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Effects of Land Surface Characteristics on Pedogenesis, Biological Soil Crust
Community Diversity, and Ecosystem Functions in a Mojave Desert Piedmont Landscape

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Soil and Water Sciences

by

Nicole Pietrasiak

September 2012

Thesis Committee:

Dr. Robert C. Graham, Chairperson

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Dr. Jeffrey R. Johansen

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The Dissertation of Nicole Pietrasiak is approved:

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ABSTRACT OF THE DISSERTATION

Effects of Land Surface Characteristics on Pedogenesis, Biological Soil Crust
Community Diversity, and Ecosystem Functions in a Mojave Desert Piedmont Landscape

by

Nicole Pietrasiak

Doctor of Philosophy, Graduate Program in Soil and Water Sciences
University of California, Riverside, September 2012
Dr. Robert C. Graham

Abiotic and biotic land surface properties are often highly heterogeneous but can assemble in a repetitive manner forming landform mosaics at a mesoscale (ten to hundreds of meters). Nonetheless, we still do not fully understand their interactions or the mechanisms involved that change these properties during landscape evolution. The goal of this work was to relate land surface properties to functional group diversity of biological soil crusts and vascular plants, ecosystem functions and pedogenesis within a Mojave Desert landscape. Seven mosaic types were visually identified that occurred on three geomorphic-aged surfaces: young bars and swales, intermediate-aged flattened bars, flattened swales and bioturbation units, and old desert pavement and shrub zones. Sixty-three randomly selected landform mosaics served as study plots. In each plot a suite of morphometrical, physical and biological variables were determined. Multivariate analysis revealed that landform mosaics are statistically distinct according to specific sets of abiotic and biotic land surface properties. Within each landform type I also detected

significant differences in functional group diversity of plants and biological soil crusts. The aggregate stability, nitrogen and carbon fixation of crusts were measured. An area based quality index (ABQI) was developed to evaluate these microbial communities based on ecological functions. The ABQI was computed for each landform mosaic and statistically compared. The ABQI was highest for bars and lowest for desert pavements. Two landform evolutionary trajectories were identified: an abiogenic and a biogenic tract. In the abiogenic track, vegetation contracted and the surface increased in physical components. In the biogenic track vegetation diversity and abundance increased, and crust cover and diversity was high. Both of these trajectories were linked to different pedogeneses. Abiogenic soils promoted vesicular and calcic horizon development, as well as sodicity and alkalinity. Organic carbon and total nitrogen decreased. Biogenic soils were well mixed. No vesicular horizon could develop and calcic horizons were weakly expressed. Furthermore, these soils increased in organic carbon and total nitrogen.

Overall, this work showed that desert landscapes are highly diverse in landform mosaics defined by abiotic and biotic land surface properties at the mesoscale. Moreover, strong linkages and feedbacks occur between physical, biotic and pedologic landscape components that over time result in quite contrasting surface features.

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1. GENERAL INTRODUCTION

1.1 Scientific Significance

About one third of the Earth's land surface is covered by desert, representing a significant portion of the terrestrial ecosystem (Goudie 2002). In California alone, about 113,000 km² are desert lands (Barbour et al. 1999), with 65,000 km² of those lands within the Mojave Desert (Norris and Webb 1990), one of the major hot desert biomes in North America.

The uniqueness of deserts is that their landscapes are composed of similar and easy to distinguish physiographic components, such as alluvial fans and playas (Peterson 1981). Additionally, land surface features like desert pavements and bar-and-swale topography, as well as soil phenomena such as vesicular horizons and caliche, are commonly found in all deserts of the globe (see Cooke et al. 1993, Turk 2012). Moreover, in recent studies of landscape ecology and biogeomorphology these features have been linked to properties of biological communities (see reviews of Viles 1988, Wainwright 2009). Knowledge gained from these landscapes allows for broad scale insights and predictions into the connections between the physical environment and biotic communities. Thus, deserts are conducive to ecological studies that integrate geomorphology, pedology, and ecology.

1.2 Broader Impact

A large area of the desert is still undeveloped. However, due to rapid population increase in the last century, desert lands are increasingly used for housing development, infrastructure, and recreation (e.g., off-road vehicle areas, golf courses) especially in developed countries, such as the United States. Despite development, we still lack detailed information about local surficial geomorphology, soils, and biodiversity for large areas of the desert. The desert ecosystem is critical for maintaining stable environmental conditions. Rapid utilization of the land can lead to major environmental and ecological problems mostly related to land surface conditions. Common problems are dust generation, water runoff, soil erosion, exotic species invasion, and habitat loss (Lovich and Bainbridge 1999, Graham et al. 2008). As a result, the increase in desert land degradation will lead to consequent loss of ecosystem components and functioning (Lovich and Bainbridge 1999, Eldridge et al. 2000, 2002, Graham et al. 2009, Read et al. 2008).

Wood et al. (2002, 2005) demonstrated that within a single landform, land surface units can differ significantly from each other, having contrasting attributes and different ecological functions. Understanding geomorphic dynamics, ecological processes, feedbacks and functions at finer scales will contribute to more precise predictions of potential disturbance effects and will help decision-making by land managers (Okin et al. 2006, Smith et al. 2004). Mesoscale land surface units also can be used to more

accurately predict and delineate soils in the desert landscape, and consequently improve soil map unit descriptions and land use interpretations in soil surveys.

1.3 Mojave Desert geomorphology and its linkage to ecological studies

Geomorphic research in the Mojave Desert at a broad scale (hundreds of meters to kilometers) has focused on stable surfaces at the upper and middle piedmont slope, including alluvial fans and fan piedmonts (McDonald 1994, Hamerlynck et al. 2002, 2004, Meadows et al. 2008). More recently, research has addressed soil geomorphic relationships in a desert mountain range (Hirmas and Graham 2011, Hirmas et al. 2011). These studies have contributed valuable information about ecosystem and hydrological processes, paleoclimatic conditions, and pedogenesis in the Mojave Desert at this scale. For example, Hirmas and Graham (2011) discovered that mountains trap significant amounts of carbonate and nitrate-rich eolian material and contribute therefore to global biogeochemical cycles. Meadows et al. (2008) studied vesicular horizon development using an alluvial fan chronosequence and demonstrated that with increasing development of this surficial horizon, hydraulic conductivity progressively decreased. In another study using an alluvial fan chronosequence, Hamerlynck et al. (2002) demonstrated that population structure and ecophysiology of two perennial shrubs could be linked to changes in soil development.

However, only two studies in the Mojave Desert have investigated mesoscale landform patterning and linked land surface properties to soil morphology, plant distribution, and ecosystem functioning (Wood et al. 2002, 2005). They demonstrated that these landscapes are not homogeneous at this finer scale and that land surface properties are important ecological drivers (Wood et al. 2002). However, their focus was limited to a specific 580,000 year old geomorphic surface that developed a distinct desert pavement from volcanic lava deposits. Consequently, it is not known if the observed patterns and processes are equally important across surfaces of differing geomorphic ages.

A major landscape component of the lower piedmont slope is the fan skirt. This topographically smooth landscape component is characterized by an assortment of geomorphic surfaces of different ages that abut each other in relatively close proximity. However, it lacks geomorphic classification at the mesoscale level as well as information about pedogenesis and ecological processes. This dissertation focuses on a fan skirt and will contribute to the fields of landscape ecology, biogeomorphology, and desert ecology, as well as pedology and geomorphology.

1.4 Research Objectives

The overarching goal of this work is to link land surface properties to the diversity of biological soil crusts, plant functional groups, pedogenesis, and ecosystem functions

within a geomorphic framework. All chapters present work obtained from studying a fan skirt chronosequence located at the Clark Mountain Wilderness Area, Mojave Desert National Preserve, California.

Chapter 2 seeks to understand the configuration, potential feedbacks, interactions and dynamics of abiotic and biotic land surface properties across a desert chronosequence. The specific objectives for this study were to: (1) describe landform unit types according to their abiotic and biotic surface properties and to discern whether land surface units are statistically discrete based on land surface properties; (2) determine whether abiotic or biotic land surface properties, or a combination of the two properties, affect statistical differentiation; (3) discern whether landform units differ in plant and biological soil crust functional group diversity; and (4) determine which abiotic surface properties significantly drive biological soil crust and plant community composition.

Chapters 3 and 4 apply the landform classification gained from Chapter 2. In particular, Chapter 3 investigates the eco-functional differences of biological soil crust community types within the fan skirt landscape. Specifically, the objectives of Chapter 3 were to: (1) determine carbon and nitrogen fixation capacity and aggregate stability of different biological soil crust types and (2) contrast how landforms of different geomorphic age differ with respect to the function of their associated crusts. An outcome of this chapter was also the development of an indicator of biological soil crust quality.

Chapter 4 describes the soils found along the chronosequence within the context of the landform classification gained in Chapter 2. Furthermore, it links land surface characteristics to soil properties and pedogenesis. Overall, this dissertation presents

linkages, feedbacks, and dynamics between the abiotic and biotic ecosystem components and integrates geomorphic, pedologic, and ecologic methodologies and concepts.

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2. BIOGEOMORPHOLOGY OF A MOJAVE DESERT LANDSCAPE – CONFIGURATIONS AND FEEDBACKS OF ABIOTIC AND BIOTIC LAND SURFACE PROPERTIES DURING LANDFORM EVOLUTION

Abstract

Investigating the morphology of landscape mosaics, the assemblage of their ecological communities, and the linkages and feedback between mosaics and communities can lead to a holistic understanding of terrestrial ecosystems. The overarching objectives of this study were to: (1) study the abiotic and biotic configurations of landscape mosaics (hereafter referred to as landforms) on a Mojave Desert chronosequence; and (2) elucidate their potential feedbacks, interactions and dynamics during landscape evolution. Seven landform mosaics distributed over three geomorphic ages were identified, including: young bars and swales; intermediate aged flattened bars, flattened swales, and bioturbation units; and old desert pavements and shrub zones. These landforms were characterized according to abiotic and biotic land surface properties. Multivariate discriminate analysis revealed landforms to be statistically distinct and predictable units that can be classified based on a specific suite of abiotic and biotic properties. Moreover, functional group diversity for vascular plant and biological soil crust communities was compared for the seven landforms. Analysis of variance revealed strong significant differences in functional group diversity according to geomorphology. Bars and shrub zones had the significantly highest functional group diversity, whereas desert pavement had the lowest functional group diversity. A third multivariate analysis, canonical correspondence analysis, was conducted to investigate relationships between abiotic land

surface properties and the abundance of both plant and biological soil crust functional groups. Specific abiotic properties were driving the distribution of these functional groups. Geomorphic age linked to surface rock size and presence of protruding rocks were the strongest drivers of the presence and absence of crust functional groups, with young bar being associated with the highest abundance. Perennial forbs were found in old-aged shrub zones with small rocks and low numbers of protruding rocks. A high clast density and a finer clast distribution were found particularly in desert pavements and flattened swales and generally inhibited crust and plant cover. Overall, two landform evolutionary trajectories were identified for the lower piedmont: abiogenic and biogenic landform evolution. These two trajectories are associated with their own unique linkages, feedbacks and dynamics of abiotic and biotic land surface properties producing a highly diverse desert landscape.

2.1 Introduction

Landscapes are configured by diverse but spatially distinctive and repetitive mosaics. These patterns bring about the following questions: (1) What are the factors that determine mosaic configuration in landscapes? (2) What structures ecological communities across these landscapes? (3) What are the feedbacks between biotic communities and landscape formation and development? Landscape ecologists and biogeomorphologists have made significant advances within the last two decades in

addressing these questions (see Viles 1988, Wainwright 2009). On the other hand, research questions and statistical hypothesis testing are often limited by the complexity of the components and their interactions within the landscape (Wiens et al. 1993). As a result, researchers often have taken a reductionist approach. However, when limiting questions to a specific taxonomic group or geomorphic process the detection of emergent properties, multiple contributing mechanistic explanations for patterns, and a holistic understanding of landscape processes is precluded (see Gaston and Blackburn 1999, Lawton 1999, Naylor et al. 2002). Also, abiotic and biotic properties of ecosystems may be tightly linked due to feedbacks between biota and their environment that were not, or maybe even cannot, be directly measured (Lawton 1999). Thus, studies that integrate methodologies from the fields of Biogeomorphology and Landscape Ecology, and considerations of contrasting reciprocal interactions and feedbacks between biotic and abiotic spatial phenomena are needed (Naylor et al. 2002, Haussmann 2011).

For multiple reasons, deserts landscapes can be model systems for such integrative, landscape ecological and biogeomorphological questions. First, desert ecosystems comprise about one third of the Earth's land surface, a significant portion of terrestrial ecosystems (Goudie 2002). Thus, understanding these ecosystems would allow for broad scale insights and predictions. Second, desert land surface components can be studied easily as mosaics of physical components including bare soil, gravel, rocks, boulder; vegetation; and biological soil crusts. These land surface components create high environmental heterogeneity and consequently, heterogeneous resource distribution. High resource diversity impacts the ecological and evolutionary responses of biota, for

example, by promoting a higher probability of species coexistence due to niche partitioning. Finally, the desert landscape is structured into geomorphic units, i.e. landforms. At a global scale, similar landform units such as alluvial fans, dunes, and playas occur in deserts (Peterson 1981). At a local scale, these landform units repeat in space. Landforms can vary in geological age, land surface properties such as percent rock cover and degree of microtopography or degree of soil development (Peterson 1981, Bedford and Small 2008), thus representing strong abiotic gradients.

In the past three decades, there has been an increasing appreciation for geomorphic impacts on biota in arid and semiarid ecosystems. So far, most studies demonstrating the driving force of geomorphology have focused on vascular plants. For example, locations within the landscape with associated differing soil properties often produce contrasting vegetation communities (Parker 1991, McAuliffe 1994, Parker 1995, Hook and Burke 2000, Buxbaum and Vanderbilt 2007, Bisigato et al. 2009).

Geomorphically related factors also influence processes at the individual plant level such as determining root morphology (Gile et al. 1998), leaf and canopy characteristics (Mauchamp et al. 1993, Sponseller and Fisher 2006), leaf water potential (Mauchamp et al. 1993, Hamerlynck et al. 2002), plant recruitment, and population dynamics, by influencing survivorship of seedlings (Mauchamp et al. 1993) or mortality of mature individuals (McAuliffe 1994, McAuliffe et al. 2007).

Substantially less work has addressed the impact of geomorphology on animals. Most research has focused on habitat needs and patch occupancy of animals, which generally are associated with spatial patterns of vegetation structure or land surface

properties (Crawford 1988, Gutschwiller and Barrow 2002, Bradford et al. 2003). In addition, there is much to learn about how geomorphology influences desert microbial communities.

Just as geomorphic patterns with associated abiotic factors influence biota, biota may act as drivers of geomorphic processes. For example, hydrological processes, sediment accumulation, and soil transformation all can be coupled to biological activity (Wainwright 2009). Within the last two decades, there has been a greater focus on understanding how biota impact particular geomorphic processes in deserts. Much of this research has been carried out on the effects of vegetation on fluvial and eolian processes (Wainwright 2009). Many studies have shown how individuals or stands of shrubs promote run-on, infiltration, and sediment trapping (i.e., Rostagno 1989, Dunkerly and Brown 1995, Hupy 2004 or see review by Ludwig et al. 1995). Likewise, bioturbation by small and medium sized mammals influences hydrological and eolian processes through burrowing activity, creating heterogeneous landscape structure. Mound building and tunneling can redistribute resources by trapping sediment and water as well as by enhancing the erosion and transport of soil loosened during burrowing activity (Alkon 1999, Bangert and Slobodchikoff 2000, Davidson and Lightfoot 2008, Schooley and Wiens 2001). At smaller spatial scales, microbial communities associated with biological soil crusts can influence both water and wind flow (Eldridge and Greene 1994, Eldridge et al. 2002, Belnap et al. 2007). Although we are beginning to discern ways in which biota influence geomorphic processes, little work has linked biota to landform evolution, especially over long timescales (centuries to >1,000,000 years).

The overarching goal of this study was to understand the configuration, potential feedbacks, interactions and dynamics of abiotic and biotic land surface properties during landscape evolution in a desert environment. The specific objectives for this study were to: (1) describe landform unit types according to their abiotic (morphometric and physical) and biotic surface properties (biological soil crust and plant functional groups) and to discern whether land surface units are statistically discrete units based on these land surface properties; (2) determine whether abiotic processes, biotic processes, or a combination of abiotic and biotic processes drive such potential differences; (3) discern whether landform units differ in plant and biological soil crust functional group richness and diversity; and (4) determine which abiotic factors significantly drive the composition of biological soil crust and plant communities.

2.2 Materials and Methods

2.2.1 Study Site

This study was conducted in the Clark Mountain Wilderness Area, at the northeastern part of the Mojave Desert National Preserve, southeastern California, USA (ca. 35° 30' N, 115° 41' W). This area is centrally located within the Mojave Desert physiographic province (Figure 1). The study area was located on the fan skirt of the lower piedmont slope. This landscape is comparable to other arid landscapes in the Mojave Desert, as well as those in the Sonoran and Great Basin Deserts.

Since the beginning of the Holocene the climate in the area has been arid, mostly resulting from the rain shadow effect of the Cordilleran Mountain Complex (MacMahon and Wagner 1985, Jannick et al. 1991, Norris and Webb 1990, Koehler et al. 2005). Mean annual precipitation is 145 mm, and mean annual temperature is 17°C, adjusted for elevational difference using NCDC Mountain Pass 1SE Meteorological Station (see Turk 2012). Annual rain events are highly variable in time and space (Osborn 1983). The precipitation is bimodal with most precipitation falling in the winter months (MacMahon and Wagner 1985). Precipitation in the winter occurs as mild rains or occasional snow events at high elevation. In late summer, monsoon thunderstorms from the Gulf of Mexico cause scattered summer pulse rain events. These localized rain events often quickly exceed the infiltration capacity of the soils, leading to rapid runoff and flash floods (Evenari 1985, Miles and Goudey 1997).

The geology of the Clark Mountain Range is highly complex. Proterozoic crystalline rocks are mixed with Paleozoic to Mesozoic sedimentary bedrock (Norris and Webb 1990, Walker et al. 1995, Schmidt and McMackin 2006, Hall 2007). For this study, I selected a watershed with the bedrock and consequential alluvial deposits of the fan skirt being composed of mostly dolomite, with minor amounts of limestone, to minimize site heterogeneity.

The soils on the western side of the Clark Mountain Range on Mojave National Preserve have not been mapped. However, soil surveys of the surrounding areas suggest that soils on younger geomorphic surfaces of the piedmont may be Typic Torriorthents

and on older surfaces they may be Typic Calciorthids. The soil moisture regime for the study area is aridic, and the soil temperature is thermic (Miles and Goudey 1997).

The watershed is characterized by patchy vegetation with characteristic shrub island/interspace micro-patterning. The dominant vegetation on the lower piedmont is an association of *Larrea tridentata* and *Ambrosia dumosa* mixed with *Ephedra nevadensis*, *Yucca schidigera*, *Yucca brevifolia*, and *Krameria* spp.

2.2.2 Field Sampling

Using remote sensing coupled with field observations, geomorphic surfaces of three different relative ages on the fan skirt were identified. Relative age determination was obtained by relating position and elevation of each surface to the active drainage (Birkeland, 1999, Watchman and Twidale 2002). Accordingly, the young surface was composed of active washes and located lowest in the landscape. The intermediate geomorphic surface was slightly elevated and some distance away from the active wash. The oldest geomorphic surface was highest in elevation compared to the other surfaces. Within those three geomorphic surfaces, seven mesoscale (10 to 100 m²) landform unit types differing in morphology were identified. Two unit types were found on young, three on intermediate, and two on old geomorphic surfaces. The selected units were easily recognizable and visually distinct, representing commonly occurring landform units within the entire Mojave Desert.

The two youngest units were the bar and swale units, which were found in active washes. They are associated with alluvial fan depositional processes. Bars were a deposit of coarse alluvial debris with a distinct convex-shaped ridge. Swales were found parallel to the bars. They were composed of fine alluvial debris deposits. In cross section, swales were distinctly concave-shaped with low microtopography. Both units were separated very easily due to a distinct unit boundary created by the visual contrast of adjoining coarse bar with fine swale alluvial debris.

The intermediate aged units were classified as flattened bars, flattened swales, and bioturbated units. Flattened bars were covered by coarse alluvial debris comparable to the young bars. However, in cross section the flattened bars were linear to slightly convex. Flattened swales were covered with fine alluvial debris and in cross section linear to slightly concave. Flattened bar and swale units were more difficult to separate from each other due to the diffuse boundary between the two units. The indistinct boundary was attributed to surface debris mixing. Bioturbated units had a large number of burrows created by small mammals such as kangaroo rats, pocket mice, or ground squirrels. They were circular to ovoid shaped units with a distinct convex-shaped mound in cross-section and distinct unit boundary. On the land surface of these units, surface rocks (= clasts) and bare soil material appeared lighter colored compared to those on the adjacent surrounding flattened bar and swale units. The clasts in the bioturbated units had white pedogenic calcium carbonate coatings and were brought up from deeper calcium-carbonate

enriched horizons by bioturbation. The bioturbation units were mostly associated with large *Larrea tridentata* shrubs.

The two units on the oldest geomorphic surface were classified as desert pavement and shrub zone. Desert pavements were barren, flat land surface units. The clasts were mixed, being composed of fine (gravel sized: 2 to 74 mm) and large (cobble sized: 74 to 120 mm) clasts. In contrast, the shrub unit was characterized by a relatively larger bare soil component and greater vegetative abundance. This unit was interspersed with the desert pavement units. It had a general slightly convex topography compared to the desert pavement.

Within a 2 km² area, a minimum of 30 replicates of each of the seven types of landform units were spatially located with GPS coordinates. Out of this pool of landform units, nine study plots of each landform unit were randomly chosen (total of 63 study plots). These plots were used to characterize land surface properties (morphometric, physical, and biological) and to test whether each unit type was statistically discrete.

Morphometric land surface properties included landform unit shape of the profile and cross section and the areal extent. Landform unit shape was determined for the profile and cross-section belonging to one of the following categories: linear, convex, slightly convex, concave, and slightly concave (Schoeneberger and Wysocki 2002). The length and width of the plots were measured and the area was estimated using elliptical geometry.

Physical land surface properties such as amount of surface clasts, as well as their properties were characterized by placing a 1 m tape perpendicular to the longest axis of a study plot at three systematic locations, as follows. The longest axis was divided into three segments. Within each segment, the 1 m tape was placed in the center of each segment, one pace away from the longest axis to allow for available undisturbed ground. Each clast touching the tape was characterized for its length and width (Folk 1980). Clast sorting was calculated using Folk's logarithmic transformation criteria and transformed to the ϕ -scale (Folk 1980). High values represent a low degree of sorting, i.e., a larger spread of clast sizes. Low values of sorting are obtained when most of the clasts have the same dimensions. Phi scale skewness and kurtosis were calculated to interpret the clast frequency distribution (Folk 1980). Skewness can be used to evaluate the symmetry of sediment or surface clast distribution. The sign and magnitude of the skewness value can be used to document whether particular size fractions preferentially are skewing the distribution. A negative sign represents that coarse and a positive sign represents that fine fractions are in excess (Folk 1980). Kurtosis is a measure of distribution peakness and can be used to detect bimodal sediment distributions. The soil embeddedness of the clasts, i.e. tight lodging of surface rocks into the soil, was recorded as presence or absence. Surface roughness describes the microtopography of a site and was recorded by placing a roller chain one pace away from the 1 m tape and calculated using the methodology of Saleh (1993).

