNLV Adams/GPSA Scholarship. Thanks to the two anonymous reviewers whose comments greatly improved this manuscript.

References

Anderson, K., Wells, S., Graham, R., 2002. Pedogenesis of vesicular horizons, Cima Volcanic Field, Mojave Desert, California. Soil Science Society of America Journal 66, 878–887.
Bachman, G.O., Machette, M.N., 1977. Calcic soils and calcretes in the southwestern United States. Open-File Report 77-794. (163 pp.).
Beard, L.S., Anderson, R.E., Block, D.L., Bohannon, R.G., Brady, R.J., Castor, S.B., Duebendorfer, E.M., Faulds, J.E., Felger, T.J., Howard, K.A., Kuntz, M.A., Williams, V.S., 2007. Preliminary Geologic Map of the Lake Mead 30′ × 60′ Quadrangle, Clark County, Nevada, and Mohave County, Arizona.
Bell, J.W., Ramelli, A.R., dePolo, C.M., Maldonado, F., Schmidt, D.L., 1999. Geologic map of the Corn Creek Springs quadrangle, Nevada. 1:24,000.
Bell, J.W., Ramelli, A.R., Caskey, S.J., 1998. Geologic map of the Tule Springs Park quadrangle, Nevada. 1:24,000.
Belnap, J., 1994. Potential role of cryptobiotic soil crust in semiarid rangelands. Proceedings — Ecology and Management of Annual Rangelands, pp. 179–185.
Belnap, J., 1995. Surface disturbances: their role in accelerating desertification. Environmental Monitoring and Assessment 37, 39–57.
Belnap, J., 2001. Comparative structure of physical and biological soil crusts. In: Belnap, J., Lange, O.L. (Eds.), Biological Soil Crusts: Structure, Function, and Management. Springer-Verlag, Berlin, pp. 177–191.