Biological characterization included determining abundance and diversity of biological soil crust community types and vascular plant functional groups using cover

and frequency quadrats. Biological crust functional type identification was made according to Pietrasiak et al. (2011a) and included: incipient algal/fungal crust, light algal crust (= unblackened algal crust), dark algal crust (= blackened algal crust), cyanolichen crust, green algal lichen crust and moss crust. Plant functional groups included: annual grasses, annual forbs, perennial grasses, perennial forbs, woody shrubs, and cacti. Ground cover was assessed using point intercept measurements of a 0.25-m² quadrat with 25 string intersections. The quadrat was systematically placed along the longest axis of the plot. A minimum of 100 cover point intercepts was required for each unit. Frequency of biotic land surface components was recorded using a 1-m² quadrat placed along the longest axis of the landform unit. Because units varied in size from 10 m² to 100 m², the number of cover and frequency quadrat placements along the longest axis of the unit was increased systematically with increases in unit size; i.e., in a 10 m² plot, quadrats were placed every meter whereas in a 100 m² plot, quadrats were placed every 10 meters. Shannon diversity (e^H) was computed using cover values. Functional group richness as number of functional groups was calculated using presence and absence data derived from frequency data.

2.2.3 Statistical analysis

Descriptive statistics for land surface properties and the following analyses were performed in SAS 9.1. Statistical differences in functional group diversity and richness between landform units were detected with ANOVA followed by a Tukey's test, using the PROC GLM statement in SAS. Several multivariate statistical analyses were

performed to distinguish and classify landform units and to investigate the factors driving the biotic communities. MANOVA is a statistical method that investigates the mean difference and statistical significance between treatments or group memberships (Tabachnik and Fidell 2007), in this case, landform unit type. Significance of the seven landform unit types as related to a combination of response variables (morphometric, biological, and physical land surface properties) was tested with the PROC GLM statement and a MANOVA model in SAS. A significant MANOVA model allows for further investigation of the data via discriminant analysis (DA). DA uses the response variables as predictor variables to classify the treatments or groups and visualize the difference in ordinal space (Tabachnik and Fidell 2007). This analysis discerns canonical correlations of morphometric, physical, and biological variables within their group memberships “landform unit type”. For both analyses, MANOVA and DA response variables were: (1) morphometric – plot area and slope shape; (2) physical – mean and median clast dimension; mean clast sorting, clast skewness and kurtosis; mean clast density; mean microtopographic roughness index and embeddedness; (3) biological – ground cover of plant and biological soil crust functional groups. Morphometric and physical variables were combined to represent abiotic factors. Dummy variables were created for slope shape for both the cross and profile shape. Only four of the five possible slope variables were considered in the analyses, since recognizing all four variables results in the identification of the fifth. Tukey tests were performed on

landform unit class means of the first two canonical variables consisting of a linear combination of the response variables in SAS. MANOVAs and DAs were run for: abiotic variables only (morphometric and physical); crust functional type only; plant functional type only; biotic variables only (crust and plant functional groups); and combined abiotic and biotic variables. For each DA, scatterplots were created to show the ordination pattern of the seven landform unit types.

A third multivariate statistical technique was performed to test which of the abiotic factors significantly drive the composition of crust and plant communities. Canonical correspondence analysis (CCA) is an analysis in which multiple dependent response variables can be related to multiple independent explanatory variables (Lepš & Šmilauer 2003). Thus, associations of physical and morphometric variables as explanatory variables with the assemblage of crust and plant functional types as response variables were investigated in CANOCO. A cover data matrix of crust and plant functional groups was used for the CCA. Perennial grasses rarely occurred in frequency quadrats and therefore were omitted as a response variable in the CCA. Explanatory variables were: (1) morphometric – plot area and slope shape; and (2) physical – mean clast dimension; mean clast sorting, skewness, kurtosis, and density; mean microtopographic roughness index and embeddedness. Median clast dimension was not included in the analysis due to high covariance with mean clast dimension.

2.3 Results

2.3.1 Landscape structure and composition: Abiotic properties

Overall, the fan skirt landscape was dominated by physical components such as gravel and cobbles with >45% cover for all unit types (Table 1) and a fan skirt mean of 67% cover of physical components with a clast density of 89% per meter. There was a general trend towards a decrease in microtopography and clast dimension, increased clast sorting, and homogeneous clast distribution with increasing geomorphic age. No bimodal clast distribution was detected for any units. Bar, flattened bar, and desert pavement had a slight excess in coarse fragments (negative sign of skewness, Table 2). Swale, flattened swale, and bioturbation units skewed slightly towards fine fragments. Bioturbation and shrub zones had a nearly symmetrical clast distribution (kurtosis near zero).

2.3.1.1 Geomorphic young surface – bars and swales

The geomorphically young swale units were dominated by physical components, in particular by gravel-sized (2 to 76 mm) clasts (Table 1). The physical land surface components were slightly lower in cover for the geomorphically young bar units (Table 1). Bar units had a greater component of cobble-sized clast components and had almost 50% fewer gravel-sized clasts as ground cover compared to swales (Table 1). Also, bar clasts were twice as large as swale clasts (mean and median, Table 2). Microtopography, as indicated by the roughness index, was more than 50% greater in bar units compared to

swales. Moreover, bars were less sorted than swales (length and width sorting $\phi > 1$, Table 2) and classified as poorly sorted. Swales were classified as moderately well sorted ($\phi > 0.75 - 1$, Folk 1980). Bar units had the highest microtopography amongst all units (highest RI, Table 2), and more rocks were embedded in the surface of bar units than in swales (Table 2).

2.3.1.2 Geomorphic intermediate-aged surface – flattened bars, flattened swales and bioturbated units

The intermediate-aged flattened swale had similar values of physical component coverage compared to the young swale (bare soil, gravel and cobble-sized clasts, Table 1). Intermediate-aged bar units had 50% lower cobble-sized fragment coverage and 50% higher coverage of gravel-sized components. In addition, mean and median clast dimensions decreased slightly in flattened bar units (Table 2). There was a slight increase in mean and median dimensions for flattened swale. Flattened bar units were still characterized by a rougher topography, poorer sorting ($\phi > 1$), and higher degree of embeddedness when compared to the flattened swale. However, roughness decreased from 2.5 to 1.7 from young to intermediate geomorphic age (Table 2).

The intermediate-aged bioturbation units had the lowest cover of physical components (less than half of land surface cover) with the lowest gravel- and cobble-sized clast cover (Table 1). These units were characterized by greater proportion of bare soil compared to the other units (Table 1). Also, bioturbated units were moderately well

sorted (Folk 1980) and had the fewest embedded clasts compared to all other units.

Microtopography was moderate, with an index value of 1.4.

2.3.1.3 Geomorphic old surface – desert pavements and shrub zone

Desert pavement units were almost completely covered by physical components (98%, Table 1), with 90% of the cover being gravel-sized clasts. Desert pavements had the lowest microtopography index value of all the units as well as the highest number of clasts embedded into the soil surface. Sorting had an intermediate value compared to the young bars and swales as well as intermediate flattened bars and swales (Table 2). Clast dimensions were coarse, but less so than bar and flattened bar units mostly attributed to coarse-sized gravel (Table 1, 2).

Shrub zone units were very similar to bioturbation units with a low cover of physical components, high cover of bare soil, moderate sorting, and low clast embeddedness. Roughness decreased almost half in shrub zone units compared to the bioturbated units (Table 2).

2.3.2 *Landscape structure and composition: Biotic properties*

Generally, three trends in biotic land surface properties could be observed with increasing geomorphic age: (1) cover and frequency of biological soil crusts and plants decreased from young bars and swales, to intermediate flattened bars and swales, to old desert pavement units; (2) biological soil crust cover increased from intermediate bioturbation units to old shrub zone units; and (3) crust and plant frequency and plant

cover was similar in intermediate bioturbation units and old shrub zone units. The greatest contrasts of plant and biological soil crust coverage were found on the two oldest geomorphic surfaces - desert pavements, with almost no biotic cover, and shrub zones, with some of the highest plant and biological soil crust coverage.

2.3.2.1 Plants

Vascular plants covered on average of 20% of the total fan skirt landscape (Table 1). Plant cover was highest in bioturbation and shrub zone units (Table 1). Plant cover for the other units ranks in decreasing order as follows: bar, flattened bar, swale, flattened swale, and desert pavement (Table 1). Percent plant frequency ranged from 26% on desert pavements to 100% in bioturbation units. Woody shrubs, annual forbs, and grasses were the most common functional groups for all units. Perennial grasses, forbs, and cacti were rare, overall, but had the highest frequency on bars and shrub zones (Table 1). Perennial grasses were only recorded in the young bars, swales and flattened swales. Perennial forbs were the most rare plant functional group and only found in shrub zones with a low frequency (Table 1).

2.3.2.2 Biological soil crusts

In general, biological soil crust cover was relatively low over the entire fan skirt area (total mean = 8%). However, it reached up to a maximum of 26% cover within some of the land surface units. The highest total crust cover was found in the bars and shrub zones with almost double the cover of the grand mean (Table 1). However, in bars

all six crust types were recorded, whereas in shrub zones only incipient and light algal crusts as well as a small percent of cyanolichen crusts were detected. Swales, flattened bars, bioturbated and shrub zone units had intermediate crust cover (Table 1). Flattened swale had a very low crust cover value (Table 1). Desert pavement was devoid of crust cover (Table 1). Lichen, moss and dark algal crusts were the most patchily distributed, with their greatest cover and frequency in young bar units. The most common crust types for all units were incipient and light algal crusts. Cyanolichen crusts were the most common non-algae dominated crust type (Table 1).

2.3.3 Land surface units as discrete statistical units based on surface properties

All five MANOVAs of abiotic ($F = 6.51$), biotic ($F = 3.62$), combined abiotic and biotic ($F = 6.68$), crust functional group ($F = 3.85$), and plant functional group ($F = 3.06$) were highly significant ($p < 0.001$) using the Wilks' Lambda significance test. Thus, in all five cases the linear combination of response variables was significantly different for at least one of the seven landform unit types in comparison to the others.

2.3.3.1 Abiotic land surface classification

Almost all seven landform units appeared as statistically distinct and widely separated units due to differences in abiotic land surface properties within the landscape as indicated in the DA scatterplot (Figure 2). The differences described by the first two linear combinations (discriminant axes) of the DA model explained a total of 77% of the variability in the data (Figure 2). The linear combination of abiotic variables representing

axis 1 explained a very large portion of the variability compared to axis 2 (discriminant axis 1 = 60%, discriminant axis 2 = 17%). Axis 1 was associated (from left to right) with a transition from concave to linear to convex morphometry as well as an increase in clast dimension, roughness and a decrease in sorting. Therefore, swales and flattened swales plotting on the left side were concave to slightly concave with smaller clasts, lower microtopography and higher clast sorting. Bars and flattened bars plotting on the right were convex to slightly convex with larger clasts, high microtopography and less sorting. Desert pavements plotted in the middle as linear units with a mix of land surface characteristics from the two plot sides. There was no significant difference between swale and flattened swale as, both plotted close to each other.

Axis two (from the lower to upper side) was associated with a transition from a convex to a more linear shape as well as an increase in clast dimension, sorting and finer clast distribution (Figure 2). These differences mostly determined the spatial separation of the bioturbated and shrub zone units from the others with bioturbated units plotting lower and the shrub zone units plotting the highest.

2.3.3.2 Biotic land surface classification

Different linear combinations were computed for discrimination of landform units using crust and plant functional group data separately (Table 3). However, patterns could be combined in a biotic DA (Figure 2). Discriminating landform units by the combined crust and plant functional group abundance data did not reveal such discrete units compared to the abiotic classification. Distinct separation of landform units in the DA

plot was only revealed for bars, shrub zones, and desert pavements. The other four units showed a gradual overlap and no distinct spatial separation. The first two discriminant axes explained slightly more of the data variability than the abiotic DA (about 78%). However, the canonical coefficients using biotic variables were weaker than in the abiotic analysis; i.e., never exceeded 1. Discriminant axis one explained about 47% of the data variation and depicted a gradient from left to right with increasing coverage of algal crust types and woody shrubs. Thus, desert pavements plotting on the left classified as units with low to no biological crust and woody shrub cover. In contrast, bars and shrub zones had high coverage of these two categories and plotted on the right (Figure 2). The second axis explained 31% of the variability and reflects a gradient shift from a purely algal dominated biological soil crust as found in shrub zones (plotted lower) to an algal crust with a lichen and moss component as found in bars (plotted higher) (Figure 2). In addition there is a trend toward higher annual forb cover (Table 3).

2.3.3.3 Combined abiotic and biotic land surface classification

Compared to the abiotic or biotic plots, the combined abiotic and biotic discriminant plot showed the widest separation of the landform units (Figure 2). Moreover, the correlation coefficient associated with the DA based on abiotic and biotic land surface properties combined had the highest values of all discriminant analyses (Table 3). However, even with the inclusion of the biotic variables, abiotic variables were still the strongest drivers of the analysis (i.e., highest canonical coefficients).

About 76% of the variability was explained with the first two discriminant axes. Axis one accounted for 45% of the variation and separated the units from left to right due to an increase of clast dimensions, microtopography, higher diversity of crust types and a shift of annuals (Table 3). In addition, the axis described a transition from concave to linear to convex landform morphometry (Table 3). Consequently, bars and flattened bars, and to some degree bioturbation units plotted on the right (Figure 2). They were classified as convex units with large clasts and high microtopography but had also higher coverage of annual grasses and greater diversity of crust functional groups including incipient crust, moss crusts and green lichen crusts (Table 3). In contrast, swales and flattened swales plotted on the left and were classified as concave, small clast covered, less roughened units with higher annual forbs coverage and lower biological soil crust diversity and coverage (Figure 2, Table 3). Desert pavement also plotted on the left side sharing more similarities in abiotic and biotic land surface characteristics of swale and flattened swales, than bar and flattened bar (Figure 2). Axis two explained 31% of the variation and just as in the abiotic DA was mostly causing the spatial separation of shrub zones and bars from bioturbation units (Figure 2). In contrast to axis 1 it depicts a gradient that combines increasing clast sorting and density, decreasing relief, increasing algal crust type diversity and woody shrub coverage, as well as decreasing cover of annual grasses (Table 3). Therefore the bioturbation units positioned lowest in the plot were classified as convex units with more heterogeneous clast sorting and more bare soil (Figure 2). They also had a higher annual grass coverage compared to the other units. On the other hand, shrub zones, bars, and to a lesser degree flattened bars were more

diverse in algal crust types with higher coverage of incipient algal/fungal, light and dark algal crusts and plotted higher (Figure 2). These units also had high woody shrub coverage (Table 3).

2.3.4 Functional group richness and Shannon diversity among the landform units

Strong significant differences in plant and biological soil crust functional group richness ($F=15.32$, $p<0.001$) and diversity ($F=10.39$, $p<0.001$) were detected among the landform units, with similar patterns in mean separation for both variables. Compared to richness, Shannon diversity index considers both richness and evenness and thus is more informative. Further evaluation will focus on interpretation of Shannon diversity data only. Overall, there was a trend for decreasing diversity observed with landform age. However, within the geomorphic surfaces, mesoscale landform units also showed significant differences in functional group diversity. Diversity of plant and biological soil crust functional groups was significantly the lowest in desert pavements and highest in bars (Figure 3). Intermediate levels of diversity were observed in flattened swales and bioturbation units. Although there was a trend for high diversity in swales, flattened bars and shrub zone units, these values were not significantly different from flattened swales and bioturbation units (Figure 3).

2.3.5 Abiotic factors related to plant and biological soil crust functional groups

Specific abiotic explanatory variables were associated with particular biological soil crust and plant functional groups (Figure 4a) and spatially separated landform units

from each other (Figure 4b). From the suite of environmental variables used in the CCA, only five were significant in the model but explained a total of 77% of the data variability (Figure 4a, b). Supporting the pattern observed from biotic DA, both environmental gradients (axis 1, 2) cause a gradual spread of the sites (Figure 4b) based on the distribution of the biological land surface components (response variables).

The first axis depicts a gradient of geomorphic age that is linked to clast size and embeddedness. Almost all biological soil crust types plotted on the right side and are found in sites of young to intermediate geomorphic age with coarse-sized embedded clasts (Figure 4a) such as bars and flattened bars (Figure 4b). On the other hand perennial forbs plotted on the left side. Their distribution was mostly driven by an increase in geomorphic age and decrease in clast size and lower clast embeddedness. These plants were highly associated with shrub zone units (Figure 4b). All other vascular plants plotted near the origin, and clear relationships to land surface characteristics were difficult to discern.

Axis 2 depicts a gradient that is associated with an increase in clast density and the change of the clast distribution towards a finer clast size (= skewness, Figure 4a, b). No biotic components except for cacti (C) grouped closely with these drivers in the upper part of the plot. Swales, flattened swales and the majority of desert pavement units were associated with these drivers and can be linked to a low abundance of biological components. In contrast, a coarser clast distribution with a lower clast density as particularly found in bars and flattened bars is linked to higher abundance of biological

soil crusts as they plot in the lower side (Figure 4a, b). Vascular plants plotted near the origin (Figure 4a).

2.4 Discussion

2.4.1 Landscape structure

At the meso-scale, the landscape of a Mojave Desert fan skirt is highly diverse in landform mosaic units. Moreover, these landform mosaics are associated with distinct assemblages of abiotic and biotic land surface properties. In general, the landscape is dominated by abiotic components, mainly gravel- and cobble-sized alluvial debris. Only shrub zone and bioturbation units had a noticeable amount of bare soil. Almost all landform units were significantly different from each other and could be classified based on the abiotic properties derived almost exclusively from the alluvial debris. The desert pavement units were almost completely composed of physical land surface components. However, some mosaics had a substantial biotic component such as bar, bioturbation, and shrub zone units, in which 30 to 50% of the land surface was composed of vascular plants and biological soil crusts. Combining abiotic and biotic land surface properties led to the best classification of landform units.

Biological soil crusts were limited in distribution. Specific landform units showed higher crust cover values as well as functional group diversity (bar and shrub zone) than others (desert pavement). This patchy distribution of crusts is similar to the

findings of other studies in the Mojave Desert (Johansen et al. 2001, Belnap 2002, Pietrasiak et al. 2011a, b). However, patchiness of crust distribution showed a consistent pattern within the geomorphic framework and was an important factor in separating the landform units in the combined abiotic and biotic discriminant analysis. Overall, bar and shrub zone units had the highest crust cover and highest crust diversity. In contrast, desert pavements were devoid of crusts. Comparable to other sites in the Mojave Desert (Johansen et al. 2001, Belnap et al. 2007, Pietrasiak et al. 2011), algal crust types were dominant, with incipient and light algal crust being the most prevalent crust types. Mosses and lichens were minor components of crusts. They were most abundant in bars. Furthermore, bars were the only units where a lichen crust type (CLC, Table 1) covered more ground than an algal crust type.

Vascular vegetation also showed a patchy distribution, with desert pavements being associated with very sparse vegetation cover and other landform units, such as bioturbation and shrub zones, with over one third of the area covered by plants. Similar to crust diversity patterns, bar and shrub zone units had the greatest plant functional group diversity. The most prevalent functional group in all units was woody shrubs, while cacti, perennial forbs and grasses were the most rare. Plants always had a greater cover than crusts. Typically, plants have a competitive advantage over biological soil crusts to establish in favorable environments (Belnap et al. 2001).

2.4.2 Implications of abiotic and biotic land surface components on geomorphic processes

Specific assemblages of land surface components can impact geomorphic processes differently (Hirmas et al. 2011). The morphological properties of surface rocks, biological soil crusts, and vascular plants have important effects on water and wind flow, sediment production and deposition, as well as erosion (Descroix et al. 2001, Wainwright 2009). For example, lateral wind and water flow is accelerated by flat surfaces such as smooth desert pavements (Wood et al. 2005) or cyanobacterial crust (Belnap 2006). At the micro-scale water flow can be accelerated on blank rock surfaces supplying water to adjacent rock-crevices (Warren-Rhodes et al. 2007). In contrast, lateral wind or water flow is slowed by any obstacle, which increases the flow turbulence and tortuosity (Descroix et al. 2001, Belnap 2006). Thus, micro-topography created by protruding surface clasts (Yair and Klein 1973), biological soil crust types that are roughened (Belnap 2006), and plant canopies and litter (Abrahams and Parsons 1991, Neave and Abrahams 2001) decreases water flow. The vertical water flow in the form of infiltration can generally be promoted by biologic components. Animal burrows and plant root channels (Abrahams and Parsons 1991, Neave and Abrahams 2001), as well as macropores formed by certain biological soil crusts (Belnap 2006) lead to increased infiltration. However, infiltration can be inhibited by tightly packed clast layers (Wood et al. 2005) or dense, soil pore clogging cyanobacterial crusts (Belnap 2006).

Sediment and dust can be naturally produced by burrowing activity of small mammals such as ground squirrels, kangaroo rats or pocket mice, all of which are

common rodents in the Mojave Desert (McAuliffe and McDonald 2006). On the other hand, sediments and dust can deposit on any object that interferes with the wind movement. Consequently, sites of deposition and accumulation are crevices between protruding rocks, as well as crevices in rugose or pinnacled biological soil crust types or individual moss phylids and lichen thalli (Hirmas and Graham 2011, Belnap 2006). Dust and coarser sediment is also trapped and accumulated around shrubs and grasses, forming mounds (Wainwright 2009). Tightly packed clasts in surfaces of desert pavement with a smooth microtopography are less efficient in dust trapping (Hirmas et al. 2011).

Eolian and fluvial erosional processes are prevented by the presence of surface rocks, biological soil crusts, plant litter, and roots (Hupy 2004, Belnap et al. 2007). Specifically, surface rocks, biological soil crust and plant litter cover the land surface protecting the underlying soil. Thus, these components reduce rill formation (Valentin and Casenave 1992) and sheet erosion. Also, biological soil crusts and plant roots function to intercept raindrop splash effect (Descroix et al. 2001, Neave and Abrahams 2001, Belnap 2006, Herrick et al. 2010), and/or promote soil aggregation and porosity (Neave and Abrahams 2001, Belnap 2006, Wainwright 2009).

By applying these known feedbacks to the landform mosaic units in this study, the following patchwork of geomorphic processes emerge. Bars, and to a lesser degree flattened bars, had rough surfaces due to extensive protruding coarse gravel and cobble cover. They also had some of the most extensive biological soil crust cover and were particularly rich in crust types promoting roughness and consequent water infiltration and dust trapping. Furthermore, substantial numbers of woody shrubs were present in these

areas. Consequently, due to the combined effect of land surface properties these units are sites with increased water infiltration and sediment and dust accretion, decreased runoff, and water and wind erosion.

In contrast, swale and flattened swale had relatively smooth surfaces due to smaller size of clasts and lower vegetation and biological soil crust abundance. If the infiltration capacity of adjacent convex shaped bars or flattened bars would be exceeded, some runoff and debris could be distributed to concave swales or flattened swales due to gravitational forces. Infiltration in these sites may still be relatively high due to the low embeddedness of the smaller sized surface gravel (see Herrick et al. 2010). Physical crust observed under fine-sized gravel in these units should limit erosion.

In contrast to these sites, desert pavement sites were characterized by the highest clast density, lowest vegetation cover, and general absence of crusts. Although clasts were highly embedded, the surface was relatively smooth, as indicated by the lowest microtopography recorded for all landform units. The densely packed gravel and cobble layer can seal the ground, protecting the underlying soil from erosion but limiting further sediment additions. These properties combine to decrease infiltration and increase runoff on desert pavements.

Bioturbated and shrub zone units are the most likely sites of sediment production due to the burrowing activity of small mammals. This sediment can be transported away by wind or runoff water. However, bare soil was recorded in <10% of the units. Gravel, vegetation, and biological soil crusts still covered a considerable portion of the ground despite the natural disturbance, which may help to trap and stabilize newly produced

sediment. However, soil stability due to crusts may be limited in the plant interspaces. Soil covered by incipient or light algal crusts is less protective against raindrop splash than lichen and moss crusts in bars and swales (Belnap 2006). Algae, fungi and cyanobacteria grow mostly within the soil matrix, leaving parts of the ground surface exposed to raindrop impacts (Belnap 2006). In contrast, lichen and mosses protrude over the soil and dissipate raindrops with their thalli or phylids. Increased infiltration rates in these units can be expected due to preferential water flow in macropores and channels created by the abundant fauna and flora.

2.4.3 Implications of geomorphology, and linked physical land surface properties, on biota

This study distinguished several abiotic land surface properties that drive photosynthetic vascular plant and biological soil crust community components. Also, different drivers impacted the abundance of biological soil crust types versus plant functional groups. The most important drivers for dark algal, lichen and moss crust abundance were variables that determine a beneficial microhabitat: a coarse surface rock size with protruding embedded rocks that have soil crevices in between them. These properties were preferentially found in bar units. The abundance of well-developed crusts with mosses and lichens can be related to physical properties and suitable habitat conditions (Pietrasiak et al. 2011a, b). Surface rocks may offer a favorable microclimate by decreasing radiation stress and improving availability and amount of moisture (Warren-Rhodes et al. 2007). Improved moisture conditions allow for longer hydration

periods of the crusts, which are linked to enhanced carbon and nitrogen fixation (Evans and Johansen 1999). In addition, roughness created by protruding clasts can aid in dust capture, promoting nutrient status, water holding capacity, and entrapment of lichen propagules (Belnap 2002, Lalley and Viles 2006).

In contrast, as seen in the CCA biplot, increasing geomorphic age shifted the crusts into communities being mainly composed of incipient and light algal crusts. This trend can be linked to an overall decreasing microtopography and clast dimensions, and to some degree increasing clast density. This change in microhabitat may be less favorable for moss and lichen crusts, with fewer soil crevices available for their colonization due to increasing clast density. Increasing geomorphic age also was associated with higher occurrence of small mammal burrowing activity in bioturbation and shrub zone units which could produce unstable microsites due to natural disturbance by bioturbation.

Greater abundance of plant functional groups was apparent with increasing geomorphic age. In particular, the abundance of perennial forbs was greatest in older shrub zone units. However, most of the plant functional groups in the CCA plotted close to the origin, and their abundance could not be fully determined by land surface characteristics. Soil properties and inter- as well as intraspecific interactions may be stronger drivers for plants at this scale. On the other hand, geomorphically old units with increased clast density, finer clast size distribution, and higher sorting as found in flattened swales and desert pavements impede both biological soil crusts and plants.

Although not directly measured, links to faunal abundance may be drawn from the knowledge of vegetation and crust abundance. For example, kangaroo rats, pocket mice and ground squirrels, which are the most abundant burrowing rodents in Mojave Desert, prefer large perennial shrubs such as *Larrea tridentata* and *Lycium andersonii* (McAuliffe and McDonald 2006). Units with a greater ground cover and diversity of shrubs (i.e, shrub zone units) would be ideal habitat patches for multiple small mammal individuals of the same or different species. Presence of small mammals can, in turn, create further surface heterogeneity by creating new habitats and facilitating overall biodiversity of these mosaics (Davidson and Lightfoot 2008). Bars and swales with high abundance of moss, lichen, and dark algal crusts may be potential habitats for arthropods and other invertebrates specialized in feeding on these resources (Belnap 2006, Darby et al. 2007). Light algal crusts, the most common crust type in the Mojave and which were preferentially found in shrub zone units in our study, may provide suitable stability for burrows used by small reptiles (Zaady and Bouskila 2002). Furthermore, units with high diversity of crust and plant functional groups may result in high diversity of animals. Thus, mapping landform mosaics may be important to discern habitats for fauna.

2.4.4 Hypothesized landform evolution

In my study I observed strong ecological and geomorphic feedbacks between landscape configuration and abiotic and biotic land surface properties over geomorphic time. With the knowledge gained in this study one can recognize two distinctively diverging trajectories of landform evolution (Figure 2.5). The first trajectory describes an

abiogenic landform evolution and the second a biogenic pathway (Figure 2.5). Both trajectories result in sharply contrasting oldest states of barren units in the abiogenic landform evolution versus the biodiversity and biotic cover-rich units of the biogenic evolution (Figure 2.5).

The trajectory of an abiogenic landform evolution is the development of a young alluvial debris deposit into a desert pavement (Figure 2.5). In this trajectory, the landscape changes from a relatively high topographic surface to one with a reduced relief changing from convex- and concave-shaped bars and swales to intermediate-aged flattened bar and swale to a flat and smooth desert pavement (Figure 2.5). A relief reduction and associated desert pavement formation occurs due to long-term geomorphic stability, sediment additions as dust-capture, embedding of clasts, and material redistribution due to gravitational and hydrological forces (McAuliffe and McDonald 2006). All of these processes smooth surface topography (Birkeland 1999). Additionally, vegetation and biological soil crust recede over time from covering a quarter to less than 1% of the ground (Table 2.1). The sharp mosaic boundaries between young bar and swale units created by the contrast of surface clast dimensions as well as roughness diminish over time. Coarse cobbles and gravel weather into smaller clasts over time (Sharp and Birman 1963, Al-Farraj and Harvey 2000). This process explains the decrease in clast size observed in the progression from bars to flattened bars (Table 2.2). Clasts from bar units mix into swale causing the slight increase of clast size in flattened swales (Table 2.2). Consequently, over geomorphic time clast sorting improves and the sharp unit boundaries disappear and become diffuse. Rock crevices that are

especially pronounced in bar units eventually get filled in with weathered surface clast material. Desert pavements on old geomorphic surfaces are ultimately large areas comprised of many historical bar and swale mosaics with negligible relief and closely packed surface clasts that seal the surface.

The second trajectory is a biogenic landform evolution - the development of a young alluvial debris deposit to a stage of bioturbation, initialized at intermediate age to eventually shrub zone units at the oldest age (Figure 2.5). The most critical driving forces for this trajectory are the biotic interactions and facilitation of flora and fauna through time that results in an alternative future state (Peters et al. 2006). Large shrubs are preferred habitats for small mammals (McAuliffe and McDonald 2006). During foraging and burrowing activities of these mammals, the abiotic processes that produced a tightly packed clast layer are interrupted (Neave and Abrahams 2001). Newly exposed bare soil and rock interspace crevices are created due to this natural disturbance and become available for crust and vascular plant colonization or redistribution with wind or water. Burrowing activity also may enhance shrub islands of fertility by promoting soil mixing, accumulating organic matter via feces and seed caches, and increasing infiltration due to increased macroporosity. Moreover, bioturbation encourages redistribution of material and resources to this spatial patch (Peters et al. 2006). Expansion of bioturbation units with one large shrub to the shrub zone unit with many shrubs (Figure 2.5) may result from (1) formation of *Larrea* clones growing outward (McAuliffe et al. 2007) while simultaneously shifting burrowing mammal activity outward; (2) preferential germination of seeds brought in by small mammals as cache

(see Alkon 1999); and (3) seed trapping by established shrubs and successful seed germination in fertile soils under nurse shrubs. Additionally, due to burrowing activity, bare soil becomes available for crust colonization (Table 2.1). Mobile and/or ubiquitous cyanobacteria, algae and fungi are pioneer colonizers that quickly can become established on newly exposed soil material and initiate crust formation (see Belnap 2006). Through time the shift of burrowing activity outward as well as its concentration under selected shrubs results in more and more soil in shrub-interspaces becoming available. This soil may be spatially isolated from burrowing disturbance and stable enough for small colonizations of non-mobile lichen and mosses.

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Table 2.1 Means and standard errors of biotic land surface properties of the seven landform unit types in the study area, Mojave Desert.

Cover (%)	Biological soil crust	Variable	Landform unit type													
			BR ^a		SW ^b		FB ^c		FS ^d		BT ^e		DP ^f		SZ ^g	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
		IC ^h	3.3	1.0	3.9	1.2	4.5	1.3	1.4	0.5	6.9	1.8	0.1	0.1	9.0	1.4
		LAC ⁱ	2.7	0.6	1.4	0.5	2.1	0.6	0.6	0.2	0.8	0.4	0.0	0.0	3.3	0.5
		DAC ^j	0.2	0.2	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		CLC ^k	5.4	1.2	1.5	0.7	1.0	0.4	1.0	0.3	0.1	0.1	0.0	0.0	0.7	0.3
		GLC ^l	1.0	0.6	0.1	0.1	0.4	0.2	0.2	0.1	0.2	0.2	0.0	0.0	0.0	0.0
		MC ^m	2.3	1.0	0.1	0.1	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		Total	14.9		7.0		8.1		3.2		8.0		0.1		13.1	
		AG ⁿ	4.9	0.8	3.4	1.7	6.3	0.6	3.0	0.8	12.6	3.0	0.1	0.1	4.3	1.2
		AF ^o	1.9	0.8	1.2	0.4	2.7	0.9	1.5	0.9	1.0	0.4	0.1	0.1	2.8	1.0
		PEG ^p	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		PEF ^q	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2
		WS ^r	15.5	3.8	5.4	1.7	11.0	2.0	8.1	3.0	20.6	2.9	0.8	0.4	24.2	4.2
		C ^s	0.2	0.2	0.2	0.2	1.3	1.3	0.6	0.5	0.1	0.1	0.0	0.0	0.6	0.4
		Total	22.6		10.2		21.2		13.3		34.3		1.0		32.1	
		Litter	5.0	0.9	4.2	1.1	5.6	1.4	4.4	0.9	8.0	1.4	0.6	0.1	9.2	1.1
		Bare Soil	1.7	0.6	2.2	0.7	2.7	0.6	4.0	0.5	8.7	1.4	4.1	0.5	7.5	1.3
		Gravel	41.1	2.7	75.9	4.3	53.6	4.4	74.8	3.5	39.9	4.8	90.8	0.9	37.9	3.2
		Cobbles	14.8	3.5	0.5	0.3	8.7	2.3	0.3	0.3	1.1	0.7	3.4	0.8	0.1	0.1
		Total	57.5		78.6		65.0		79.2		49.7		98.3		45.5	
		Frequency	100.0	0.0	89.3	8.9	93.1	3.5	84.4	7.3	95.0	3.3	18.5	4.0	100.0	0.0
		Biological soil crust	90.4	5.7	69.0	12.6	79.4	10.5	64.4	12.8	67.2	7.9	8.5	3.3	92.0	4.1
		LAC ⁱ	6.7	6.7	1.9	1.9	1.9	1.9	0.0	0.0	0.0	0.0	0.0	0.0	1.9	1.9
		DAC ^j	91.6	3.5	59.8	13.3	63.0	13.5	62.7	11.9	7.2	3.6	0.0	0.0	18.3	8.4
		CLC ^k	77.9	7.7	16.4	7.9	48.5	15.0	23.7	10.4	2.2	2.2	0.0	0.0	3.9	2.6
		GLC ^l	55.2	13.8	13.4	6.4	16.3	9.3	6.4	3.5	0.0	0.0	0.0	0.0	12.1	4.8
		MC ^m	100.0		89.3		93.1		84.4		95.0		18.5		100.0	
		Total														

Table 2.1 (continued)

Variable	Landform unit type													
	BR ^a		SW ^b		FB ^c		FS ^d		BT ^e		DP ^f		SZ ^g	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Frequency	96.2	2.6	81.9	7.0	91.7	4.4	84.8	8.7	100.0	0.0	23.7	6.5	95.9	2.7
Vascular plants	91.1	6.8	68.9	14.2	87.8	8.1	93.3	4.7	81.1	9.5	25.8	6.5	88.1	5.1
AG ⁿ	2.2	2.2	1.6	1.6	0.0	0.0	2.2	2.2	0.0	0.0	0.0	0.0	0.0	0.0
AF ^o	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.8	3.1
PEG ^p	87.5	4.4	61.6	6.2	71.3	3.7	62.2	7.5	87.2	5.8	14.1	1.6	88.3	4.8
PEF ^q	9.7	4.6	3.7	2.4	2.8	2.8	3.0	2.0	2.8	2.8	0.0	0.0	6.7	3.2
WS ^r	96.2		81.9		91.7		93.3		100.0		25.8		95.9	
C ^s														
Total														

^a BR = bar^b SW = swale^c FB = flattened bar^d FS = flattened swale^e BT = bioturbated^f DP = desert pavement^g SZ = shrub zone^h IC = incipient algal/fungal crustⁱ LAC = light algal crust^j DAC = dark algal crust^k CLC = cyanolichen crust^l GLC = green algal lichen crust^m MC = moss crustⁿ AG = annual grasses^o AF = annual forbs^p PEG = perennial grasses^q PEF = perennial forbs^r WS = woody shrubs^s C = cacti

Table 2.2 Means and standard errors of abiotic land surface properties of the seven landform unit types in the study area, Mojave Desert.

Variable	Landform unit type														
	BR ^a		SW ^b		FB ^c		FS ^d		BT ^e		DP ^f		SZ ^g		
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
Clast length	Mean (mm)	28.6	1.3	13.2	0.7	25.0	1.8	15.4	1.0	16.0	0.4	23.6	1.1	14.7	0.5
	Med. (mm)	21.7	1.7	11.3	0.6	18.8	2.0	13.0	0.9	13.1	0.5	19.7	0.8	12.2	0.5
	Sorting (ϕ)	1.11	0.08	0.77	0.03	1.13	0.10	0.84	0.07	0.87	0.07	1.03	0.09	0.80	0.04
	Skew. ^j	-0.14	0.09	-0.25	0.10	-0.16	0.10	-0.17	0.13	-0.30	0.11	0.08	0.15	-0.20	0.09
	Kurt. ^k	-0.20	0.17	0.39	0.28	-0.48	0.13	0.20	0.12	0.31	0.46	-0.14	0.22	-0.01	0.09
Clast width	Mean (mm)	19.4	0.8	8.9	0.4	16.5	1.2	10.0	0.6	9.8	0.8	15.5	0.7	9.3	0.7
	Med. (mm)	14.3	1.0	7.5	0.4	12.5	1.3	8.5	0.6	8.4	0.8	12.9	0.6	7.9	0.6
	Sorting (ϕ)	1.10	0.08	0.78	0.02	1.10	0.09	0.80	0.06	0.84	0.07	0.99	0.09	0.78	0.04
	Skew. ^j	-0.24	0.11	-0.29	0.07	-0.18	0.09	-0.17	0.11	-0.27	0.09	0.00	0.18	-0.18	0.08
	Kurt. ^k	-0.19	0.15	0.13	0.33	-0.34	0.16	0.07	0.20	-0.04	0.15	0.10	0.34	-0.04	0.06
Clast den. ^e	N	58.6	6.6	127.5	16.3	71.1	8.5	111.6	13.8	94.8	15.4	75.0	4.5	83.5	11.0
RI		2.5	0.1	0.9	0.1	1.7	0.1	0.8	0.1	1.4	0.1	0.5	0.0	0.8	0.1
Areal ext.	m2	90	12	104	12	121	19	161	22	84	20	2859	1383	799	281
Embedd. ^f	N	7.7	0.6	2.5	0.4	8.0	0.6	2.7	0.5	2.0	0.3	8.5	1.0	3.7	0.6

^a BR = bar

^b SW = swale

^c FB = flattened bar

^d FS = flattened swale

^e BT = bioturbated

^f DP = desert pavement

^g SZ = shrub zone

^e Clast den. = clast density

^f Embedd. = clast embeddedness

^j Skew = skewness

^k Kurt = kurtosis

Table 2.3 Total-sample standardized canonical coefficient calculated in the five discriminant analyses. Important coefficients (>1.00) are highlighted in bold, intermediate (>0.50 - 1.00) are italics.

Predictor variables		Abiotic		Biotic		Abiotic and biotic		CFG ^a		PFG ^b	
		DA1 ^c	DA2 ^d	DA1 ^c	DA2 ^d	DA1 ^c	DA2 ^d	DA1 ^c	DA2 ^d	DA1 ^c	DA2 ^d
Clast length	Mean	5.56	-2.01	-	-	5.45	2.68	-	-	-	-
	Med	-5.50	3.56	-	-	-6.99	-1.71	-	-	-	-
	Sort	-1.31	2.26	-	-	0.43	-6.04	-	-	-	-
	Skew. ^j	0.27	-3.52	-	-	<i>-0.55</i>	<i>0.56</i>	-	-	-	-
	Kurt. ^k	0.08	0.37	-	-	0.27	<i>-0.37</i>	-	-	-	-
Clast width	Mean	-4.50	<i>-0.74</i>	-	-	-4.70	-1.85	-	-	-	-
	Med	5.36	<i>0.50</i>	-	-	7.13	2.05	-	-	-	-
	Sort	1.16	0.33	-	-	<i>-0.80</i>	5.85	-	-	-	-
	Skew. ^j	<i>-0.19</i>	<i>-0.27</i>	-	-	<i>0.80</i>	<i>-0.23</i>	-	-	-	-
	Kurt. ^k	<i>-0.18</i>	0.17	-	-	<i>-0.16</i>	<i>0.54</i>	-	-	-	-
Clast d. ^e		<i>-0.03</i>	<i>0.03</i>	-	-	0.26	1.82	-	-	-	-
RI		2.02	<i>-0.56</i>	-	-	4.07	0.44	-	-	-	-
Embed. ^f		<i>0.82</i>	<i>0.94</i>	-	-	0.49	<i>0.86</i>	-	-	-	-
x sect ^g	lin	2.01	1.19	-	-	2.28	0.04	-	-	-	-
	conv	3.03	<i>-0.09</i>	-	-	3.64	<i>-0.32</i>	-	-	-	-
	sconv. ^l	2.99	<i>0.90</i>	-	-	3.47	<i>0.99</i>	-	-	-	-
	conc	<i>-0.15</i>	0.03	-	-	0.04	0.21	-	-	-	-
pro sect ^h	lin	<i>-0.14</i>	<i>-0.04</i>	-	-	<i>-0.13</i>	<i>0.52</i>	-	-	-	-
	conv	<i>0.61</i>	-1.31	-	-	1.03	-2.35	-	-	-	-
	sconv.	0.14	<i>-0.10</i>	-	-	<i>-0.03</i>	2.27	-	-	-	-
	conc	<i>0.84</i>	<i>-0.87</i>	-	-	1.41	-1.70	-	-	-	-
Plot area		0.18	0.28	-	-	0.02	0.13	-	-	-	-
FGC ⁱ	IC ^m	-	-	<i>0.68</i>	<i>-0.61</i>	<i>0.87</i>	1.02	0.03	<i>0.91</i>	-	-
	LAC ⁿ	-	-	0.46	<i>-0.30</i>	0.02	1.04	0.20	<i>0.85</i>	-	-
	DAC ^o	-	-	0.09	<i>-0.45</i>	0.33	<i>0.64</i>	<i>-0.05</i>	0.33	-	-
	CLC ^p	-	-	0.41	<i>0.79</i>	0.02	<i>-0.08</i>	<i>0.92</i>	<i>-0.33</i>	-	-
	GLC ^q	-	-	0.23	<i>0.91</i>	<i>0.51</i>	0.31	<i>0.54</i>	<i>-0.42</i>	-	-
	MC ^r	-	-	0.40	<i>0.65</i>	<i>0.59</i>	0.31	<i>0.55</i>	0.04	-	-

Table 2.3 (continued)

Predictor variables	Abiotic		Biotic		Abiotic and biotic		CFG ^a		PFG ^b	
	DA1 ^c	DA2 ^d	DA1 ^c	DA2 ^d	DA1 ^c	DA2 ^d	DA1 ^c	DA2 ^d	DA1 ^c	DA2 ^d
AG ^s	-	-	0.35	0.26	0.78	-2.87	-	-	0.60	-1.09
AF ^t	-	-	0.21	0.66	-0.69	0.14	-	-	0.16	0.71
PEG ^u	-	-	0.00	0.00	0.00	0.00	-	-	0.00	0.00
PEF ^v	-	-	0.01	-0.14	0.10	-0.30	-	-	0.02	0.33
WS ^w	-	-	0.85	-0.06	-0.14	1.20	-	-	1.07	0.58
C ^x	-	-	0.06	0.03	-0.55	0.42	-	-	-0.23	0.09

^a CFG = biological soil crust functional groups

^b PFG = plant functional groups

^c DA1 = discriminant axis 1

^d DA2 = discriminant axis 2

^e Clast d. = clast density

^f Embedd. = clast embeddedness

^g x sect. = slope cross section

^h pro sect. = slope profile section

ⁱ FGC = functional group cover

^j Skew = skewness

^k Kurt = kurtosis

^l sconv. = slightly convex

^m IC = incipient algal/fungal crust

ⁿ LAC = light algal crust

^o DAC = dark algal crust

^p CLC = cyanolichen crust

^q GLC = green algal lichen crust

^r MC = moss crust

^s AG = annual grasses

^t AF = annual forbs

^u PEG = perennial grasses

^v PEF = perennial forbs

^w WS = woody shrubs

^x C = cacti

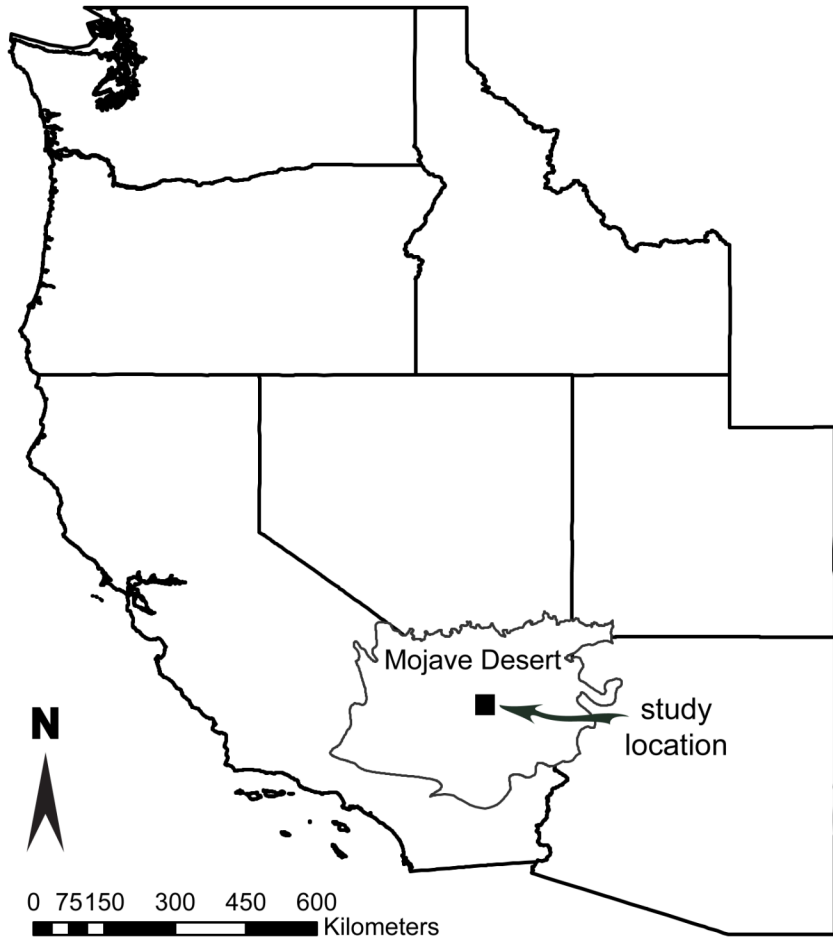


Figure 2.1 Map of the study location within the Mojave Desert of the western U.S.