Belnap, J., 2006. The potential roles of biological soil crusts in dryland hydrologic cycles. Hydrological Processes 20, 3159–3178.
Belnap, J., Gardner, J.S., 1993. Soil microstructure in soils of the Colorado Plateau: the role of the cyanobacterium *Microcoleus vaginatus*. Great Basin Naturalist 53, 40–47.
Belnap, J., Kaltenecker, J., Rosentreter, R., Williams, J., Leonard, S., Eldridge, D.J., 2001. Biological Soil Crusts: Ecology and Management. Technical Reference 1730-2. (118 pp.).
Belnap, J., Phillips, S.L., Troxler, T., 2006. Soil lichen and moss cover and species richness can be highly dynamic: the effects of invasion by the annual exotic grass *Bromus tectorum*, precipitation, and temperature on biological soil crusts in SE Utah. Applied Soil Ecology 32, 63–76.
Belnap, J., Phillips, S.L., Herrick, J.E., Johansen, J.R., 2007. Wind erodibility of soils at Fort Irwin, California (Mojave Desert), USA, before and after trampling disturbance: implications for land management. Earth Surface Processes and Landforms 32, 75–84.
Beraldi-Campesi, H., Hartnett, H.E., Anbar, A., Gordon, G.W., Garcia-Pichel, F., 2009. Effect of biological soil crusts on soil elemental concentrations: implications for biogeochemistry and as traceable biosignatures of ancient life on land. Geobiology 7, 348–359.
Bowker, M.A., 2007. Biological soil crust rehabilitation in theory and practice: an underexploited opportunity. Restoration Ecology 15, 13–23.
Bowker, M.A., Belnap, J., 2008. A simple classification of soil types as habitats of biological soil crusts on the Colorado Plateau, USA. Journal of Vegetation Science 19, 831–840.
Bowker, M.A., Belnap, J., Davidson, D.W., Phillips, S.L., 2005. Evidence for micronutrient limitations of biological soil crusts: importance to arid-lands restoration. Ecological Applications 15, 1941–1951.
Bowker, M.A., Belnap, J., Davidson, D.W., Goldstein, H., 2006. Correlates of biological soil crust abundance across a continuum of spatial scales: support for a hierarchical conceptual model. Journal of Applied Ecology 43, 152–163.
Bowker, M.A., Belnap, J., Davidson, D.W., 2010. Microclimate and propagule availability are equally important for rehabilitation of dryland N-fixing lichens. Restoration Ecology 18, 30–33.
Brock, A.L., Buck, B.J., 2005. A new formation process for calcic pendants from the Pahranagat Valley, Nevada, USA, and implication for dating Quaternary landforms. Quaternary Research 63, 359–367.
Brock, A.L., Buck, B.J., 2009. Polygenetic development of the Mormon Mesa, NV petrocalcic horizons: geomorphic and paleoenvironmental interpretations. Catena 77, 65–75.
Brostoff, W.N., 2002. Cryptobiotic crusts of a seasonally inundated dune–pan system at Edwards Air Force Base, western Mojave Desert, California. Journal of Arid Environments 51, 339–361.
Buck, B.J., Kipp, J.J., Monger, H.C., 2002. Inverted clast stratigraphy in an eolian archaeological environment. Geoarchaeology 17, 665–687.
Buck, B.J., King, J., Etyemezian, V., 2011. Effects of salt mineralogy on dust emissions, Salton Sea, California. Soil Science Society of America Journal 75, 1958–1972.
Bull, W.B., 1991. Geomorphic Responses to Climatic Change. Oxford University Press, New York.
Burt, R. (Ed.), 2004. Soil Survey Laboratory Methods Manual, SSIR No. 42, Version 4.0. USDA-NRCS National Soil Survey Center, Lincoln, NE.
Campbell, S.E., 1979. Soil stabilization by a prokaryotic desert crust: implications for Precambrian land biota. Origins of Life 9, 335–348.
Campbell, S.E., Seeler, J., Golubic, S., 1989. Desert crust formation and soil stabilization. Arid Soil Research and Rehabilitation 3, 217–228.
Canton, Y., Sole-Benet, A., Lazaro, R., 2003. Soil-geomorphology relations in gypsiferous materials of the Tabernas Desert (Almerıa, SE Spain). Geoderma 115, 193–222.
Christenson, G.E., Purcell, C., 1985. Correlation and age of Quaternary alluvial-fan sequences, Basin and Range province, southwestern United States. In: Weide, D.E. (Ed.), Soils and Quaternary Geology of the Southwestern Unitersity States: Geological Society of America Special Paper, 203, pp. 115–122.