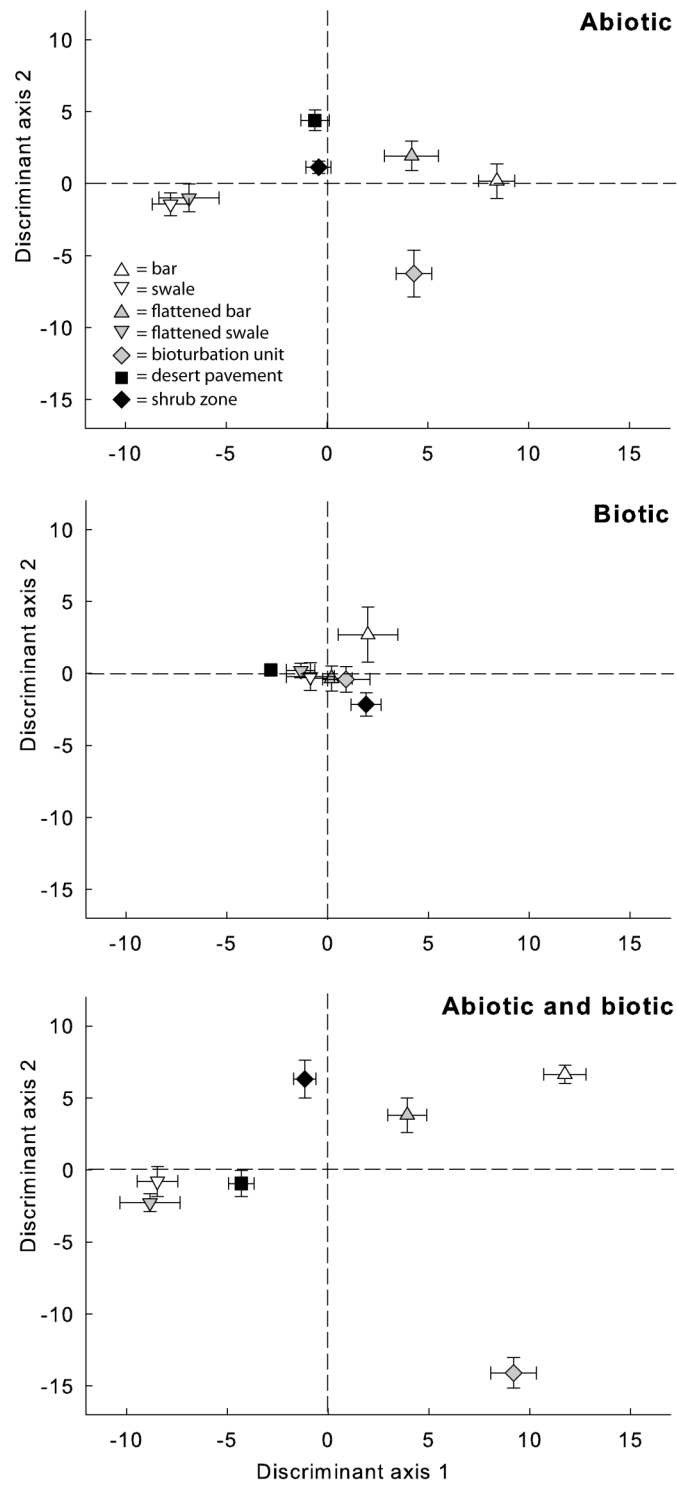


Figure 2.2 Discriminant analysis plots for abiotic and biotic land surface properties showing the first two axes. Error bars on centroids represent one standard deviation. White symbols represent units found on young, grey represent units on intermediate and black represents units on old geomorphic surfaces.

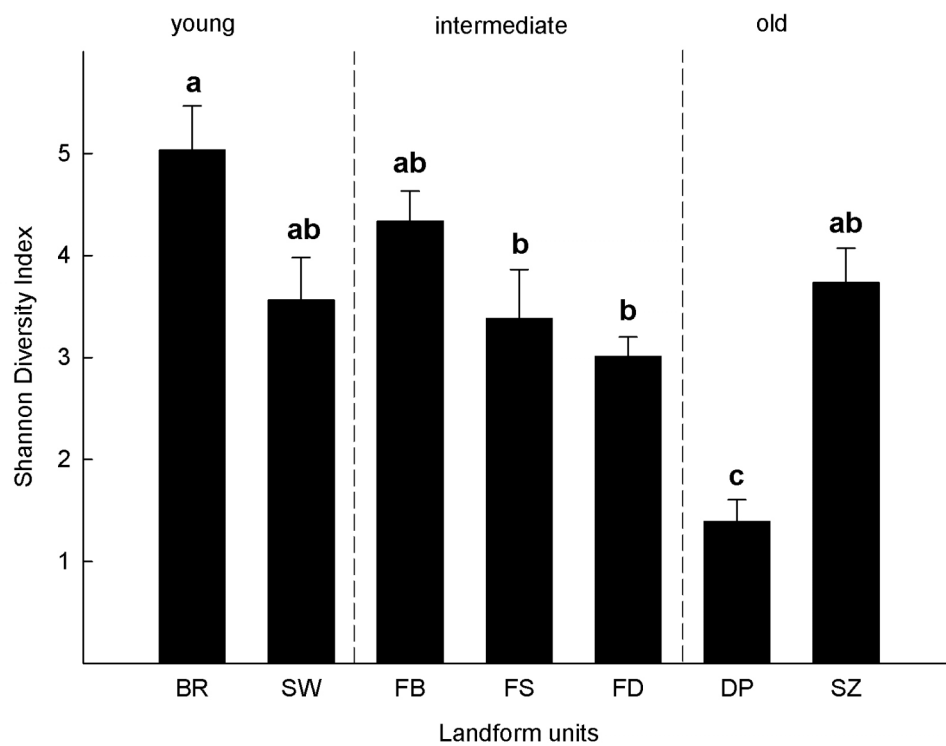


Figure 2.3 Bar graph showing Shannon diversity index values of crust and plant functional group diversity between the seven landform units. Letters above bars indicate significant difference between landform units.

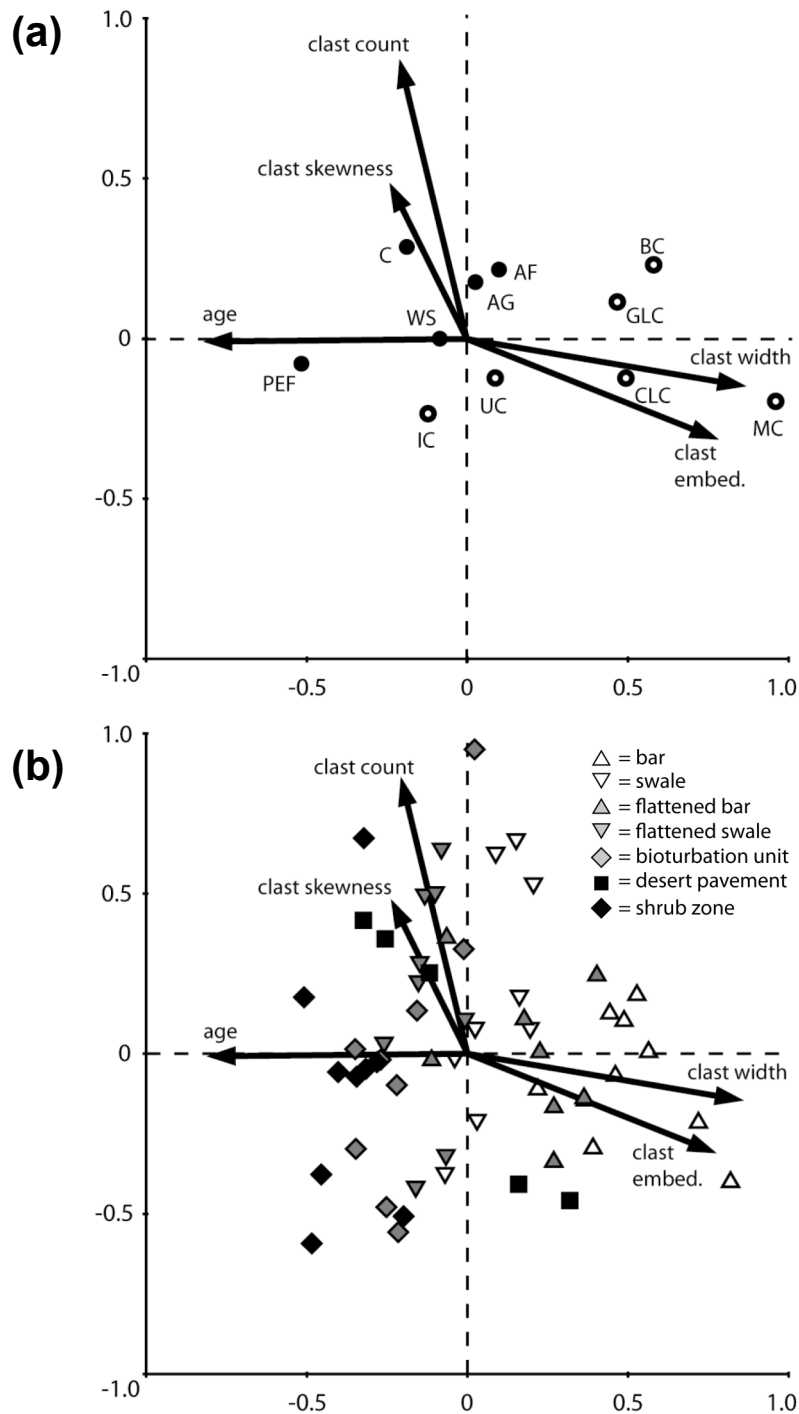


Figure 2.4 CCA biplots for (a) crust and plant functional groups (IC = Incipient algal crust, UC = light algal crust, BC = dark algal crust, CLC = cyanolichen crust, GLC = green algal lichen crust, MC = moss crust, AG = annual grasses, AF = annual forbs, PEF = perennial forbs, C = cacti, WS = woody shrubs) and (b) study plots. Biplots are showing significant explanatory abiotic variables only. Axis 1 (horizontal) explains 49% and axis 2 (vertical) explains 18% of the total variability.

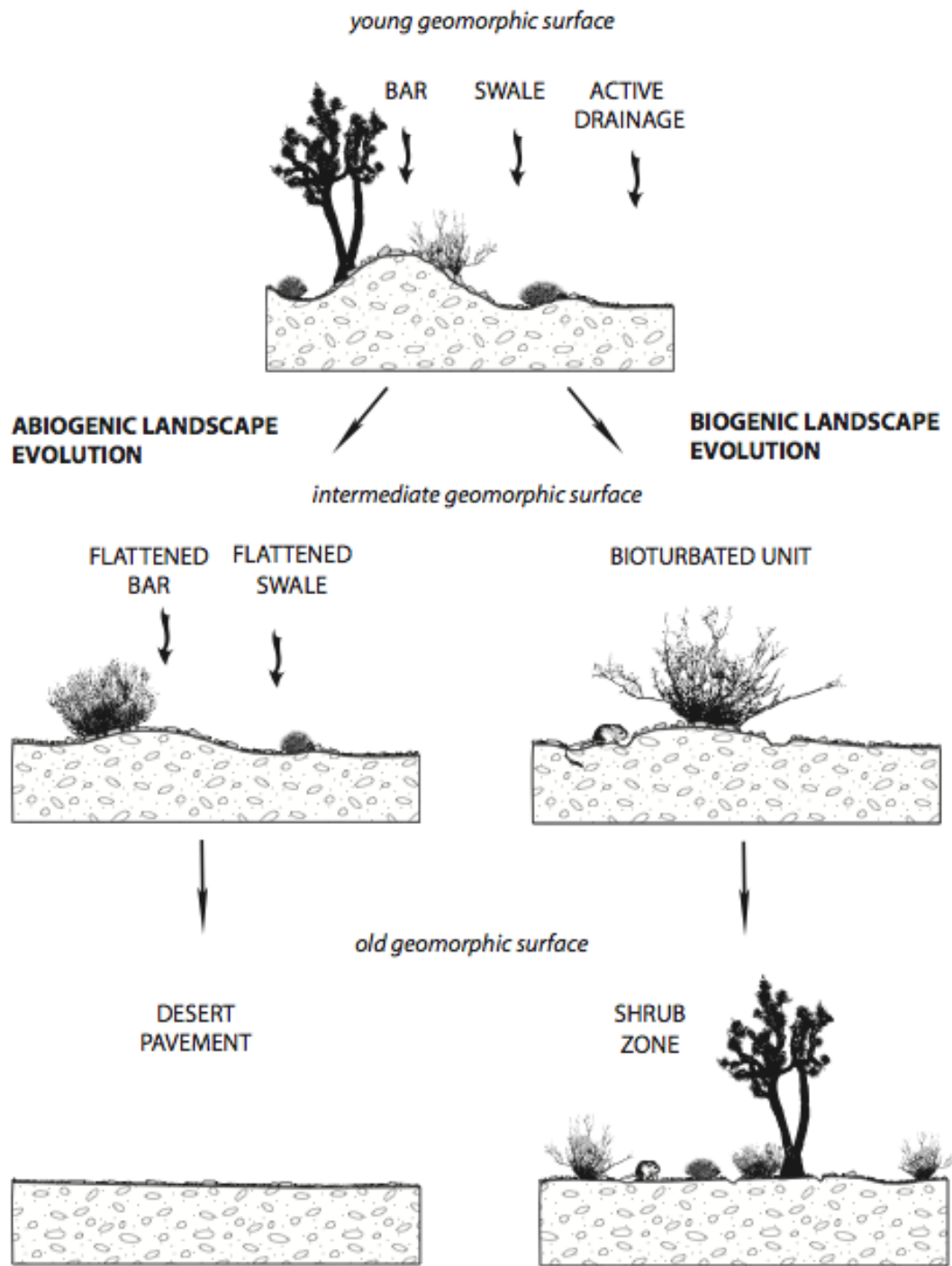


Figure 2.5 Hypothesized mechanistic scheme of abiogenic and biogenic landform evolution of a fan skirt in the Mojave Desert. Components not drawn to scale.

3. ECOLOGICAL FUNCTIONS VARY AMONG BIOLOGICAL SOIL CRUST TYPES AND WITHIN LANDFORMS AS INDICATED BY THE ABQI – AN AREA BASED QUALITY INDEX

Abstract

Deserts are resource poor ecosystems that are currently threatened by anthropogenic disturbance. Biological soil crusts, established at the soil surface, help maintain resources through their multiple eco-functional roles. The goal of this study was to investigate the differences of multiple ecological functions among different types of soil crust communities. Nitrogen and carbon fixation, soil stability, and hydrological properties were assessed for eight crust community types collected in the Mojave Desert. Crust types included: incipient algal/fungal, fungal, light algal, cyanolichen, green algal lichen, rough moss, hairy moss, and dark moss crust. Cyanolichen crust outperformed all other crusts in multi-functionality whereas incipient crust had the poorest performance. Furthermore, an area based quality index (ABQI) was developed that integrated all four major ecological functions at a given site. This index was then used to compare the quality of biological soil crusts occurring in seven distinct landforms in a desert landscape. Geomorphically young sites with high micro-topography, as well as sites with high vegetation cover, diversity and burrowing activity, had the greatest index values. Geomorphically old, barren desert pavements with high surface rock density had the lowest index values. The ABQI is an integrative area-based metric that focuses on ecological function rather than taxon. After broad-scale validation it has potential to be an important and rapid assessment tool for land managers.

3.1 Introduction

Arid and semiarid environments are resource-limited and fragile ecosystems. Nevertheless, these environments cover over one third of the terrestrial earth surface (Goudie 2002). Despite the extent of desert landscapes on the planet, arid and semi-arid ecosystems face major threats from anthropogenic encroachment. Historically being exposed mainly to livestock grazing, minor human settlement, and oil and mineral extraction (Greene 1983), arid and semiarid lands are now heavily impacted by the rapid human population increase and its associated environmental threats such as urban sprawl, infrastructural and commercial development, as well as various recreational land uses (Lovich and Bainbridge 1999). While the desert animal and vascular plant communities are sensitive to these disturbances, probably the greatest threat to continued ecosystem health is the loss of soil. Desert landscapes are characterized by having a low, and patchy vegetation cover and their soils are often not as protected from erosion as in wetter temperate or tropical regions that have a continuous vegetation cover. The barren plant interspaces are covered by a combination of rock, gravel, and soil, with the amount of exposed soil varying widely among different landscapes. In general, these soils have only a thin fertile soil surface layer. Major environmental and ecological problems such as dust generation, rapid water runoff, sediment production, soil erosion, exotic species invasion, and habitat loss can be related to the loss of this thin layer (Lovich and Bainbridge 1999, Herrick et al. 2010). Once the soils are lost to erosion, soil fertility, texture, and structure do not recover within a human lifespan.

Biological soil crusts are essential components in these environments. Their importance to arid and semi-arid ecosystems has been widely established in numerous studies (see reviews of Evans and Johansen 1999, Belnap et al. 2001, Belnap and Lange 2003). Especially important is their role in stabilizing soil surfaces through the production of wind and water-stable aggregates (Carpenter and Chong 2010). Contributions to soil fertility represent secondary but critical roles. Biological soil crusts contain free-living and lichenized heterocytous cyanobacteria that are capable of fixing significant amounts of atmospheric nitrogen (MacGregor and Johnson 1971, Evans and Johansen 1999). Consequently, they can be major sources of nitrogen for associated vascular plant communities or soil food webs (Evans and Ehleringer 1993, Belnap 2002, Darby et al. 2010). Biological soil crusts also fix substantial amounts of carbon when their abundance is high and moisture is available (Lange et al. 1992). The fixed carbon accumulates in living crust biomass, available for consumption by bacteria and microfauna in the soil, but is also invested in sticky extra-cellular polysaccharides or root-like structures that contribute to soil particle aggregation (Mazor et al. 1996, Belnap and Gardner 1993, Belnap et al. 2003, Bowker et al. 2008, Darby et al. 2010). Thus, biological soil crusts act as a fertile mantle in many if not most deserts of the world (Garcia-Pichel et al. 2003).

The ecosystem functions of biological soil crusts have been studied worldwide, and researchers now have determined that not all crusts are equal with respect to physiological and ecosystem processes (Belnap 2002, Housman et al. 2006, Strauss et al. 2012, see review of Lange 2003). Though, most crusts have some functionality with

respect to nitrogen fixation, photosynthetic carbon fixation, hydrology, soil stability, and soil fertility, the importance of biological soil crusts varies widely based upon soil properties, precipitation patterns, geomorphology and crust community assemblage. In this study I investigated the eco-functional properties of contrasting biological soil crust community types within a single Mojave Desert landscape. There were two questions of great interest, (1) How do key ecosystem functions vary among different crust types? (2) How do landforms of contrasting geomorphic age differ with respect to the function of their associated soil crusts?

To date, no clear integrative method of assessing differences in ecosystem function or significance of the crusts to a particular landscape has been formulated. A desired outcome of this study was to develop an indicator of soil crust quality in a region based both upon percent cover and an integrated assessment of ecosystem function for the crust community. Such an indicator of crust importance could inform management and become a powerful tool for identifying conservation priorities.

3.2 Materials and Methods

3.2.1 Study Site

The study area is centrally located within the Mojave Desert physiographic province (ca. 35° 30' N, 115° 41' W, Figure 3.1). The study area is on the fan skirt landscape of the lower piedmont slope in the Clark Mountain Wilderness Area, northeastern Mojave Desert National Preserve, USA. This landscape is comparable to other arid landscapes in the Mojave Desert, as well as those in the Sonoran and Great Basin Deserts.

The climate is arid, mean annual precipitation is 145 mm, and mean annual temperature is 17°C, adjusted for elevational difference using NCDC Mountain Pass 1SE Meteorological Station (see Turk 2012). Annual rain events are characterized by a high variability in temporal and spatial distribution (Osborn 1983). The precipitation is bimodal. Most precipitation in this region falls in the winter months as mild rains or occasional snow (MacMahon and Wagner 1985). In late summer, monsoon thunderstorms can cause scattered summer pulse rain events which may exceed the soil infiltration capacity and lead to rapid runoff and flash floods (Evenari 1985, Miles and Goudey 1997).

Soil parent material is alluvium composed mostly of Mesozoic dolomite. Eolian dust is an important component of older soils. While the soils of this area have not been mapped, soil surveys from the surrounding areas suggest the soils to be Typic Torriorthents or Typic Calciorthids. Three geomorphic surfaces varying in geomorphic

age were identified on the fan skirt (Chapter 2). Relative age determination was obtained by relating position and elevation of each surface to the active drainage (Birkeland 1999, Watchman and Twidale 2002). Amongst these three surfaces, finer-scaled landform units can be distinguished. Seven statistically distinct landform units were previously defined as: bar and swale on the young geomorphic surface, flattened bar, flattened swale and bioturbation units on intermediate aged surfaces, and desert pavement and shrub zone units on the oldest geomorphic surfaces (Chapter 2). The entire area is characterized by patchy vegetation with characteristic shrub island/interspace micro-patterning. The dominant vegetation on the lower piedmont is an association of *Larrea tridentata* and *Ambrosia dumosa* mixed with *Yucca schidigera*, *Yucca brevifolia*, *Ephedra nevadensis*, and *Krameria* spp.

3.2.2 Soil crust collection and soil stability

Within a 2 km² area, eight predominant biological soil crust types were identified: incipient algal/fungal crust, fungal crust, light algal crust, green algal lichen crust, cyanolichen crust, rough moss crust, hairy moss crust, and darkened moss crust (Table 3.1). Two additional crust types could be distinguished as dark algal and smooth moss crust. These two crust types have been identified as important components of the landscape in other Mojave regions, such as the granitic areas of Joshua Tree National Park (Pietrasiak et al. 2011a, b). However, in the Clark Mountain study site these crust types were so rare that an insufficient amount of sample material could be collected for laboratory experimentation. At least ten replicates per crust type were collected at

random locations in April 2011. Samples were kept dry and cool (ca. 4 °C) until laboratory measurements. An additional five replicates per crust type were sampled in the field to conduct the field stability test following Herrick et al. (2001).

3.2.3 Crust type abundance among landform units

Within a 2 km² area, a minimum of 30 replicates of each of the seven types of landform units were spatially located with GPS coordinates. Out of this pool of landform units, nine study plots of each landform unit were randomly chosen (total of 63 study plots). The area was determined by measuring the length and width of the plots and estimating area using elliptical geometry. Ground cover was assessed using point intercept measurements of a 0.25-m² quadrat with 25 points (string intersections). The quadrat was systematically placed along the longest axis of the plot. A minimum of 100 cover point intercepts was required for each unit. Since units varied in size from 10 m² to 100 m², the number of cover quadrat placements along the longest axis of the unit was increased systematically with increase in unit size; i.e., in a 10 m² plot, quadrats were placed every meter whereas in a 100 m² plot, quadrats were placed every 10 meters.

Land surface characterization of ground cover included both physical and biological components as follows: (1) biological crust types; (2) plant functional groups: annual grasses, annual forbs, perennial grasses, perennial forbs, woody shrubs, cacti; and (3) physical components of bare soil, gravel, and cobbles. Composite soil samples containing nine sub-samples were taken along transects of each landform unit using soil cores. Soil samples were air-dried and stored until laboratory analysis. Composite

samples were then sieved through a 2-mm-mesh to separate gravel. Litter was removed, and biological soil crust aggregates were pressed through the mesh. Total nitrogen and carbon of composites was determined by dry combustion with an elemental analyzer (Carlo-Erba, Milan, Italy; Nelson and Sommers, 1996). Composite samples were sent to the Pedology Laboratory at University of Kansas for total organic carbon and total inorganic carbon (TIC) determination. TIC was determined with coulometric titration (Engleman et al. 1985). Total organic carbon was obtained by subtraction of TIC from total carbon. Three 1.5 g subsamples from each composite sample were analyzed for chlorophyll *a* analysis using a DMSO extraction protocol (Johansen et al. 2001).

3.2.4 Nitrogen fixation

In the laboratory, five crust samples per type were weighed and their volume was determined with a 3D scanner. The density of the crust was calculated and recorded along with thickness. Crust samples were then placed into a sterile microcosm and covered. A preliminary test determined that a 24 hr rehydration period followed by a 48 hr experimental incubation period were required to achieve detection of ^{15}N enrichment. Thus, prior to ^{15}N incubation, samples were moistened to field capacity and kept in a natural light/dark cycle at room temperature for 24 h to allow for sufficient activation of metabolism during rehydration.

Twenty ml of the microcosm air was replaced with 20 ml of 98 atom% isotopic enriched ^{15}N gas (Cambridge Isotope Laboratories Inc., Massachusetts, USA).

Composite control samples had no air exchanged. Incubation occurred in a growth

chamber with a 16 hr light ($236 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) and 8 hr dark cycle. After incubation, samples were immediately dried in an oven at $65 \text{ }^\circ\text{C}$ for 48 hr. Dry crusts were then crushed through a 2-mm mesh sieve and the gravel was removed and weighed (= bulk density correction). To homogenize the samples, sieved and crushed crusts were further ground with mortar and pestle until the processed soil passed through a 100- μm -mesh sieve. Nitrogen fixation rates for each crust type were calculated according to Warembourg (1992).