Dane, J.H., Topp, C. (Eds.), 2002. SSSA Method of Soil Analysis, Part 4-Physical Methods. Soil Science Society of America, Inc., Madison, WI.
Danin, A., Ganor, E., 1991. Trapping of airborne dust by mosses in the Negev Desert, Israel. Earth Surface Processes and Landforms 16, 153–162.
Danin, A., Dor, I., Sandler, A., Amit, R., 1998. Desert crust morphology and its relations to microbiotic succession at Mt. Sedom, Israel. Journal of Arid Environments 38, 161–174.
DeFalco, L.A., Detling, J.K., Tracy, C.R., Warren, S.D., 2001. Physiological variation among native and exotic winter annual plants associated with microbiotic crusts in the Mojave Desert. Plant and Soil 234, 1–14.
Eghbal, M.K., Southard, R.J., 1993. Micromorphological evidence of polygenesis of three aridisols, western Mojave Desert, California. Soil Science Society of America Journal 57, 1041–1050.
Eldridge, D.J., Greene, R.S.B., 1994. Microbiotic soil crusts: a review of their roles in soil and ecological processes in the rangelands of Australia. Australian Journal of Soil Research 32, 389–415.
Escudero, A., Martinez, I., de la Cruz, A., Otalora, M.A.G., Maestre, F.T., 2007. Soil lichens have species-specific effects on the seedling emergence of three gypsophile plant species. Journal of Arid Environments 70, 18–28.
Evans, R.D., Belnap, J., 1999. Long-term consequences of disturbance on nitrogen dynamics in an arid ecosystem. Ecology 80, 150–160.
Friedmann, E.I., Galun, M., 1974. Desert algae, lichens and fungi. In: Brown, G.W. (Ed.), Desert Biology. Academic Press, New York, pp. 165–212.
Garcia-Pichel, F., Pringault, O., 2001. Cyanobacteria track water in desert soils. Nature 413, 380–381.
Gile, L.H., Peterson, F.F., Grossman, R.B., 1966. Morphological and genetic sequences of carbonate accumulation. Soil Science 101, 347–360.
Goossens, D., 1995. Field experiments of aeolian dust accumulation on rock fragment substrata. Sedimentology 42, 391–402.
Goossens, D., 2008. Techniques to measure grain-size distributions of loamy sediments: a comparative study of ten instruments for wet analysis. Sedimentology 55, 65–96.
Goossens, D., Buck, B., 2009. Dust emission by off-road driving: experiments on 17 arid soil types, Nevada, USA. Geomorphology 107, 118–138.
Gorelow, A.S., Skrbac, P.H., 2005. Climate of Las Vegas, NV. National Weather Service, Las Vegas, NV.
Hamerlynck, E.P., McAuliffe, J.R., McDonald, E.V., Smith, S.D., 2002. Ecological responses of two Mojave Desert shrubs to soil horizon development and soil water dynamics. Ecology 83, 768–779.
Harden, J.W., Taylor, E.M., Hill, C., Mark, R.K., McFadden, L.D., Reheis, M.C., Sowers, J.M., Wells, S.G., 1991. Rates of soil development from four soil chronosequences in the southern Great Basin. Quaternary Research 35, 383–399.
Herrick, J.E., Van Zee, J.W., Belnap, J., Johansen, J.R., Remmenga, M., 2010. Fine gravel controls hydrologic and erodibility responses to trampling disturbance for coarse-textured soils with weak cyanobacterial crusts. 83, 119–126.
House, P.K., 2005. Using geology to improve flood hazard management on alluvial fans — An example from Laughlin, Nevada. Journal of the American Water Resources Association 41, 1431–1447.
House, P.K., Buck, B.J., Ramelli, A.R., 2010. Geologic Assessment of Piedmont and Playa Flood Hazards in the Ivanpah Valley Area, Clark County, Nevada (online only). NBMG Report 53.
Issa, O.M., Trichet, J., Defarge, C., Coute, A., Valentin, C., 1999. Morphology and microstructure of microbiotic soil crusts on a tiger bush sequence (Niger, Sahel). Catena 37, 175–196.
Kaltenecker, J.H., Wicklow-Howard, M.C., Rosentreter, R., 1999. Biological soil crusts in three sagebrush communities recovering from a century of livestock trampling. USDA Forest Service Proceedings RMRS-P-11.
Kidron, G.J., Barzilay, E., Sachs, E., 2000. Microclimate control upon sand microbiotic crusts, western Negev Desert, Israel. Geomorphology 36, 1–18.