A literature search on nitrogen fixation in biological soil crusts was conducted to establish global reference data (Table 3.2). Most past studies on nitrogen fixation rates employed the acetylene reduction method. For comparison of acetylene reduction data with ^{15}N data, the commonly used conversion ratio of 3:1 C_2H_4 to N_2 (Hardy et al. 1968) was applied.

3.2.5 Carbon fixation

The remaining five crust type replicates were used for photosynthetic carbon fixation experiments. Crust samples were wetted to field capacity and then incubated for 2 hours at ambient light and room temperature to allow for rehydration as well as to activate metabolism and photosynthesis. Handling of fragile incipient crusts was supported by metal-wired mesh baskets. Maximal CO_2 assimilation was measured with an infrared gas analyzer (LiCor model 6400, Lincoln, NE, USA) at a photosynthetic photon flux density of $1600 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at ambient relative humidity and temperature. The flow rate was set to $400 \mu\text{mol} \cdot \text{s}^{-1}$ and the reference CO_2 partial pressure to 400

ppm. Maximal carbon assimilation was computed depending on surface area of each crust type replicate. A literature search established global carbon fixation reference data (Table 3.3).

3.2.6 Statistical analysis

Descriptive statistics for land surface properties and the following analyses were performed in SAS 9.1. Data were log-transformed when variances were significantly ($p < 0.01$) unequal based on Levine's test of homogeneity of variances (e.g., nitrogen fixation, carbon fixation). ANOVA was used to detect statistical differences in treatment means (or the means of log-transformed data) using the PROC GLM statement in SAS 9.1. A less conservative post-hoc multiple comparison test (LSD) was used to make pair-wise comparisons of means following ANOVA since ANOVA results were highly significant (< 0.001). A less conservative post-hoc test lessens the risk of committing a type II error, a great concern when the risk of a type I error in the ANOVA is demonstrated to be very small.

3.3 Results

3.3.1 Differences in crust function

Nitrogen fixation varied significantly ($p < 0.0001$) among crust types based on evaluation of \log_{10} -transformed data (Figure 3.2). ^{15}N incorporation into crust ranged from below detection to over 100 000 $\text{nmol N}_2 \text{ m}^{-2} \cdot \text{hr}^{-1}$. Cyanolichen crusts had significantly higher nitrogen fixation rates than all other crust types (mean $\log_{10}(x) = 4.90$, unaltered mean = 83 403 $\text{nmol N}_2 \text{ m}^{-2} \cdot \text{hr}^{-1}$). The hairy moss, darkened moss, and green lichen crusts also showed detectable rates of nitrogen fixation (mean $\log_{10}(x) = 3.88, 3.61, 3.51$, respectively, and unaltered means = 10 475, 7173, 5814 $\text{nmol N}_2 \text{ m}^{-2} \cdot \text{hr}^{-1}$), but were not significantly different from each other. Roughened moss crust (mean $\log_{10}(x) = 2.91$, unaltered mean = 2721 $\text{nmol N}_2 \text{ m}^{-2} \cdot \text{hr}^{-1}$) and light algal crust (mean $\log_{10}(x) = 2.72$, unaltered mean = 734 $\text{nmol N}_2 \text{ m}^{-2} \cdot \text{hr}^{-1}$) showed significantly more nitrogen fixation than fungal crust or incipient algal-fungal crust. The incipient (mean $\log_{10}(x) = 1.29$, unaltered mean = 102 $\text{nmol N}_2 \text{ m}^{-2} \cdot \text{hr}^{-1}$) and fungal crust types (below detection) were significantly different from each other and from all other crust types.

Carbon fixation varied significantly among crust types ($p < 0.0001$). Cyanolichen crust had the highest carbon fixation rates (mean = 10.89 $\mu \text{mol CO}_2 \text{ m}^{-2} \cdot \text{s}^{-1}$), but did not differ significantly from the darkened moss crust (mean = 9.04 $\mu \text{mol CO}_2 \text{ m}^{-2} \cdot \text{s}^{-1}$). Carbon fixation was lower for the other crust types and ranks in decreasing order as follows: hairy moss (mean = 6.60 $\mu \text{mol CO}_2 \text{ m}^{-2} \cdot \text{s}^{-1}$), roughened moss (mean = 6.19 $\mu \text{mol CO}_2 \text{ m}^{-2} \cdot \text{s}^{-1}$), and green lichen crust (mean = 4.97 $\mu \text{mol CO}_2 \text{ m}^{-2} \cdot \text{s}^{-1}$). Light algal

crust, incipient algal-fungal crust, and fungal crust had significantly less carbon fixation than all of the above crusts (mean $\leq 1.0 \mu\text{mol CO}_2 \text{ m}^{-2} \cdot \text{s}^{-1}$). For full comparison of log-transformed data among crust types see Figure 3.3.

The stability test demonstrated that most crusts had the maximal stability possible with this metric (Figure 3.4). Cyanolichen, darkened moss, hairy moss, roughened moss and green lichen crust had values of 6 for all replicates. Fungal crust had a stability mean of 5.8, which was not significantly different from all of the other crusts. Light algal crust had significantly lower stability than all above crust types (mean = 4.2). Incipient algal-fungal crust had significantly less stability than all other crust types (mean = 2.4).

With respect to hydrological properties, all crusts at this site were rugose. This microtopography leads to fairly rapid infiltration as well as reduced rates of overland flow. This classification is based on the ranked classification scheme of Belnap (2006). No smooth, pinnacled, or rolling crusts were seen in any of the areas studied in this work.

3.3.2 Calculation of the Area-Based Quality Index

The Area-Based Quality Index (ABQI) was calculated using the four functional components discussed above. The strategy for matrix formation was to create classes for the components that would at least theoretically cover the range of possible values for the components for all deserts of the world based upon reported values in the literature as well as our measurements. Once classes are calculated for the crusts of an area, they are summed to give a composite metric ranging from a minimum value of 1 to a maximum of 20. This metric is then multiplied by the cover area for the crust in the community under

assessment. This area-based product is the Area-Based Quality Index (ABQI), and theoretically ranges from 0 for sites devoid of crusts to a maximum of 20 for continuous crust cover with maximal ecosystem function.

When rates of nitrogen fixation are compared among biological soil crusts of the world, values ranged widely from undetectable ($< 1 \text{ nmol N}_2 \text{ m}^{-2} \cdot \text{h}^{-1}$) to $5.5 \times 10^6 \text{ nmol N}_2 \text{ m}^{-2} \cdot \text{h}^{-1}$ (Table 3.2). Values for all of the crust types that I observed in the Mojave Desert were not available in the peer-reviewed literature, because of the high diversity of crust types available in California. Crusts representing light algal crust, dark algal crust, and cyanolichen crust have often been studied, and rates were available for these crust types from several deserts of the world (Table 3.2). Included in the historical data were arid and semiarid regions from North America, Asia, the Middle East, Africa and the Arctic, encompassing cold deserts and hot deserts, steppe, savannah, and tundra. The range of values spanning 7 orders of magnitude makes establishment of the classes for nitrogen fixation relatively easy, the exponent of the rate of fixation can be used as the class. In the unlikely event that nitrogen fixation rates exceed $10^7 \text{ N}_2 \text{ m}^{-2} \text{ h}^{-1}$ in some future study, a larger value can be used for this metric, possibly expanding the range of the present ABQI.

Carbon fixation had a narrower range than nitrogen fixation: $< 1.0 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \cdot \text{s}^{-1}$ to $10.9 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \cdot \text{s}^{-1}$ (Table 3.3). Selecting classes for this parameter was more subjective. Natural breaks in rates occurred at about $3.0 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \cdot \text{s}^{-1}$ as well as between 5.0 and $6.0 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \cdot \text{s}^{-1}$, and these were chosen as class boundaries (Table 3.4). The range in this metric is 0-4. Rates were found from arid and semiarid

regions of Europe, North and South America, Africa, and the Middle East (Table 3.3). Maximal rates for all sites in this study, as well as those reported in the literature, were for cyanolichen crust and darkened moss crust. In a regional comparison, high rates were also reported from the Colorado Plateau (Lange et al. 1998).

Classes for the stability component were already established by Herrick et al. (2001) and therefore fully incorporated as a metric for the ABQI. The stability classes range from 0 to 6 (Table 3.4). Hydrology is a qualitative metric and its four classes are based on the ranked classification scheme in Belnap (2006). Smooth soils with no topography, which include thin, flat or flaky biological soil crusts of depression areas, generally have poor water absorptivity, infiltration, and retention, and this class is given a score of 1. Most crusts of the hot arid deserts have a rugose, low relief microtopography, and are given a score of 2. Pinnacled crusts with a rich lichen component such as those typically found in the sandy and silty soils of the Colorado Plateau were given a score of 3. Rolling crusts often found in cold arid regions are typically dominated by mosses and have the highest absorptivity, infiltration, and water retention rates, and were given a score of 4 (Table 3.4).

3.3.3 Evaluation of the ABQI

The quality metric for each type of crust was calculated based on five replicates within type. The ABQI was calculated for each study plot by summing the products of the metric and cover value for each crust type. This allowed statistical comparison of the ABQI for all seven landforms (Figure 3.5). The bar had the highest index values, with a

mean value of 2.62. The ABQI showed decreasing values for landforms according to a temporal series of abiotic development (Figure 3.5), from geomorphically young to geomorphically old: bar and swale > flattened bar and flattened swale > desert pavement. The trend of decreasing function with landform age was disrupted through biotic activity (bioturbation). In the bioturbated plots, the ecosystem function index was nearly as high as in bar sites, and did not differ significantly from those sites. The shrub zone also had an elevated ABQI, although less so than the bioturbated plots.

If taken as a whole, the ABQI values displayed a fairly Gaussian distribution in the Clark Mountains. These values were tested using both the skewness and kurtosis statistics and found to be neither skewed nor peaked. This is of value, as it means that statistical comparisons among landforms can be made without violating the assumption of normality, at least in the present case.

The ABQI was evaluated in comparison to three other ecosystem traits measured as part of this study. ABQI was significantly correlated with total soil nitrogen ($R^2=0.266$, $p = 0.017$, based on sample size of 21) and total soil organic carbon ($R^2=0.254$, $p = 0.024$, based on sample size of 21). Photosynthetic biomass as estimated by chlorophyll a ($\text{ng} \cdot \text{g}^{-1}$ soil) was less correlated ($R^2=0.177$, $p < 0.001$, based on sample size of 63) but still significant.

3.4 Discussion

3.4.1 Ecosystem functions vary among biological soil crust types

The eight different crust community types showed substantially varying levels of ecosystem function, particularly with regards to nitrogen and carbon fixation. The most broadly varying ecosystem function measured and compared among crust types was nitrogen fixation, demonstrating very different nitrogen fixing capacities among crust types. The differences observed in ecological functions may be linked to the specific crust community assemblages in each crust type. This was not the focus of this study but should be investigated in the future.

Overall, lichen and moss crusts performed best among all ecological functions. The crust type with the overall highest values for all ecosystem functions studied was cyanolichen crust, which was mainly dominated by *Collema tenax* and *Collema coccophorum*. Cyanolichen crusts had significantly higher nitrogen fixation than all other types, and had significantly greater carbon fixation than all other crust types except darkened moss crust. This finding is in agreement with the results of others (Lange et al. 1998, Belnap et al. 2002, Lange 2003). Traits that support these high fixation rates may be the carbon concentrating mechanism (CCM) observed in these lichens (Badger et al. 1993), the high nitrogen fixation capacity of the cyanobacterial symbiont (see Lange et al. 1998) and the prolonged water holding capacity due to the gelatinous nature of the lichen thalli (Lange et al. 1998). Thus, landscapes that support a substantial ground cover

of these cyanolichens, especially with *Collema* spp. may be more fertile in terms of nitrogen and carbon inputs than areas lacking this crust type.

The high nitrogen fixation rates of moss crusts were unexpected. Moss crusts are likely to be associated with nitrogen-fixing cyanobacteria, as reported by Wu et al. (2009) and Zhao et al. (2010). Examination of Clark Mountain hairy moss crusts revealed small colonies of lichenized cyanobacteria (i.e. *Collema*) growing among the bases of the mosses on the soil as well as on the phyllids. The green lichen crusts had observable cyanobacterial colonies growing in between the lichen squamules, and this likely explains the occurrence of nitrogen fixation of these communities.

The lower carbon fixation of green algal lichen crust compared to cyanolichen crusts could be attributed to the lack of CCM since the photobionts in these lichens are eukaryotic algal taxa (Lange et al. 1998). Light algal crusts were low in both nitrogen and carbon fixation. These crusts lack a significant component of heterocytous free-living cyanobacteria (Garcia-Pichel and Belnap 1996, Belnap 2002, Garcia-Pichel et al. 2003). Typically, the dominant community components in these crusts are filamentous non-heterocytous cyanobacteria such as *Microcoleus* and *Leptolyngbya* species. Minor nitrogen fixation may occur through heterotrophic fixation of symbiotic bacteria living in the sheath material of these filamentous cyanobacteria (Steppe et al. 1996) or due to sparsely abundant free-living heterocytous cyanobacteria (Garcia-Pichel and Belnap 1996). Thus, one would expect a low nitrogen fixation rate.

Fungal crusts at the Clark Mountains were mostly found embedded underneath a litter layer adjacent to perennial woody shrubs (especially with *Larrea tridentata*). Those

crusts are generally devoid of cyanobacteria and are associated with a rich heterotrophic microbial community (Pietrasiak, personal observation). In contrast to Zaady et al. (1998) heterotrophic nitrogen fixation was minimal in fungal crusts from the Clark Mountains. This would support Skujins' (1981) assumptions that heterotrophic nitrogen fixation is of minor importance. However, I speculate that it may not be due to the lack of carbon as Skujins hypothesized. Carbon is much more abundant within the soils underneath desert shrubs than compared to soils from intershrub spaces (Charley and West 1975, Zaady et al. 1998, Schlesinger et al. 1996). But in addition to carbon, nitrogen is also more abundant than in the less fertile plant interspaces (Schlesinger et al. 1996). Incipient algal-fungal crusts had very low fixation rates, which is also consistent with expectations since these crust have very low biomass and low diversity of biological soil crust community components.

Nitrogen fixation rates in the Clark Mountains are similar to those published from other hot deserts, even given the fact that most researchers used the acetylene reduction method and a 3:1 conversion ratio (Table 3.2). Globally, light algal crust is the most variable crust type with values varying over several orders of magnitude. The greatest variability in the fixation data exists within cold arid environments, with substantial variation among several crust types. Temperate crusts had the highest overall values for all crusts studied, and this finding has been hypothetically linked to less limiting moisture and temperature conditions (Zhao et al. 2010). Consequently, a regional climatic signal may be an important determinant of nitrogen fixation rates in addition to differences in community types or composition. In contrast, carbon dioxide assimilation rates were

comparable with almost all previously published data. Within crust types, dark algal crusts were most variable in performance even across physiographic provinces (Table 3.2).

This is the first instance in which different crust community types have been compared based on their stability index values. Previous studies using Herrick's stability test focused instead on the relationships between soil aggregate stability and total crust cover, or reported mean values of mixed community crusts (Bowker et al. 2008, Chaudhary et al. 2009, Carpenter and Chong 2010, Herrick et al. 2010). In my study, most of the crusts had high stability values, and this measure did not distinguish well among crust types with respect to ecosystem function differences. Even fungal crusts had relatively high stability values. Only incipient crusts showed depressed stability values. These findings indicate that all crusts contribute to stability even if they do not play significant roles in nitrogen and carbon fixation. Thus, prevention of erosion due to water and wind represents the major ecosystem function that is common to all crust types. The supremacy of the stability function over all other functions can be linked to a wide array of traits that support soil aggregation such as extra cellular polysaccharides of cyanobacteria and eukaryotic algae, the rhizomorphs of lichens and mosses, or the sticky glomalin produced by fungi (Belnap et al. 2001, Bird et al. 2002). All crusts had rugose microtopography, so in the case of Clark Mountain crusts, this trait was not a useful distinguishing characteristic.

3.4.2 Implementation and Evaluation of the ABQI

Biological indicators of ecosystem health, such as indices of biotic integrity, have been typically based on taxon-centered approaches. For example, the large number of indicators of freshwater stream condition are all based on taxonomy of a particular group of organisms: Index of Biotic Integrity (IBI) based on fish (Karr 1981), a variety of indices (MIBI, B-IBI, MBII, ICI) based on macroinvertebrates in streams (Chirhart 2003, Genet and Chirhart 2004, Kerans and Karr 1984, Klemm et al. 2003, Ohio Environmental Protection Agency 2007), and a number of indices (LBI, GDI, TSI, TDI, etc.) based on diatoms (Kelly and Whitton 1985, Lange-Bertalot 1979, Rosati et al. 2003, Rumeau and Coste 1988). The same has been done using birds (BirdIBI - O'Connell et al. 1998) and plants (PIBI – Simon et al. 2001, Rothrock et al. 2008) for wetland evaluation. Such species- or taxon-based indices have not been developed to assess desert soil crust communities. Biological soil crusts comprise many phyla often having very distant related phylogenetic relationships to each other. Thus, the great challenge lies in the acquisition of the taxonomic expertise to identify and distinguish among bacteria, cyanobacteria, eukaryotic algae, fungi, lichens, and bryophytes. In addition, due to their microscopic morphology, field identification is problematic, and even laboratory determination based on morphology alone is challenging (West 1990, Eldridge and Rosentreter 1999) and requires further molecular identification (Flechtner et al. in press).

Some indicators of biological crust integrity have been proposed, but have not been widely adapted by managers. Belnap (1998) recommended an index based primarily on microtopography and coarse taxonomic resolution of moss and lichen

presence. The index had a non-linear scale of 1 to 10, and was standardized to area using cover values for each class of crust similar to the ABQI. Belnap's index was developed in Arches National Park in the Colorado Plateau, and while it could probably be applied to other Colorado Plateau sites, it is not very applicable outside of that physiographic region. Extensive pinnacled crusts of the Colorado Plateau are not found in the Mojave Desert, the Chihuahuan Desert, the Southern Sonoran Desert, or the Great Basin. Nonetheless, the categories were well defined and could likely be assigned by other workers in the field without training, an important criterion for metric implementation.

Tongway (1994) developed indices of landscape health using soil and vegetation attributes for arid and semi-arid soils in Australia. Eldridge and Koen (1998) tested four of these indices for rangeland condition related to biological soil crusts in Australia, including stability, infiltration, nutrient cycling, and degradation. Their indices were based on 17 metrics that could be assessed in the field and then summed to give a score for each of the indices. Their indices were not based on area, and were not integrated into a single index. However, these indices could potentially be used as a composite to assess landscape health independent of Tongway's system.

The ABQI has a number of advantages over the indices developed by earlier workers. It is relatively easy to determine and is based on tests that are fairly standard and widely applied, including nitrogen fixation, photosynthetic carbon fixation, and stability. Assessment of a new site would require (1) field evaluation of crust types and cover for each of those crust types; (2) field determination of stability; (3) collection of crust fragments for the fixation experiments; (4) determination of nitrogen and carbon

fixation in a laboratory setting, perhaps at a facility providing such assays for a fee. Managers and researchers could be quickly trained for the field work and it is likely that different teams would obtain reliable results that could be compared between different regions of the world. The index is scaled between 1 and 20, and is applicable to all regions because it is function-based rather than taxonomy-based. The index is also easy to interpret. Since it consists of four metrics, it is even possible that the crusts could be assessed by evaluating these metrics individually as well as in the combined integrated index. Finally, the ABQI could be a powerful management tool for assigning conservation priorities. While all crusts have value to the workers that study them, this index will provide a quantitative unbiased assessment of the ecological significance of crusts in the landscapes where they occur.

The question that remains open at this time is the sample size required for an accurate, repeatable ABQI determination for a site of interest. Certainly, a representative number of quadrats or line transects must be read to accurately estimate crust cover. If different crust categories are to be scored, as in this study, the sample size must be large enough to quantify those crust types. Stability is a quick assay, and it is likely that 5 tests in each crust type could be done rapidly and easily. Microtopography is also quickly assessed even for novice workers if they have access to the field guides that differentiate crust types (Rosentreter et al. 2007). Sample size for fixation rates is the most problematic as these assays require equipment and expertise, or funding if an outside laboratory is chosen to run the assays. The sample size for fixation trials probably depends in part upon the number of different crust types discerned during cover

quantification. Very rare crust types (<1.0% cover) provide too little material to evaluate fixation and are frequently missed in field quantification. In the event that few crust types are tested, 10 assays are recommended. With a higher diversity of crusts five replicate assays per crust type is likely sufficient. In order to obtain a representative estimate of fixation, samples for trials should be broadly dispersed in the community being studied.

The ABQI gives a good indication of contributions of crust communities to ecosystem function, and has clear use as a management tool for preserving high function communities. However, the ABQI has broader potential uses. In particular, it can be used to assess the ecological impacts of proposed anthropogenic disturbance. Deserts are currently targeted for energy development, including photovoltaic facilities, wind farms, and solar collector power plants. This kind of disturbance is very different from the well-studied physical disturbance due to livestock, off-road vehicles, and hikers. The ABQI provides a quantitative measure that goes beyond simple cover estimates, and degradation of ecosystem function will be more readily detected using this approach. The ABQI can also be used to assess natural recovery or inoculum-enhanced recovery (Buttars et al. 1998, Kubečková et al. 2003) following disturbance. Total crust cover in some areas can actually recover fairly rapidly (Johansen et al. 1984, Johansen and Rushforth 1985, Johansen and St. Clair 1986, Pietrasiak et al. 2011), but studies of ecosystem function recovery indicate that this kind of recovery, particularly nitrogen fixation, takes much longer (Anderson et al. 1982, Belnap 1993, Belnap et al. 2001, Belnap and Eldridge 2003). The ABQI is an integrative metric, combining cover and abundance with

ecological function. It remains to be tested in other desert regions, but based upon this study in the Mojave Desert, the metric appears to have great promise. Certainly the approach is one that can be adopted in most desert regions of the world.

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Table 3.1 Crust type and landform classification used in this study.

Crust type code	Crust type identification	Description
IC	incipient algal/fungal crust	weakly consolidated, soft crust that breaks apart easily but displays fungal hyphae or cyanobacterial filaments, dominant components are fungi and/or cyanobacteria
FC	fungal crust	embedded underneath a litter or sand layer, fungal hyphae clearly visible, dominant components are fungi
LAC	light algal crust	inconspicuous colored crust dominantly composed of cyanobacteria and eukaryotic algae
CLC	cyanolichen crust	lichen crust that has cyanobacteria as the photobiont
GLC	green algal lichen crust	lichen crust that has green algae as the photobiont
RMC	rough moss crust	moss crust with minor hair-like extensions on phyllus, brownish when dry, green to brown-green when moist
HMC	hairy moss crust	moss crust with extensive hair-like extensions on phyllus that appear like whitish-grey carpets
DMC	dark moss crust	clearly blackened, moss-dominated crust
Landform Code	Landform identification	Description
BR	bar	Young, convex geomorphic surfaces, found in active washes, high proportion of cobble-sized surface rocks and soil crevices between rocks, high microtopography
SW	swale	Young, concave geomorphic surfaces, found in active washes, high proportion of fine- to medium-sized gravel, fewer and smaller soil crevices between rocks, lower microtopography than BR
FB	flattened bar	Slightly convex to linear, intermediate-aged geomorphic surfaces, elevated above active washes, still high proportion of cobble-sized surface rocks, but fewer soil crevices between rocks, decreased microtopography
FS	flattened swale	Slightly concave to linear, intermediate-aged geomorphic surfaces, elevated above active washes, still fine- to medium-sized gravel, fewer and smaller soil crevices between rocks, decreased microtopography
FD	bioturbated unit	Convex intermediate-aged geomorphic surfaces, vegetation cover high in unit center with many burrows from small mammals, most bare soil
DP	desert pavement	Linear, old geomorphic surfaces, highest elevation compared to active wash, barren, vegetation poorest, high density of clasts with lowest microtopography of all landforms
SZ	shrub zone	Slightly convex, old geomorphic surfaces, highest elevation compared to active wash, vegetation rich, lower density of clasts with modest microtopography and bare soil

Table 3.2 Nitrogen fixation rates ($\text{mmol N}_2 \text{ m}^{-2} \cdot \text{hr}^{-1}$) of biological soil crust types collected in various arid and semiarid regions of the world. Acetylene reduction rates were converted using the standard 3:1 conversion ratio. Number indicated in parentheses represents the equivalent metric score if ABQI classification is used.

Reference	Location	Climate	IAFC	FC	LAC	DAC	CLC	GLC	DMC	MC	LWC
This paper	Mojave Desert	hot arid	ND (0)	ND (0)	7.3E+02 (3)	-	8.3E+04 (5)	5.8E+03 (4)	7.2E+03 (4)	2.7E+03 (4)	-
Hartley & Schlesinger 2002	Chihuahuan Desert	hot arid	-	-	-	3.0E+00 (1)	-	-	-	-	-
Housmann et al. 2006	Chihuahuan Desert	hot arid	-	-	3.5E+02 (3)	1.4E+03 (4)	-	-	-	-	-
Eskew and Ting 1978	Colorado Desert	hot arid	-	-	-	-	4.4E+04 (5)	-	-	-	-
MacGregor and Johnson 1971	Sonoran Desert	hot arid	-	-	-	2.6E+05 (6)	-	-	-	-	-
Zaady et al. 1998	Negev Desert	hot arid	-	-	-	3.4E+05 (6)	-	-	-	-	-
Issa et al. 2001	Niger Sahel	hot arid/ savanna	-	-	1.2E+04 (5)	1.4E+04 (5)	-	-	-	-	-
Skarpe and Henrikson 1986	Kalahari	savanna	-	-	2.0E+05 (6)	2.3E+06 (6)	-	-	-	-	-
Johnson et al. 2005	Colorado Plateau	cold arid	-	-	2.2E+03 (4)	1.6E+04 (5)	-	-	-	-	-
Belnap 1996	Colorado Plateau	cold arid	-	-	7.3E+00 (1)	6.0E+00 (1)	2.4E+01 (2)	-	-	-	-
Evans and Belnap 1999	Colorado Plateau	cold arid	-	-	-	-	4.0E+00 (1)	-	-	-	-
Belnap 2002	Colorado Plateau	cold arid	-	-	2.7E+03 (4)	1.7E+04 (5)	4.2E+04 (4)	-	-	-	-
Jeffries et al. 1992	Colorado Plateau	cold arid	-	-	2.3E+04 (5)	3.4E+04 (5)	-	-	-	-	-
Housmann et al. 2006	Colorado Plateau	cold arid	-	-	1.0E+03 (4)	1.5E+03 (4)	-	-	-	-	-

Table 3.2 continued

Reference	Location	Climate	IAFC	FC	LAC	DAC	CLC	GLC	DMC	MC	LWC
Zhao et al. 2010	Shaanxi Province	cold arid	-	-	9.0E+03 (4)	-	6.8E+04 (5)	-	-	4.5E+04 (5)	-
Wu et al. 2009	Gurbantung-gut Desert	cold arid	-	-	3.3E+03 (4)	-	3.0E+03 (4)	-	-	6.8E+02 (3)	-
Liu et al. 2009	Mongolia	temperate dry	-	-	7.3E+04 (5)	5.3E+05 (6)	-	-	-	-	-
Su et al. 2011	Tenger Desert	temperate dry	-	-	5.5E+06 (6)	2.3E+06 (6)	-	-	-	8.7E+05 (6)	-
Stewart et al. 2011	Arctic	tundra	-	-	-	-	5.0E+04 (5)	-	-	2.8E+04 (5)	9.0E+03 (4)

Table 3.3 Maximal carbon fixation rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \cdot \text{s}^{-1}$) of biological soil crust types collected in various arid and semiarid regions of the world. Number indicated in parentheses represents the equivalent metric score if ABQI classification is used.

Reference	Location	Climate	IAFC	FC	LAC	DAC	CLC	GLC	DMC	MC	LWC
This paper	Mojave Desert	hot arid	0.79 (1)	0.55 (1)	1.01 (1)	1.75* (2)	10.89 (4)	4.97 (3)	9.04 (4)	6.19 (4)	-
Pietrasiak unpublished	California chaparral	xeric	-	-	-	-	-	-	-	-	1.17 (1)
Grote et al. 2010	Chihuahuan Desert	hot arid	-	-	1.93 (2)	3.49 (3)	-	-	-	-	-
Housmann et al. 2006	Chihuahuan Desert	hot arid	-	-	0.41 (1)	1.00 (1)	-	-	-	-	-
Lange et al. 1994	Namib	hot arid	-	-	-	-	-	3.98 (3)	-	-	-
Lange et al. 1993	Judean Desert	hot arid	-	-	-	-	2.49 (2)	1.79 (2)	-	-	-
Housmann et al. 2006	Colorado Plateau	cold arid	-	-	0.46 (1)	0.58 (1)	-	-	-	-	-
Jeffries et al. 1993a	Colorado Plateau	cold arid	-	-	0.19 (1)	0.35 (1)	-	-	-	-	-
Jeffries et al. 1993b	Colorado Plateau	cold arid	-	-	0.11 (1)	0.19 (1)	-	-	-	-	-
Lange et al. 1998	Colorado Plateau	cold arid	-	-	-	-	7.00 (4)	-	-	-	-
Grote et al. 2010	Colorado Plateau	cold arid	-	-	3.03 (2)	2.84 (2)	-	-	-	-	-
Phillips and Belnap 1998	Colorado Plateau	cold arid	-	-	-	1.50 (1)	-	-	-	-	-
Lange et al. 1997	Central European Steppe	temperate	-	-	-	-	-	5.9 (3)	-	-	-
San Jose and Bravo 1991	Orinoco Llanos, Venezuela	Savanna	-	-	-	5.00 (3)	-	-	-	-	-

Table 3.4 Metric components of the area based quality index (ABQI) for biological soil crusts based on ecological functions.

(1) maximal nitrogen fixation (if acetylene reduction method was used, the assumed conversion is 3 nmol C₂H₄ m⁻² h⁻¹ = 1 nmol N₂ m⁻² h⁻¹)

0 = no detection

1 = 1 - 10¹ nmol N₂ m⁻² h⁻¹

2 = 10¹ - 10² nmol N₂ m⁻² h⁻¹

3 = 10² - 10³ nmol N₂ m⁻² h⁻¹

4 = 10³ - 10⁴ nmol N₂ m⁻² h⁻¹

5 = 10⁴ - 10⁵ nmol N₂ m⁻² h⁻¹

6 = >10⁵ nmol N₂ m⁻² h⁻¹

(2) maximal carbon fixation

0 = no detection

1 = 0.1 – 1.5 μmol CO₂ m⁻² s⁻¹

2 = 1.6 – 3.0 μmol CO₂ m⁻² s⁻¹

3 = 3.1 – 6.0 μmol CO₂ m⁻² s⁻¹

4 = > 6.1 μmol CO₂ m⁻² s⁻¹

(3) soil aggregate stability (according to Herrick et al. 2001)

0 = structure-less soil, too unstable to sample

1 = 50% aggregate loss within 5 s of water immersion

2 = 50% aggregate loss within 5-30 s of water immersion

3 = 50% aggregate loss within 30-300 s of water immersion or <10% of soil remains after 5 dipping cycles

4 = 10-25% of soil remains after 5 dipping cycles

5 = 25-75% of soil remains after 5 dipping cycles

6 = 75-100% of soil remains after 5 dipping cycles

(4) hydrological impact (adapted from Belnap 2006)

1 = smooth crusts with no microtopography; often thin, flat crusts mainly composed of cyanobacteria and/or fungi with low absorptivity, infiltration, and water retention.

2 = rugose crusts with moderately low microtopography, cyanobacteria and algae dominated with sparse patches of mosses and lichen; absorptivity, infiltration and water retention are moderate.

3 = pinnacled crusts with high microtopography expressed as pedicelled mounds; presence of frost heaving events, high abundance of cyanobacteria and lichens; absorptivity, infiltration are high, and water retention is highest.

4 = rolling crusts with slightly rolling microtopography; moss and lichen dominated; extended periods of frost heaving; absorptivity, infiltration are highest, water retention are high.

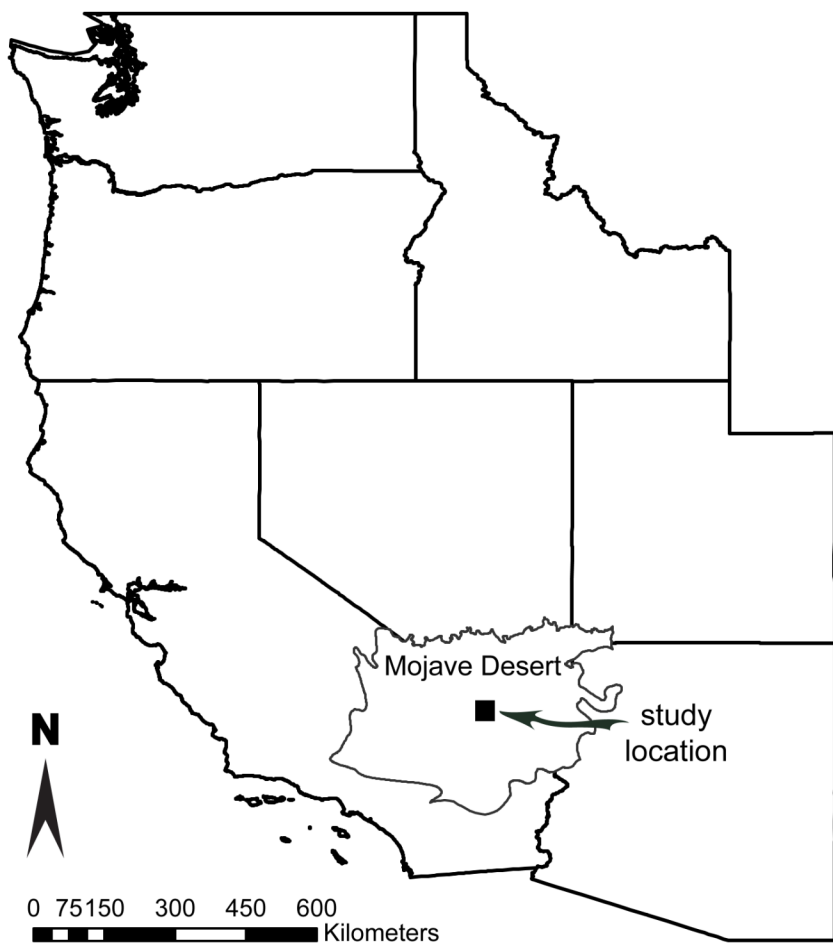


Figure 3.1 Map of the study location within the western U.S.

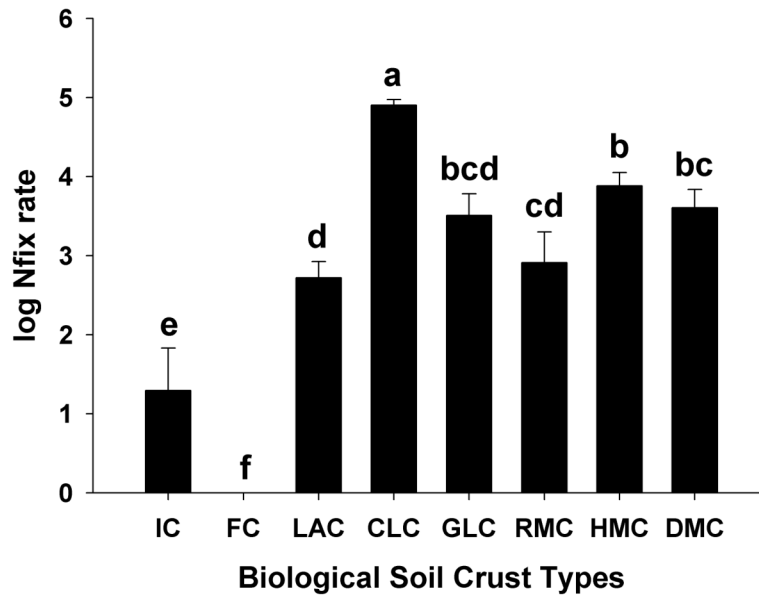


Figure 3.2 Log-transformed nitrogen fixation rates of biological soil crust types collected at the study location, Mojave Desert. Lowercase letters represent significant differences detected with ANOVA and the LSD test.

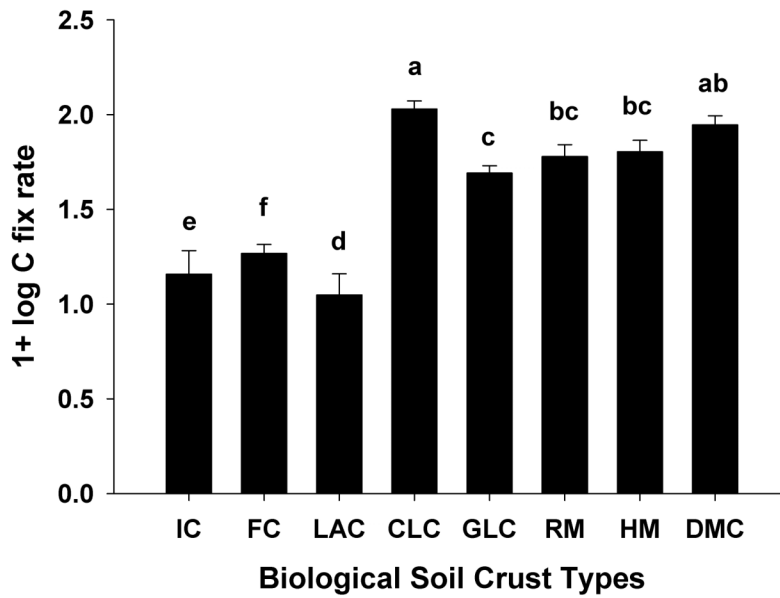


Figure 3.3 Log-transformed maximal photosynthetic carbon fixation rates of biological soil crust types collected at the study location, Mojave Desert. To correct negative log values 1 was added to each value. Lowercase letters represent significant differences detected with ANOVA and the LSD test.

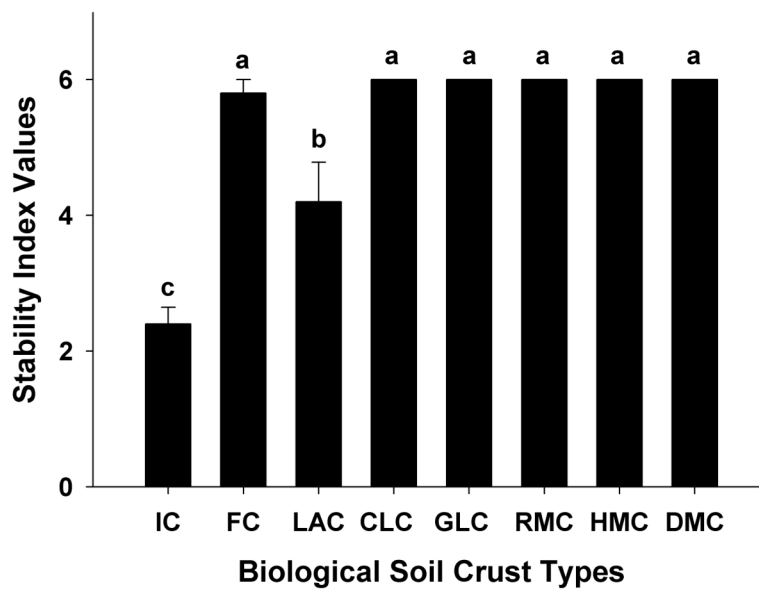


Figure 3.4 Herrick's stability index values of biological soil crust types collected at the study location, Mojave Desert. Lowercase letters represent significant differences detected with ANOVA and the LSD test.

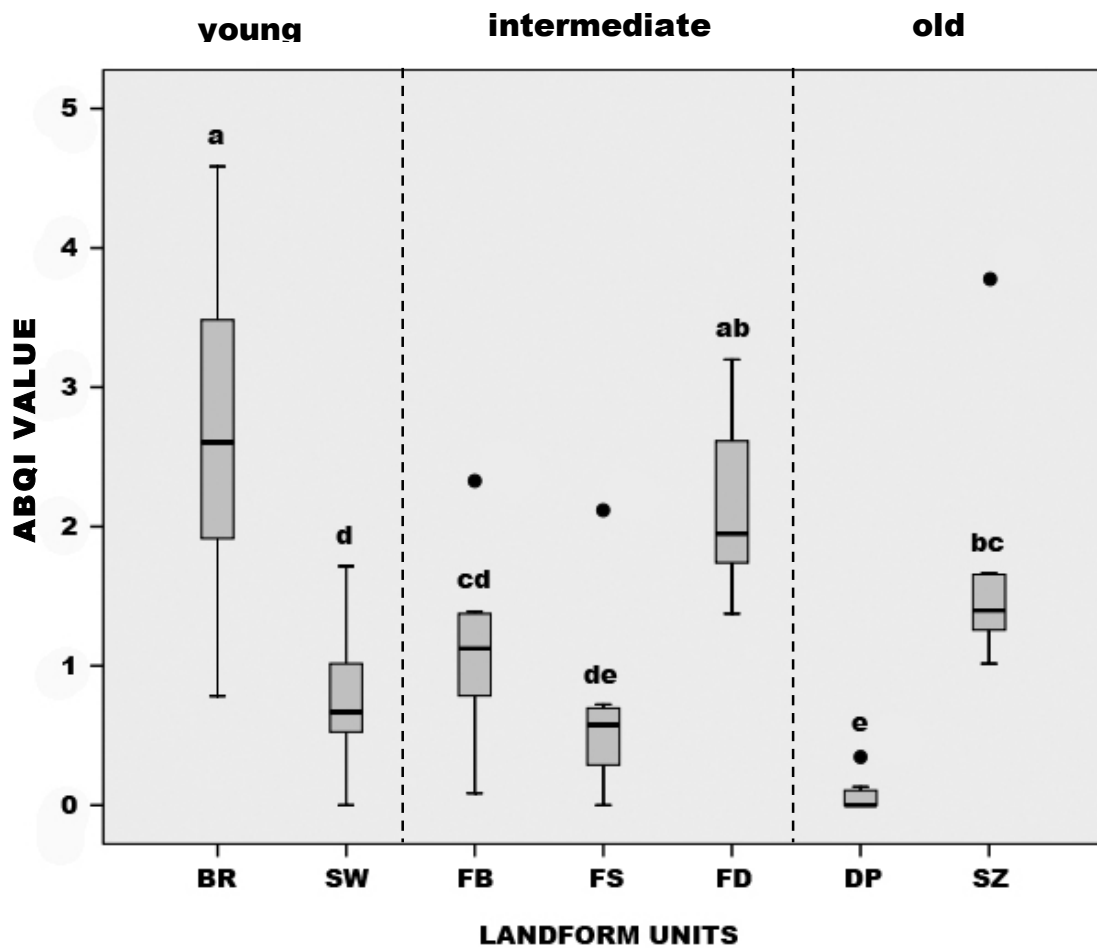


Figure 3.5 Box and Whisker plot of the Area Based Quality Index among the seven landform units studied. Dots above the boxes represent extreme values. Lower case letters represent significant differences detected with ANOVA and the LSD test. BR = bar, SW = swale, FB = flattened bar, FS = flattened swale, FD = Bioturbation unit, DP = desert pavement, and SZ = shrub zone.

4. SOIL-BIOGEOMORPHOLOGY OF A PIEDMONT FAN SKIRT, MOJAVE DESERT, CA.

Abstract

Landscapes consist of abiotic and biotic land surface components. Abiotic components are the morphometric shape of the land surface and the presence of boulders, rocks, gravel, and bare soil. Biotic components include the cover of vegetation or biological soil crusts. Drastic changes of these biotic and abiotic land surface characteristics occur during desert landscape evolution. These changes can be especially prominent at a mesoscale (tens to hundreds of meters). This study investigated the linkages of these land surface changes to pedogenesis in an alluvial fan skirt landscape. Geomorphic surfaces of three different ages, harboring seven landform unit types, were used as the geomorphic framework. These landforms have been previously characterized and defined by abiotic and biotic land surface properties and were distinguished as: young bars and swales; intermediate-aged flattened bars, swales, and bioturbation units; and old desert pavements and shrub zone units. The specific objectives of this work were to (1) determine the relationship between specific land surface characteristics and soil chemical, and physical properties, and (2) to develop a mechanistic explanation of fan skirt pedogenesis that is related to landform evolution. The morphologies of twenty-one soils were described in manually excavated pits and classified following a standard soil survey protocol. All morphological soil horizons were sampled to a depth of 60 cm for a suite of physical and chemical analyses. Properties analyzed included: soil texture and percent rock fragments; bulk density; soluble phosphate, ammonium, nitrate, elemental sulfur,

calcium, magnesium, potassium, and sodium; total nitrogen; organic and inorganic carbon; and electrical conductivity. Sodium absorption ratio and calcium carbonate equivalent were calculated. Multivariate analyses were used to observe patterns in soil properties related to geomorphology, age, and land surface characteristics. These analyses demonstrated that land surface characteristics and geomorphic age are strongly predictive of specific soil properties. Specifically, sodicity, salinity, and a finer texture could be related to presence of a tightly interlocking dense clast layer at the surface. Organic carbon, total nitrogen, nutrients, and soil aggregation could be associated with the presence of biological soil crust, vegetation, and small mammal activity. Accordingly, two pedogenic trajectories were discovered: one dominated by abiotic processes and the other by biotic processes. Within both, I observed distinct changes in soil morphological characteristics. Strongly developed vesicular and calcic horizons developed over time from abiotic pedogenesis, whereas these were absent or more weakly developed in the biotic system. This detailed study demonstrated that mesoscale land surface heterogeneity can lead to predictive relationships of ecosystem components as well as a mechanistic understanding of pedogenesis that is linked to contrasting abiogenic and biogenic landform evolutionary trajectories.

4.1 Introduction

Landscapes and their component landforms are characterized by unique combinations of abiotic and biotic land surface properties. These surficial properties can enhance environmental heterogeneity and resource distribution. If the heterogeneity is organized in a predictable way, it can aid our understanding of nature's complexity. Moreover, it allows for powerful hypothesis testing of the roles of land surface properties in geomorphic, pedologic, and ecological processes and functions.

Land surface properties can be especially diverse in desert ecosystems. For example, bare soil, gravel, rocks, and boulders are physical components often occupying large areal extents (Wood et al. 2002, Pietrasiak et al. 2011, Hirmas et al. 2011). Biological components include animal mounds and burrows, vascular vegetation, and biological soil crusts, creating conspicuous biological landform mosaics in the present or past (Johansen et al. 2001, McAuliffe and McDonald 2006). Deserts are also unique because spatial differences of mosaics can be easily observed in the field or through remote sensing at varying scales. Thus, one can easily recognize different landscape or landform mosaics at the broadscale (hundreds of meters to kilometers), mesoscale (several to tens of meters) or even microscale (less than one to two meters) due to differences in land surface properties. Moreover, these mosaics are spatially repetitive allowing one to potentially include the spatial units in a classification system, test linkages of surface features to ecosystem processes, and extrapolate knowledge gained in one area to similar landscapes elsewhere at local, regional, and even global scales.

Landform mosaics that vary in land surface properties can concomitantly vary in soil properties and development (Peterson 1981). Land surface properties may influence surficial and subsurficial pedological processes such as soil formation, hydrology, accumulation, loss, mixing, and transformation (Yair and Klein 1973, Wood et al. 2002, Meadows et al. 2008, Hirmas et al. 2011). For example, land surface characteristics such as a dense clast cover or presence of physical soil crusts result in the formation of vesicular surface soil horizons which then can be linked to multiple geomorphic processes such as increasing sediment storage, decreasing infiltration, and increasing runoff (Turk and Graham 2011). Microtopography, created by protruding gravel and cobbles or biological soil crusts, is linked to dust accumulation and increasing infiltration (Yair and Klein 1973, Blank et al. 1996, Pérez 1997, Reynolds et al. 2006, Belnap 2006). Large coverage by biological soil crusts can also positively affect organic matter accumulation and biological weathering at the microscale (Pérez 1997, Souza-Egipsy et al. 2004). Soil mixing can be promoted by small mammals living in close association with large perennial shrubs (McAuliffe and McDonald 2006, Schafer et al. 2007). Thus, surficial features represent strong drivers in geomorphic, pedologic, and ecologic processes. However, most insights into pedological and geomorphic processes have been gained from studies either of broadscale chronosequences or at a finer scale such as investigations on single geomorphic surface.