Kleiner, E.F., Harper, K.T., 1977. Soil properties in relation to cryptogamic groundcover in Canyonlands National Park. Journal of Range Management 30, 202–205.
Lazaro, R., Canton, Y., Sole-Benet, A., Bevan, J., Alexander, R., Sancho, L.G., Puigdefabregas, J., 2008. The influence of competition between lichen colonization and erosion on the evolution of soil surfaces in the Tabernas badlands (SE Spain) and its landscape effects. Geomorphology 102, 252–266.
Li, X.R., He, M.Z., Zerbe, S., Li, X.J., Liu, L.C., 2010. Micro-geomorphology determines community structure of biological soil crusts at small scales. Earth Surface Processes and Landforms 35, 932–940.
Machette, M.N., 1985. Calcic soils of the southwestern United States. In: Weide, D.L. (Ed.), Soils and Quaternary Geomorphology of the Southwestern United States. Geological Society of America, Boulder, CO, pp. 1–21.
McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, OR.
McFadden, L.D., Wells, S.G., Dohrenwend, J.C., 1986. Influences of Quaternary climatic changes on processes of soil development on desert loess deposits of the Cima Volcanic Field, California. Catena 13, 361–389.
McFadden, L.D., Wells, S.G., Jercinovich, M.J., 1987. Influences of eolian and pedogenic processes on the origin and evolution of desert pavements. Geology 15, 504–508.
McFadden, L.D., McDonald, E.V., Wells, S.G., Anderson, K., Quade, J., Forman, S.L., 1998. The vesicular layer and carbonate collars of desert soils and pavements: formation, age and relation to climate change. Geomorphology 24, 101–145.
McFadden, L.D., Eppes, M.C., Gillespie, A.R., Hallet, B., 2005. Physical weathering in arid landscapes due to diurnal variation in the direction of solar heating. GSA Bulletin 117, 161–173.
McKenna Neuman, C., Maxwell, C., 2002. Temporal aspects of the abrasion of microphytic crusts under grain impact. Earth Surface Processes and Landforms 27, 891–908.
McKenna Neuman, C., Maxwell, C.D., Boulton, J.W., 1996. Wind transport of sand surfaces crusted with photoautotrophic microorganisms. Catena 27, 229–247.
Meadows, D.G., Young, M.H., McDonald, E.V., 2008. Influence of relative surface age on hydraulic properties and infiltration on soils associated with desert pavements. Catena 72, 169–178.
Monger, H.C., Bestelmeyer, B.T., 2006. The soil-geomorphic template and biotic change in arid and semi-arid ecosystems. Journal of Arid Environments 65, 207–218.
Noffke, N., Knoll, A.H., Grotzinger, J.P., 2002. Sedimentary controls on the formation and preservation of microbial mats in siliciclastic deposits: a case study from the upper Neoproterozoic Nama Group, Namibia. PALAIOS 17, 533–544.
Page, W.R., Lundstrom, S.C., Harris, A.G., Langenheim, V.E., Workman, J.B., Mahan, S.A., Paces, J.B., Dixon, G.L., Rowley, P.D., Burchfiel, B.C., Bell, J.W., Smith, E.I., 2005. Geologic and Geophysical Maps of the Las Vegas 30′ × 60′ Quadrangle, Clark and Nye Counties, Nevada, and Inyo County, California. 1:100,000.
Peterson, F.F., 1981. Landforms of the Basin and Range, Defined for Soil Survey. Technical Bulletin, 28 (52 pp.).
Peterson, F.F., Bell, J.W., Dorn, R.I., Ramelli, A.R., Ku, T.L., 1995. Late Quaternary geomorphology and soils in Crater Flat, Yucca Mountain area, southern Nevada. GSA Bulletin 107, 379–395.
Ponzetti, J.M., McCune, B.P., 2001. Biotic soil crusts of Oregon's shrub steppe: community composition in relation to soil chemistry, climate, and livestock activity. The Bryologist 104, 212–225.
Quade, J., 2001. Desert pavements and associated rock varnish in the Mojave Desert: how old can they be? Geology 29, 855–858.
Reheis, M., 2006. A 16-year record of eolian dust in Southern Nevada and California, USA: controls on dust generation and accumulation. Journal of Arid Environments 67, 487–520.
Reheis, M.C., Sowers, J.M., Taylor, E.M., McFadden, L.D., Harden, J.W., 1992. Morphology and genesis of carbonate soils on the Kyle Canyon fan, Nevada, U.S.A. Geoderma 52, 303–342.