In the Mojave Desert soil-geomorphic research has addressed broadscale patterns on stable surfaces at the upper and middle piedmont slope, including alluvial fans and fan piedmonts as well as on lava flows (Wells et al. 1985, McDonald 1994, Schafer et al.

2007, Meadows et al. 2008). More recently, research has addressed soil geomorphic relationships in the mountains (Hirmas and Graham 2011, Hirmas et al. 2011). These studies contributed valuable knowledge about broadscale ecosystem processes, paleoclimatic conditions, and pedogenesis. Within these broadscale landscapes, finer land surface mosaics can be recognized and deserve a thorough investigation and mechanistic understanding (McAuliffe 1994). Apparently, only two interrelated studies in the Mojave Desert have investigated mesoscale landform patterning (Wood et al. 2002, 2005). These thorough studies focused on a single geomorphic surface, yet several mesoscale mosaics were identified based on contrasting differences in land surface characteristics. Wood et al. (2002) described three desert pavement and three bare ground mosaics that differed largely in percent clast, shrub, and biological soil crust cover. Moreover, these surficial differences could be linked to differences in soil morphology and ecosystem functions (Wood et al. 2005). Desert pavement mosaics had well developed vesicular horizons near the surface, underlain by subsurface horizons enriched in clay, salts, and carbonates. These soils had limited infiltration, percolation, and leaching depth. In contrast, bare ground areas lacked a distinct vesicular horizon and had coarser-textured soils with greater infiltration and deeper leaching fronts. Nonetheless, since this detailed study was limited to one geomorphic surface, it is not known if mesoscale patterning and processes are equally important across a chronosequence.

A major landscape component of the lower piedmont slope is the fan skirt. This landscape component is a relatively smooth landscape with a low slope gradient (< 2%).

It is characterized by an assortment of differently aged geomorphic surfaces (current washes and fan terraces) that abut each other in relatively close proximity. These surfaces lack a geomorphic classification at the mesoscale level, and pedogenesis and ecological processes at this level are consequently poorly understood.

In this study I investigated the mechanisms of mesoscale soil formation and development according to changes in land surface characteristics across a fan skirt chronosequence. I hypothesized that land surface characteristics are key indicators for soil development. My goals were to (1) determine if a change in soil properties can be linked to a landform change, and (2) relate specific soil properties to land surface characteristics.

4.2 Materials and Methods

4.2.1 Study Site

The study area was located on an alluvial fan skirt covering the western lower piedmont of the Clark Mountains at an elevation of ca. 1050 m. This area lies centrally within the Mojave Desert physiographic province (ca. 35° 30' N, 115° 41' W, Figure 4.1). The entire area, including the Clark Mountains and their western watersheds, is part of the northeastern portion of the Mojave National Preserve and comprises mostly undisturbed wilderness areas.

The climate of the study area has been arid since the beginning of the Holocene due to the Cordilleran rain shadow and Holocene climatic conditions. During the Pleistocene, cooler and moister conditions prevailed (Jannick et al. 1991, Norris and Webb 1990). Mean annual precipitation is 145 mm, and mean annual temperature is 17°C (adjusted for an elevation difference using NCDC Mountain Pass 1SE Meteorological Station, see Turk 2012). Annual rain events are bimodal and highly variable in temporal and spatial distribution (Osborn 1983). Most precipitation falls in the winter months (November to April) as mild rains or occasional snow (MacMahon and Wagner 1985). In late summer (August to September), monsoon thunderstorms occasionally cause scattered pulse rain events, which often can exceed the infiltration capacities of the soils (Evenari 1985, Miles and Goudey 1997).

The geology of the Clark Mountain Range is highly complex and composed of Proterozoic crystalline rocks mixed with Paleozoic to Mesozoic sedimentary bedrock (Norris and Webb 1990, Walker et al. 1995, Schmidt and McMackin 2006, Hall 2007). A watershed of the western piedmont was selected for the study. Both the bedrock and consequential alluvium deposits are composed primarily of dolomite, with minor limestone occurrences, and have minimal across-site heterogeneity.

The soil parent material was dolomite alluvium, as well as incorporated eolian dust in older soils. The soil moisture regime for the study area is aridic and the soil temperature regime is thermic (Miles and Goudey 1997). The soils of the entire Clark Mountains Wilderness Area in the Mojave National Preserve have not been mapped.

The fan skirt consisted of three types of geomorphic surfaces of varying ages. Relative age determination was obtained by relating position and elevation of each surface to the active drainage (Birkeland 1999, Watchman and Twidale 2002). Finer scaled landform units were distinguished amongst these three surfaces. Previous work (Chapter 2) on land surface characterization identified seven statistically distinct landform units which were defined as: bar and swale on the young surfaces; flattened bar, flattened swale, and bioturbation units on intermediate-aged surfaces; and desert pavement and shrub zone units on the oldest surfaces.

The fan skirt had patchy cover of both vegetation and biological soil crust. The dominant vegetation on the lower piedmont was an association of *Larrea tridentata* and *Ambrosia dumosa* mixed with *Yucca schidigera*, *Yucca brevifolia*, *Ephedra nevadensis*, and *Krameria* spp. The dominant soil crust community was light algal crust, fungal crust, and incipient algal/fungal crust, with occasional patches of lichen and moss crusts.

4.2.2 Field sampling and soil descriptions

A minimum of 30 study plot locations of each of the seven landform types were mapped. Out of this study plot pool, three representative soil study plots for each landform were randomly chosen (= total of 21 study locations). At each plot, land surface properties were characterized, including morphometric, physical, and biotic properties. Data on land surface properties and detailed descriptions of procedures used are given in Chapter 2 and are only briefly presented here.

Morphometric land surface properties included topographic shape (profile and cross section, Schoeneberger et al. 2002) and the areal extent. Physical land surface properties included number of surface rocks (= clasts) per meter, clast dimension (length and width, Folk 1980), microtopography as expressed as a roughness index (Saleh 1993), clast embeddedness as presence or absence, and clast distribution characteristics. Clast distribution characteristics included sorting, skewness, and kurtosis and were computed according to Folk (1980). High sorting values represent low degrees of sorting, i.e., a larger spread of clast sizes. Low sorting values occur when clast size is homogeneous. Skewness evaluates the symmetry of the clast distribution. Its sign and magnitude can be used to document an excess of coarse- or fine-sized clasts. For example, a clast distribution that has coarse-sized clasts in excess has a negative sign and a distribution with more fine-sized clasts has a positive sign (Folk 1980). Kurtosis can be used to detect bimodal sediment distributions.

Biological characterization included determining the cover of total biological soil crust and cover of vascular plant functional groups. Plant functional groups included: annual grasses, annual forbs, perennial grasses, perennial forbs, woody shrubs, and cacti. Ground cover was assessed using point intercept measurements of a 0.25-m² quadrat with 25 string intersections. A minimum of 100 cover point intercepts was required for each unit.

In each plot a soil pit was excavated by hand in the intershrub space at a representative location, i.e., at least 0.5 m from plot edges where properties could be transitional. Descriptions were made using Schoeneberger et al. (2002) and included

characterization of soil morphological features such as soil structure, root distribution, presence and degree of clay and/or calcium carbonate accumulation. Carbonate morphology was classified after Gile et al. (1966). Morphological horizons of each soil profile were sampled for later laboratory analyses. In most soils at least three peds per soil horizon were obtained for bulk density analysis.

4.2.3 Laboratory Analysis

After collection in the field, soil samples were air dried overnight and stored for laboratory analysis. Samples were sieved with a 2-mm-mesh to separate the gravel fraction from the fine earth component. Any coarse litter was removed and soil aggregates, including biological soil crust, were crushed through the sieve mesh. Soil physical characterization included percent rock fragments, particle size distribution, and bulk density. Total rock fragment content was determined gravimetrically. Sand was separated by wet sieving with a 53- μm -mesh sieve and weighed to obtain percentages. Percent clay was determined with the hydrometer method with chemical (10% sodium hexametaphosphate) and physical dispersion pretreatment. Clay values were corrected for soil moisture, solution temperature, and a blank hexametaphosphate solution (Gee and Or 2002). Bulk density was determined by the paraffin-coated clod method and corrected for gravel content following Hirmas and Furquim (2006).

Chemical characterization included electrical conductivity (EC); pH; soluble nitrate, phosphates, and ammonium; total soluble base cations; total soluble sulfur;

sodium absorption ratio (SAR); total carbon (TC); total inorganic carbon (TIC); total organic carbon (TOC); and total nitrogen (TN). Soil pH and EC were determined on 1:1 soil extracts using a 15 g subsample of each horizon (U.S. Salinity Laboratory Staff, 1954). Samples were shaken for 1 hr and centrifuged for 6 min at 2000 rpm. Soil pH and EC were measured in solution phase with a Corning 320 pH meter and a YSI conductivity meter. Soil solution was then filtered using ashless Whatman 42 filter paper. Filtered solutions were used to colorimetrically determine soluble nitrate, phosphates, and ammonium by a Technicon autoanalyzer (Mulvaney 1996). Soluble base cation and sulfur content was determined on a 1:5 soil:water filtered extract using ICP-OES (PerkinElmer, Waltham, MA). Base cation content was then used to compute SAR (U.S. Salinity Staff 1954). Due to high dolomite content in the soil sample, calcium carbonate equivalent could not be determined with standard procedures as outlined in the National Soil Survey Center (1996). Soil samples were ground with a ball mill to pass a 100 μm mesh and then oven dried at 105°C and stored in airtight vials. Ground samples were sent to the Pedology Laboratory at University of Kansas for carbon determination. Total inorganic carbon (TIC) was determined with continuous coulometric titration (Engleman et al. 1985, Hirmas et al. in press) and total carbon (TC) by dry combustion (Jackson et al. 1992). TIC represented total geogenic and pedogenic inorganic carbon. Total organic carbon was obtained by subtraction of TIC from TC. Calcium carbonate equivalent (CCE) by weight was determined from TIC data.

4.3.4 Statistical analysis

Statistical analyses using soil data obtained from morphological horizons are difficult because classification of basic experimental units is sometimes unclear or highly variable. For example, in a soil survey along a chronosequence, or even within one geomorphic surface, not all soils may belong to the same order or even suborder. Furthermore, replicate soils within the same order or geomorphic unit type may not possess the exact same morphologic horizonation. For example, within Aridisols the replicate profiles may not consistently possess a calcic horizon, or may have slightly different horizons, e.g., Av/Bt/Bk/Cr versus Av/Btk/Cr, or horizons may have different depths or thicknesses. Thus, a weighed average transformation of soils data is commonly used for statistical comparisons. After preliminary data exploration of soil chemical and physical properties for each soil horizon studied, four soil depths were chosen as weighed average depths: 0 to 2cm, 2 to 10cm, 10 to 40 cm, and 40 to 60 cm.

Principal component analysis (PCA), an indirect multivariate gradient analysis that aims to detect patterns of a suite of dependent variables, was used to discern patterns in the soil chemical and physical properties of the four soil depths. I also tested whether these patterns could be associated with specific landforms. Variables investigated included water-soluble ions ($\text{PO}_4^{3-}\text{-P}$, $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, K^+ , Na^+ , Ca^{2+} , Mg^{2+}), elemental sulfur (S), SAR, TN, TOC, EC, pH, CCE, bulk density (BD), percent sand and clay, percent fine and medium gravel combined (f & m gr), and coarse gravel (co gr). TIC was omitted due to high co-variation with CCE. Percent silt was also omitted

since percent clay and sand results in the computation of percent silt. A data matrix was developed for each of the weighted average soil depths (total of four matrices).

Canonical correspondence analysis (CCA), a multivariate analysis in which multiple independent environmental variables are related to multiple dependent variables (Lepš & Šmilauer 2003), was used to investigate whether abiotic and biotic land surface properties are linked to the underlying soil properties of the four depths. A data matrix was developed for each of the weighted average soil depths and related to a matrix of land surface characteristics. Dependent variables were $\text{PO}_4^{3-}\text{-P}$, $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, S, K, Na, Ca, Mg, SAR, TN, TOC, EC, pH, CCE, BD, and percent sand, clay, f&m gr, and co gr percentages. Explanatory variables included the following properties: (1) abiotic: morphometric slope shape; clast dimension, sorting, skewness, kurtosis, and density; microtopographic roughness index and clast embeddedness; (2) biotic: cover of biological soil crust and plant functional groups; and (3) relative geomorphic age. Since no absolute data on geomorphic age were available a dummy variable was created where 1 represented young, 2 represented intermediate age, and 3 represented old. All multivariate analyses were conducted with CANOCO software (Lepš & Šmilauer 2003).

4.3 Results

4.3.1 Soil morphology, taxonomic classification and geomorphic age estimation

The soils investigated in this study exhibit distinct variation in soil morphological characteristics among the three geomorphic ages and seven mesoscale landforms (Table 4.1, 4.2, Figure 4.2). Vesicular horizons (Av) were a common surface feature but did not occur ubiquitously among the seven landform units (Table 4.1, 4.2, Figure 4.2). They were lacking or weakly developed in bar, shrub zone, and bioturbation unit soils (Figure 4.2). Vesicular horizons were discontinuous and thinly (1 cm) developed in swales, but increased in thickness and continuity in flattened bar and swales and were thickest (up to 10 cm) and continuously developed under desert pavements (Figure 4.2). Non-vesicular A-horizons in bioturbation and shrub zone units were relatively thick compared to the other soils and ranged from 10 cm up to almost 30 cm.

Soil structure in the A horizons followed two trends. The first trend was an increase in structure size and distinctiveness in the chronosequence from young bars and swales to intermediate flattened bars and swales, to old desert pavements (Figure 4.2). Specifically, soil structure changed from 1) moderate, medium to thick platy in biological soil crusts with underlying moderate, medium sub-angular (bar and swale landforms), to 2) weak to moderate medium sub-angular blocky/fine prismatic (flattened bar and swale), to 3) distinct medium to coarse prismatic (desert pavement) (Figure 4.2). The second trend in soil structure was driven by biological processes. Surface soil horizons of bioturbation zones and shrub zones were similar and were characterized as thick platy

due to biological crusts and medium to coarse subangular blocky/granular underneath (Figure 4.2).

Soil texture had the most drastic changes in the surface horizons. It followed a similar pattern with loamy sand/sandy loam changing to sandy loam/loam to silt loam in the bar and swale to flattened bar and swale to desert pavement chronosequence (Figure 4.3). In contrast, bioturbation and shrub zone units had loamy sand and sandy loam textures (Figure 4.3).

The most common subsurface horizons in almost all soils were Bk, BC and BCK horizons. Bioturbation units and shrub zones commonly had weakly developed B-horizons (Bw). Bkk and Bkkq horizons were found in desert pavement soils. Soil structure in subsurface horizons of young and intermediate-aged soil was not as common or distinct and was usually associated with plant roots. The best-developed structure was found in the old soils (desert pavement and shrub zone soils) (Figure 4.2). Carbonate morphology increased over geomorphic time in B-horizons (Table 4.1). However, the strongest carbonate buildup was recognized in the sequence: bar and swale (Stage I) to flattened bar and swale (Stage I/I+) to desert pavement (Stage II+/III). Classification of carbonate morphology in bioturbation unit and shrub zone soils never exceeded Stage I+.

The soils in all soil pits studied had an ochric epipedon. Three morphological subsurface features were identified: cambic and calcic horizons and durinodes. The calcic horizon was the most common subsurface horizon for all soils. Occurrences of a calcic horizon increased over geomorphic time (Table 4.1). Bar, swale and shrub zone soils generally lacked a calcic horizon. Calcic horizons were best developed in desert

pavement units. Desert pavements were also the landform where durinodes were identified. Cambic horizons occurred only in bioturbation and shrub zone soils.

Soils of the fan skirt chronosequence were classified into two soil orders: Entisols and Aridisols. In general, the soils of the young geomorphic surface with bar and swale topography were identified as Orthents and Fluvents. The difference between the two was the irregular amount of organic carbon in subsequent horizons in the Fluvents. The soils of the intermediate-aged surfaces were a mix of Orthents and Calcids (Table 4.3). Desert pavement soils of the old geomorphic surfaces were classified as Calcids and the shrub zone soils were mostly Cambids with one Calcid.

Calcium carbonate morphology (Gile et al. 1966) of the B horizons were used to obtain an age estimation of the geomorphic surfaces by comparisons with nearby dated alluvial fan surfaces of the Soda Mountain and Providence Mountain piedmonts (Table 4.4). Thus, I estimate the young geomorphic surfaces to be between 500 to 1000 years old. Analog calcium carbonate stage the intermediate surfaces would be around 4000 years old. These surfaces would be of Holocene age. The old surfaces may range between 10,000 to 50,000 years old and may have formed during the late Pleistocene.

4.3.2 Patterns of chemical and physical soil properties

PCA analysis revealed distinct patterns of chemical and physical soil properties among the seven landforms and three geomorphic surfaces. Due to high variability, data were divided into two general data sets. One contained soils from abiotically structured landforms (flattened bars and swales, desert pavements) and the other had soils from

biologically active landforms (bioturbation and shrub zone units). Bar and swale soils were incorporated into both data sets as incipient soils.

4.3.2.1 PCA of abiotically-structured soils

Surface and subsurface horizons were associated with different and quite contrasting sets of soil properties depending on geomorphic age. These contrasts can be observed by the spatial separation of white to grey to black landform symbols that were associated with particular bundles of soil property vectors in all four PCA plots (Figure 4.4). All four PCA scatterplots explained 50 to 60% of the data variation in the first two component axes. The differences were most distinct in the 0 to 2 and 40 to 60 cm soil depths, 2 to 10 and 10 to 40 cm soil depths represented intermediate patterns, with 2 to 10 cm being more similar to the 0 to 2 cm depth and 10 to 40 cm being more similar to the 40 to 60 cm depth (Figure 4.4). The uniqueness of the 10 to 40 cm soil depth was the association of high calcium carbonate content of the fine earth fraction with increasing geomorphic age that was linked to the typical occurrence of calcic horizons in these depths. The data presentation that follows will focus on the 0 to 2 cm surface and 40 to 60 cm subsurface depths.

The first principal component axis of the 0 to 2 cm PCA explained 40.7% of the variation. It depicts a chronologic trend from young soils that plotted on the left to intermediate aged soils that plotted near the origin, and finally to old soils that plotted on the right (Figure 4.4). The young soils that plotted on the left were generally enriched in particular nutrients including nitrate, potassium, sulfur, calcium; total organic carbon and

nitrogen, calcium carbonate expressed as CCE and coarse and skeletal texture including percent sand, fine, medium, coarse gravel and cobbles. In contrast old surface soils were characterized by increasing values of sodium (sodium and SAR), soluble phosphate and ammonium, magnesium, a finer soil texture (clay) and high bulk density. Principal component axis 2 explained an additional 19.6% of the variability and was correlated primarily with increasing EC values from the lower to the upper plot site. This second gradient was less clearly linked to geomorphology since no distinct pattern with any particular landform was observable.

The principal component axis of the 40 to 60 cm subsurface horizon also explained a large amount of the variability (30.2%) and similarly depicted a geomorphic age gradient. Thus, young soils plotted on the left, old soils on the right and intermediate-aged soils close to the origin. Young soils, as in the 0 to 2 cm depth, had more organic matter, sandier texture, and generally higher percentages of gravel and cobble-sized fragments. In contrast to the 0 to 2 cm soil depth, nitrate, sulfur and calcium values were low in young soils. On the other hand, older soils had high values of these three soil components. In addition these soils were finer textured (increase in clay content), sodic (high in sodium and SAR) and saline (high EC) at this subsurface depth. Soluble phosphate values and bulk density were also high. The second PCA axis separated the sites according to higher pH that correlated with finer texture and finer rock fragments in the lower plot and coarser rock fragment size in the upper plot. This gradient explained 24.1% of the variation.

4.3.2.2 PCA of biotically-structured soils

Principal component analyses using a biotic model were, in general, very similar to each other in all four soil depths and explained more than 50% of the data variability (Figure 4.5). Similar to the abiotic model, in all four plots the first axis depicted a geomorphic aging trend. Moreover, for almost all soil properties a particular set was associated with young soils and a particular set with old soils that was consistent throughout the soil depths. Therefore young incipient soils were coarse textured and skeletal, with low nutrient and organic matter plotting on the opposite side from old soils (left side, Figure 4.5). After initiation of bioturbation, soils tended to increase in organic matter, increase in nutrients, become finer textured, and incorporate salts throughout the entire profile. Old soils plotted on the right side and grouped around TOC, TN, clay, Na, SAR, Mg, K, CA, EC, and S (Figure 4.5). The second PCA was less clearly associated with a distinct gradient. Some association between fine and coarse texture and presence of ammonium versus nitrate was indicated (Figure 4.5).

4.3.3 *Linking land surface characteristics to soil properties*

Multivariate CCA revealed that chemical and physical properties increased or decreased in response to an increase in geomorphic age and change in land surface characteristics for all four soil depths of the seven landforms studied. The linkages can be observed in the CCA biplots (Figure 4.6 and 4.7) as specific environmental variables (plot vectors) associated with specific soil response variables (crosses in the plot). All four analyses explained >80% of the data variability within the first two axes.

Geomorphic age was the strongest driver for all four CCA's and was closely correlated with the first axis (Figure 4.6. and 4.7) in agreement with the patterns observed in the PCA. Thus, just as in the PCA plots, in the CCA plots geomorphic age was the prime contributor to spatial separation of landform units from left to right (white to grey to black colored symbols). Surface clast properties were generally tightly correlated with axis two in all four CCAs. Vascular plants and biological soil crust vectors were generally found in a diagonal position between axis one and two in the third quadrant and may represent a third gradient that is not depicted in the biplot.

In the first analysis (0 to 2 cm), an increase in the number of soil-embedded clasts and geomorphic age was associated with high values of SAR, sodium cations, soluble phosphate, ammonium ions and to a lesser degree of EC, percent clay and magnesium cations. A higher microtopography and clast size was linked to the amount of cobbles found in this soil depth. There was a weak association of higher microtopography, total biological soil crust, and annual grass cover with higher values of bulk density, pH, CCE, nitrate, TOC, TN, sulfur, calcium and percent sand and fine and medium gravel. However these response variables grouped closely to the plot origin, meaning that they contributed less to the weighting of the samples.

In the second analysis (2 to 10 cm), increases in geomorphic age and to a lesser degree perennial forbs were associated with high values of SAR, sodium cations, soluble phosphate and ammonium ions and to a lesser degree, values of EC, percent clay and magnesium cations. Perennial forbs associated closely with calcium, magnesium, and EC, but the relationship was weak. The number of soil-embedded clasts, clast kurtosis,

and clast skewness were correlated with sulfur concentrations. Slope convexity could be related to amount of cobbles found in the soil. Crust cover and annual forbs were weakly associated with higher values of bulk density, pH, CCE, nitrate, TOC, TN, and percent clay, sand, and fine and medium gravel.

The next two CCA's investigated the relationship in the subsurface horizons. In the 10 to 40 cm soil depth plot, geomorphic age correlated closely with high values of sodium in soil solution and consequently high values of SAR on the right side. Also, number of embedded clasts, and the clast distribution parameters kurtosis and sorting were associated with increases in magnesium and calcium cations and EC.

Microtopography was linked to the percent of cobbles in the profile and plotted on the left. Interestingly, presence of woody shrubs and annual forbs was linked to higher values of soluble phosphate, nitrate, ammonium, potassium, TOC, TN, bulk density, CCE, percent sand, clay, fine and medium gravel, and coarse gravel.