Reynolds, R., Neff, J., Reheis, M., Lamothe, P., 2006. Atmospheric dust in modern soil on aeolian sandstone, Colorado Plateau (USA): variation with landscape position and contribution to potential plant nutrients. Geoderma 130, 108–123.

Rivera-Aguilar, V., Godinez-Alvarez, H., Moreno-Torres, R., Rodriguez-Zaragoza, S., 2009. Soil physico-chemical properties affecting the distribution of biological soil crusts along an environmental transect at Zapotitlan drylands, Mexico. Journal of Arid Environments 73, 1023–1028.

Robins, C.R., Buck, B.J., Williams, A.J., Morton, J.L., House, P.K., Howell, M.S., Yonovitz, M.L., 2009. Comparison of flood hazard assessments on desert piedmonts and playas: a case study in Ivanpah Valley, Nevada. Geomorphology 103, 520–532.

Schafer, D.S., Young, M.H., Zitzer, S.F., Caldwell, T.G., McDonald, E.V., 2007. Impacts of interrelated biotic and abiotic processes during the past 125,000 years of landscape evolution in the Northern Mojave Desert, Nevada, USA. Journal of Arid Environments 69, 633–657.

Schoeneberger, P.J., Wysocki, D.A., Benham, E.C., Broderson, W.D., 2002. Field Book for Describing and Sampling Soils, Version 2.0. Natural Resources Conservation Service, National Soil Survey Center, Lincoln, NE.

Shachak, M., Lovett, G.M., 1998. Atmospheric deposition to a desert ecosystem and it implications for management. Ecological Applications 8, 455–463.

Simonson, R.W., 1995. Airborne dust and its significance to soils. Geoderma 65, 1–43.

Sowers, J.M., Amundson, R.G., Chadwick, O.A., Hardin, J.W., Jull, A.J.T., Ku, T.L., McFadden, L.D., Reheis, M.C., Taylor, E.M., Szabo, B.J., 1989. Geomorphology and pedology on the Kyle Canyon Alluvial Fan, southern Nevada. In: Rice, T.J. (Ed.), Soils, geomorphology, and pedology in the Mojave Desert, California, Nevada: Field Tour Guidebook for the 1989 Soil Science Society of America Annual Meeting Pre-Meeting Tour, October 12–14, 1989. SSSA, pp. 93–112.

Soil Survey Staff, 2007. Soil survey of the Clark County area, NV.

Thomas, A.D., Dougill, A.J., 2006. Distribution and characteristics of cyanobacterial soil crusts in the Molopo Basin, South Africa. Journal of Arid Environments 64, 270–283.

Thomas, A.D., Dougill, A.J., 2007. Spatial and temporal distribution of cyanobacterial soil crusts in the Kalahari: implications for soil surface properties. Geomorphology 85, 17–29.

Wang, W.B., Yang, C.Y., Tang, D.S., Li, D.H., Liu, Y.D., Hu, C.X., 2007. Effects of sand burial on biomass, chlorophyll fluorescence and extracellular polysaccharides of man-made cyanobacterial crusts under experimental conditions. Science in China. Series C, Life Sciences 50, 530–534.

Wells, S.G., Dohrenwend, J.C., 1985. Relict sheetflood bed forms on late Quaternary alluvial-fan surfaces in the southwestern United States. Geology 13, 512–516.

Wells, S.G., McFadden, L.D., Dohrenwend, J.C., 1987. Influence of late Quaternary climatic changes on geomorphic and pedogenic processes on a desert piedmont, eastern Mojave Desert, California. Quaternary Research 27, 130–146.

Williams, A.J., 2011a. Co-development of BSCs and Soil-Geomorphology. Co-Development of Biological Soil Crusts, Soil-Geomorphology, and Landscape Biogeochemistry in the Mojave Desert, Nevada, U.S.A. — Implications for Ecological Management. University of Nevada, Las Vegas (Ph.D. Dissertation).

Williams, A.J., 2011b. Biological Soil Crusts and the Fertile Island Effect. Co-Development of Biological Soil Crusts, Soil-Geomorphology, and Landscape Biogeochemistry in the Mojave Desert, Nevada, U.S.A. — Implications for Ecological Management. University of Nevada, Las Vegas (Ph.D. Dissertation).

Williams, A.J., Buck, B.J., Beyene, M.A., 2012. Biological soil crusts in the Mojave Desert USA: micromorphology and pedogenesis. Soil Science Society of America Journal 76, 1685–1695.

Wood, Y.A., Graham, R.C., Wells, S.G., 2005. Surface control of desert pavement pedologic process and landscape function, Cima Volcanic field, Mojave Desert, California. Catena 59, 205–230.

Young, M.H., McDonald, E.V., Caldwell, T.G., Benner, S.G., Meadows, D.G., 2004. Hydraulic properties of a desert soil chronosequence in the Mojave Desert, USA. Vadose Zone Journal 3, 956–963.

Zaady, E., Offer, Z.Y., 2010. Biogenic soil crusts and soil depth: a long-term case study from the Central Negev desert highland. Sedimentology 57, 351–358.