The 40 to 60 cm analysis showed an overall similar pattern. Geomorphic age, together with clast size, associated with SAR, sodium, sulfur, calcium, magnesium, and EC on the right side. Woody shrubs, annual forbs, and microtopography were closely linked to soluble phosphate, nitrate, ammonium, potassium, TOC, TN, bulk density, CCE, percent sand, clay, fine and medium gravel, and coarse gravel.

4.4 Discussion

4.4.1 Land surface properties and geomorphic age are linked to soil properties

This study demonstrated that land surface characteristics are strongly predictive of specific soil characteristics. Remarkably, the relationships were not just limited to the surface horizons. Subsurface soil properties still could be associated tightly with land surface characteristics. Thus, several patterns for surface and subsurface horizons were recognized and evaluated.

4.4.1.1 Surface horizons

At the surface and in the subsurface, the presence and amount of coarse gravel and cobbles was positively correlated with greater microtopography, larger mean clast size, and convex slope morphometry. These attributes have their origin in the initial depositional differences between alluvial debris deposited as a bar or in a swale. Bar-and-swale/channel topography is a commonly observed fluvial feature on channel beds of alluvial fans, fan piedmonts, and fanskirts (Wells et al. 1987, McFadden et al. 1989, Cooke et al. 1993, McDonald 1994, Pietrasiak personal observation). Specifically, it describes the undulating pattern of differently sorted debris that was deposited on a braided streambed during a high-magnitude flow event (Cooke et al. 1993, Powell 2009). Bars contain coarse water-laid sediments, such as gravel and cobbles, and are topographic highs. Swales are topographic lows that are dominated by finer particles such as fine gravel and sands.

Cover of biological soil crusts and annual plants indicated some weak positive associations with the amount of organic matter components (TOC and TN) and nutrients (e.g. nitrate and calcium) in the surface 10 cm of the soils in the CCA plots. This was not surprising since both crusts and annual plants aid in organic matter addition, accumulation, decomposition, and nutrient leaching at the microscale (Pérez 1997, Evans and Johansen 1999, Belnap et al. 2001, DeFalco et al. 2001, Belnap and Lange 2003, Sperry et al. 2006). For example, decaying tissues of annual vascular plants and microbial organisms in biological soil crusts, as well as soil fauna feeding on them, ultimately add organic carbon to the surface soil horizons. With low biological decomposition rates (Vanderbilt et al. 2008) and temporally limited microbial respiration in deserts (Huxmann et al. 2004), total organic carbon can accumulate within the very top few centimeters of the soil in shrub interspaces (Pérez 1997, Huxmann et al. 2004, Pietrasiak unpublished data). However, some decomposition of annual plant roots, litter and microbiological soil crust biomass may increase available nutrients in solution when soils are moist (Sperry et al. 2006, DeFalco et al. 2001). This may explain the increased level of soluble nitrate and calcium in the surface soil. An increase of nitrate in solution could also be from cell leakage of biological soil crust organisms when exposed to wetting/drying cycles (Johnson et al. 2005).

The weak relationships of pH, coarse soil texture, CCE, and bulk density with land surface properties are less clear. These variables grouped between biological soil crust, annual plants, clast size, and microtopography vectors close to the plot origin. Both biological and physical properties could affect, covary, or counteract with these soil

properties. For example, a sandy texture is found in young soils of bar and swale soils and may reflect the incipient texture of deposited alluvial debris. However, fine sand particles could also be added through entrapment by annual plants and biological soil crusts. Higher values of pH and bulk density plotted closest to the origin with a tendency to the right side of the plot. I expected these variables to show a greater increase with geomorphic age than observed. Physical and biological land surface vectors may counteract each other, causing high data variability and thus their close position to the plot origin. An increase in pH is often linked to an input of alkaline dust, which is commonly trapped and accumulates in the soil over time (Harden et al. 1991), especially in desert pavement soils. Therefore I would have expected pH to plot further to the right, being associated with clast embeddedness and geomorphic age. However, some other factors may influence pH as well and mask a clear relationship with these vectors.

Bulk density at the soil surface increased with presence of thicker vesicular horizons in the soils studied. This may be related to the continued shrink and swell processes, as well as silt and clay translocation, which compact the peds (Anderson et al. 2002). However, bulk density also increased somewhat in the presence of biological soil crust and vascular plants in comparison to skeletal single-grained soil horizons. Thus, physical and biological processes both impact bulk density but may counteract each other. As a result, bulk density plotted close to the plot origin.

The third distinct relationship was the association of high clast embeddedness and a finer clast distribution (= high skewness) with high salinity and sodicity, as well as soluble potassium, ammonium, and phosphate in the top 10 cm. A high clast

embeddedness and skewness indicate a well-developed desert pavement that has a monolayer of densely packed, interlocking clasts. I found strongly developed vesicular horizons underneath all desert pavements. These horizons were formed during long-term trapping and accumulation of fine dust particles by the original rough surface of protruding clasts (McFadden et al. 1987). Dust particles are often salt rich when derived from playa sources (Reynolds et al. 2006, Reynolds et al. 2007). Such dust trapping and deposition of salty fines was indicated by the finer texture and high amounts of salts and sulfur in this soil horizon.

Both desert pavement and the vesicular horizon have been linked to decreased infiltration and percolation of rainwater (Young et al. 2004, Wood et al. 2005, Schafer et al. 2007). However, depending on the intensity and duration of rain events, vesicular horizons may be slowly or partially wetted. The vesicular horizons observed were fine textured and characterized by high bulk density and soil pore discontinuity. Furthermore, they had a distinct prismatic structure with an accumulation of distinct clay films sealing their bottom layer. Therefore, I hypothesize that some rain events can cause enough wetting from the top that this horizon undergoes saturated conditions, since percolation may be difficult past the clay films. The water-holding capacity is high due to fine texture, and the clast layer on top inhibits evaporative water losses, thereby prolonging the saturation phase. During this saturation, anaerobic redox-reactions may take place that produce large amounts of ammonium and phosphate potentially gained from allochthonous dust salts and minerals that accumulated in the surface. The horizon eventually dries but oxygenation may be slower due to pore discontinuity. In addition,

microbes that could oxidize these products may cease metabolic activity while the soil is drying out. Consequently, not all reduction products will get oxidized and transferred into another redox state. Presence of desert varnish found on autochthonous non-dolomitic clasts in the pavement support this finding. Future research could investigate this interesting phenomenon.

4.4.1.2 Subsurface horizons

Just as was observed in the surface horizons, clast embeddedness and clast distribution attributes promoted elevated sodicity and salinity in the subsoil. Clast embeddedness and clast distribution attributes, such as finer sorting, and skewness to finer particles, can be associated with presence of well-developed desert pavement. As mentioned above, infiltration into desert pavement soils is limited. Thus leaching depth is shallow and salts remain in near-surface depths (Wood et al. 2005).

Interestingly, higher values of organic matter, bulk density, calcium carbonate content, pH, and nutrients occurred in the subsoil of shrub interspaces on those landforms with greater total cover of woody shrubs and annual forbs compared to landforms with low plant cover. In the peer-reviewed literature, the soils beneath perennial shrubs has long been considered as “islands of fertility” (Charley and West 1975, Schlesinger et al. 1996, Schlesinger and Pilmanis 1998). These vegetation-enhanced fertile soils are known to be richer in carbon, nitrogen, and other essential elements (Charley and West 1975, Rostagno et al. 1991, Gallardo and Schlesinger 1992, Schlesinger et al. 1996). But this study demonstrated that in some landform mosaics the impact of plants may not be

limited to the soil directly beneath the plants. Roots can extend into and explore much of the intershrub spaces (Wilcox et al. 2004). They add organic carbon to these spaces, improve soil structure, and increase bulk density in skeletal single-grained soils that initially lack aggregation as observed in this study. Presence of roots may also support higher calcium carbonate values because calcium carbonate preferentially precipitates close to roots (Gutiérrez-Jurado et al. 2006).

4.4.2 Pedogenesis

Pedogenesis can be explained by Simonson's conceptual model of soil genesis (Simonson 1959). The aim of this model is a mechanistic understanding of soil formation. Soil formation is a result of four processes: additions, removals, transfers, and transformations. In the following paragraphs pedogenesis will be elucidated using this conceptual framework. Moreover, such soil forming processes are linked to the specific changes at the land surface through time. Thus, landform evolution drives changes in selected properties either at the surface, in the subsurface, or throughout the entire profile. Similar to the earlier described landform evolution (Chapter 2), pedogenesis followed two trajectories: one dominated by abiotic processes and the other by biotic processes. Both trajectories reflect different processes that produced differences in soil morphology and development.

4.4.2.1 Pedogenesis dominated by abiotic processes

Soil morphological observations, taxonomic classification, and multivariate analysis all revealed evidence of a distinct abiotic trajectory of soil development. Moreover, this trajectory is tightly associated with an abiogenic dominated change of land surface properties over time.

The soils on the alluvial fan skirt clearly differed depending on the timing of parent material depositional events. During periods of major erosion, fluvial activity deposited weathered debris from the mountains as alluvium on the piedmont (Cooke et al. 1993). This erosional/depositional event could have been initiated by tectonic activity or climatic change (Cooke et al. 1993). After reaching geomorphic stability, freshly deposited alluvial material exhibits a bar-and-swale topography. Over time, physical weathering, gravitational translocation of sediment and debris from topographic highs to lows, pedogenesis, dust deposition and accumulation, and erosion smooth the relief. This results in the sequence of (1) bar-and-swale, to (2) flattened bar-and swale, to (3) an almost even desert pavement unit (Chapter 2). This geomorphic change is associated with changes in land surface characteristics. Particularly, surface clast size and surface roughness decreases, clast density, skewness, and cover increases, and vegetation and biological soil crust cover contracts (see Chapter 2). At the desert pavement stage, the geomorphic surface is relatively sealed and stabilized by a densely packed and interlocking clast monolayer, so the underlying vesicular horizons and other horizons are protected from erosion for long periods of time (Cooke et al. 1993, McAuliffe et al. 2007). A similar trajectory of desert pavement development has been reported for

various arid landscapes; e.g., terraces (Al-Farraj and Harvey 2000), lava deposits (Wells et al. 1985, Valentine and Harrington 2011), alluvial fans (Pelletier et al. 2007, and moraines (Bockheim 2010).

Throughout the evolution of the alluvial fan skirt surfaces, tight interactions also exist between land surface properties and pedogenesis, hydrology, and ecosystem function. For example, rough surfaces of freshly deposited alluvial debris (gravel and cobbles) found on bars and swales create microtopography. Microtopography in turn alters the flow of water and wind and traps fine sediments (Yair and Klein 1973, Wells et al. 1985, Gillette and Stockton 1989, Blank et al. 1996, McDonald et al. 1995).

Dust is an important factor contributing to soil development in arid and semiarid landscapes. Accumulation rates of 2 to 20 g m⁻² yr⁻¹ have been reported for the Mojave Desert (Wells et al. 1987, 1990, Reheis et al. 1992, 1995, McFadden and Weldon 1987, Elliot and Drohan 2009). Dust sources are playas and piedmont surfaces with low vegetation cover (Wells et al. 1985, Reheis et al. 1989, Musick and Gillette 1990, Reheis 2006). Over time, deposited dust washes into cracks underneath surface clasts, lifting them up and building up a fine-textured layer. This process is inferred in A horizons of the sequence: bar and swale - flattened bar and swale - desert pavements as soil changed from loamy sand and sandy loam to loams and silt loams. During this accumulation period the fine-textured material is exposed to drastic and continued wetting and drying cycles especially during summer pulse precipitation events. Some rainwater infiltrates into the fine layer forcing gas displacement from soil pores. However not all the gas escapes due to a lack of pore continuity leaving a great portion of gas bubbles entrapped.

These pores are preserved once the soil layer dries, forming a vesicular horizon (McFadden et al. 1986, Anderson et al. 2002, Turk and Graham 2011). A continuation of wetting and drying cycles leads to enlargement of pores and formation of prismatic soil structure as observed in the old desert pavement soils of this study (Table 4.2).

The Av horizon has major effects on hydrology. With increasing Av horizon development, infiltration decreases until a threshold is reached and infiltration rate becomes constant (Young et al. 2004, McAuliffe et al. 2007, Meadows et al. 2008). Due to the water deficit and resulting lack of leaching, subsoil horizons accumulate salts, carbonates, and/or gypsum (Wood et al. 2005, Graham et al. 2008, Hirmas and Graham 2011). Decreased infiltration also results in increased runoff. The generated runoff can provide additional water input to areas that support plant growth and have higher infiltration rates. The amount of water redistributed may be a function of tortuosity of the overland waterflow path, which is determined by land surface properties.

The input of calcium-rich dust, in addition to local weathering of the dolomitic parent material, is mostly responsible for the formation of the calcic horizons in the intermediate and old soils. These horizons form by dissolution and eluviation of calcium carbonate from surface horizons and subsequent precipitation in subsurface horizons (Gile et al. 1966, Reheis et al. 1989, Hirmas and Graham 2011). Dissolution and precipitation of calcium carbonate is due to inorganic chemical changes, microbial activity, and/or root respiration. A well-developed calcic horizon can be a barrier for root penetration, but this phenomenon was not observed in this study.

Two desert pavement soils and one shrub zone soil had moderately well developed durinodes. Silica sources may be autochthonous chert, eroded material from upslope, and allochthonous dust and fine sand. The dissolution of silica from this material is promoted by the high pH environment caused by the presence of sodium carbonate (Na_2CO_3). The dissolved silica moves down the profile with occasional waterfronts and precipitates as amorphous opaline silica in the subsurface horizons where the waterfront stops.

4.4.2.2 Pedogenesis dominated by biotic processes

The alternative trajectory of biotic process-dominated pedogenesis proceeds from (1) young alluvial debris deposits (bar and swale) largely unimpacted by plants and animals; to (2) a stage in which bioturbation becomes significant, initialized in intermediate age; to (3) old age shrub zone units. The driving force of this trajectory is the presence of biological activity, especially the higher abundance of woody shrubs and associated presence of burrowing small mammals. At the land surface, foraging and burrowing activities of these animals prevent the formation of a tight interlocking clast layer (Neave and Abrahams 2001), expose new bare soil, displace subsurface debris to the surface, and create new soil crevices between surface rocks. Soil mixing is promoted throughout the profile depending on the depth of the animal burrows. Bioturbation units expand to a shrub zone over time due to biological facilitation (i.e., ecological species interactions that promote resource availability), growth habits of perennial shrubs, sand trapping, continued soil mixing, and resource redistribution (Alkon 1999, McAuliffe et

al. 2007, Chapter 2). Although Hans Jenny (1941) clearly highlighted biota as one of the factors of soil formation, my study may be the first to illustrate the potential for animals to route pedogenesis into a completely different direction.

Soil morphological observations, taxonomic classification, and data gained from multivariate analysis can all be tied to this trajectory. As compared to the abiotic trajectory, dust still can be trapped in these landforms due to roughness created by surface clasts, biological soil crusts, and vegetation, and consequently added to the soils. However, no vesicular horizon was formed despite the additions of fines. All A horizons had a very sandy texture on the young, intermediate, and old surfaces and no significant increase of clay and silt could be detected in the surface horizon as age increased. Indeed, soil textures of the fine earth fraction were close to homogeneous throughout the entire soil profile. This soil texture homogenization could be attributed to the continued animal disturbance. Bioturbation activity may also contribute to minor sediment losses by exposing fresh material that can be eroded by wind and water (Douglass and Bockheim 2006). However, biological soil crusts in bioturbation- and shrub-zone units are dominated by algae and cyanobacteria which have been shown elsewhere to quickly colonize freshly exposed soil material if moisture is available (Kidron et al. 2008).

Despite low litter and root decomposition rates in desert ecosystems and limited translocation of organic matter during sporadic rain events, total organic carbon and nitrogen content still increased over geomorphic time. Organic carbon and nitrogen also could be added to the soil from the leachates of plant, litter, and biological soil crusts. Nitrogen is also added to desert soils by dry and wet deposition (Brooks 2003).

Biotic soils lacked of well-developed calcic horizons. Soil development may be inhibited by constant mixing of the soil material, resulting in the development of cambic horizons rather than calcic horizons. Furthermore, in these coarse-textured soils with many krotovina and root channels, water can infiltrate easier and percolate much more freely, resulting in deeper leaching of calcium carbonates and salts, similar to the findings of Wood et al. (2005).

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Table 4.1 Soil morphological features among the seven landform units on a lower piedmont in the Mojave Desert. X's represent occurrence out of 3 replicate soils: X = 1/3 occurrences; XX = 2/3 occurrences; XXX = 3/3 occurrences.

Soil morphology	Young surface		Intermediate surface			Old surface	
	BR ^a	SW ^b	FB ^c	FS ^d	BT ^e	DP ^f	SZ ^g
Surface							
Vesicular horizon		XX	XX	XXX	X	XXX	
Ochric epipedon	XXX	XXX	XXX	XXX	XXX	XXX	XXX
Subsurface							
Cambic horizon					X		XXX
Calcic horizon		X	XX	X	XX	XXX	X
Durinodes						XX	
Carbonate stage after Gile et al. 1966	I	I	I/I+	I/I+	I	II+/III	I+

^a BR = bar

^b SW = swale

^c FB = flattened bar

^d FS = flattened swale

^e BT = bioturbated

^f DP = desert pavement

^g SZ = shrub zone

Table 4.2 Soil profile descriptions for one representative soil of each landform.

Horizon ^a	Depth (cm)	Bndy ^b	Munsell color dry	moist	Txtr ^c	Strct ^d	Ped/Void ^e surf feat	Roots ^f	Pores ^g	Efv ^h	CaCO ₃ ⁱ morph	Comments
Bar (1BRIN): Typic Torrifuvent												
P	2-0	as					10YR 7/2 fpr caf					discontinuous
A	0-1	as	10YR6/3	10YR4/4	ls	2mpl		1vft	3vf&fir	sl		well crusted, structure due to BSC many fungi many fungi
AB	1-25	gw	10YR6/4	10YR4/4	grsl	1msbk	10YR 7/2 fpr caf	1fc 2mc	3vf&fir 1mir, 1fdt	sl		
BC	25-46	gw	10YR6/3	10YR4/4	xgrls	1fsbk	10YR 7/2 fpr caf	3vf&fc 1m&cc	3vf&fir 1mir,	st		many fungi, root mats
Bck	46- 57+		10YR6/3	10YR4/6	vgrls	sgr	10YR 7/2 fpr caf	1vf&fc	3vf&fir	st		fungi rare

Table 4.2 (continued)

Horizon ^a	Depth (cm)	Bndy ^b	Munsell color		Txtr ^c	Strct ^d	Ped/Void ^e surf feat	Roots ^f	Pores ^g	Efv ^h	CaCO ₃ ⁱ morph	Comments
			dry	moist								
Swale (1SWIN): Typic Torrifluvent												
P	1-0	as					10YR8/2 fpr caf					discontinuous
Av	0-1	as	10YR6/3	10YR4/4	sl	1th-impl	10YR8/2 vfpr caf		3vf+f ve	sl		some fungi, incipient, non- continuous vesicular peds
A	1-8	aw	10YR6/3	10YR4/4	grsl	1m-tkpl 1msbk	10YR8/3 vfpr caf	1vf	3vf+f+	sl		some fungi, very loose
Bw	8-16	aw	10YR6/3	10YR4/6	vgrls	1msbk	10YR8/1 fp-dpr caf	1vf+fc	3vf+f+	st		many fungi,
Bk1	16-36	aw	10YR6/3	10YR4/6	vgrls	1fsbk	10YR8/1 cp-dpr caf	2vi&ft 1mt	m ir* 3vf+f ir*	st		many fungi
Bk2	36-47	aw	10YR6/3	10YR4/6	grls	1fsbk	10YR8/1 cdpr caf	2vf&ft	3vf+f+	st		some fungi, structure is in soil
Bk3	47-57	cw	10YR6/3	10YR4/6	vgrsl	sgr	10YR8/1 cdpr caf	2vft	m ir 3vf+f ir	st		pockets, root mats some fungi, root mats
Bck	57-69+		10YR6/3	10YR4/6	vgrls	sgr	10YR8/1 cdpr caf		2vf+f ir	st		root mats

Table 4.2 (continued)

Horizon ^a	Depth (cm)	Bndy ^b	Munsell color		Txtr ^c	Strct ^d	Ped/Void ^e surf feat	Roots ^f	Pores ^g	Efv ^h	CaCO ₃ ⁱ morph	Comments
			dry	moist								
Flattened bar (1FBIN): Typic Torriorthent												
P	2-0	aw					10YR8/3 fppr caf					desert varnish on a non-dolomitic clast with 7.5YR4/6 color on bottom of the clast
Av	0-6	as	10YR6/4	10YR4/4	vgrsl	1 tml 3m- cosbk	10YR8/3 fppr caf		2vf+fir 3vf	sl		
A	6-15	cs	10YR6/4	10YR4/4	vgrsl	1 mgr	10YR8/3 fp-dpr caf	1 vfc	3vf+fi m ir*	sl		some fungi, salt crystals: 10YR6/1, 10YR8/1, 7.5YR6/6
Bk1	15-25	cw	10YR6/3	10YR4/4	vgrls	1 msbk	10YR8/2 cdpr caf	2vf+fc 1mc	3vf+fi m ir*	st		some fungi, root mats associated with carbonate coating of big clasts
Bk2	25-33	cs	10YR6/3	10YR4/4	xgrls	sgr	10YR8/2 fp-dpr caf	2vfc 3fc 2mc	3vf+fi m ir*	st		some salt crystals
Bk3	33-44	gw	10YR6/3	10YR4/4	vgrsl	sgr	10YR8/1 cdpr caf	3vf&fc	3vf+fi m ir*	st		rootmats
BC	44-56+		10YR6/3	10YR4/4	xgrsl	sgr			3vf+fi ir*	st		some salt crystals

Table 4.2 (continued)

Horizon ^a	Depth (cm)	Bndy ^b	Munsell color		Txtr ^c	Strct ^d	Ped/Void ^e surf feat	Roots ^f	Pores ^g	Efv ^h	CaCO ₃ ⁱ morph	Comments
			dry	moist								
Flattened swale (1FSIN): Typic Torriorthent												
P	1-0	vs					10YR7/2 cp-dpr caf					dense clast cover
Av1	0-2	as	10YR6/4	10YR4/4	grsl	1 vfpr, 1 fsbk 1 tnp1	10YR7/2 fppr caf	1 vft	3vf ir 3vf-m ve	sl		some fungi, vesicular horizon discontinuous many fungi,
Av2	2-9	aw	10YR6/4	10YR4/4	l	3f-mpr 3msbk	10YR8/1 fppr caf	3vfc	3vf ir* 3vf-m ve	st		
Bk1	9-20	cw	10YR6/3	10YR4/4	xgrsl	sgr	10YR8/1 cp-cpr caf	3vf+fc 1cc	3vf+f ir*	st		many fungi, root mats, salt crystals causing gravel conglomerate
Bk2	20-31	cw	10YR6/3	10YR4/4	vgrls	sgr	10YR8/1 cp-cpr caf	2vf+fc	3vf+f ir*	st		many fungi, salt crystals on gravel undersides
BC	31-48	cs	10YR6/4	10YR4/4	xgrls	sgr	10YR8/1 fp-cpr caf	2vf+fc	2c ir* 3vf+f ir*	st		some fungi, root mats, salt crystals on gravel undersides
BC	48-58+		10YR6/4	10YR4/4	vgrls	sgr	10YR8/1 fp-cpr caf		3vf ir*	st		root mats, some salt crystals

Table 4.2 (continued)

Horizon ^a	Depth (cm)	Bndy ^b	Munsell color		Txtr ^c	Strct ^d	Ped/Void ^e surf feat	Roots ^f	Pores ^g	Efv ^h	CaCO ₃ ⁱ morph	Comments
			dry	moist								
Bioturbation unit (1FDIN): Typic Haplocambid												
A1	0-4	aw	10YR5/3	10YR4/4	grls	1mpl, 2msbk	10YR8/2 fppr caf	3vft	3vf+ft m ir	sl		incipient and light algal crust, many fungi many fungi,
A2	4-12	aw	10YR6/3	10YR4/4	grsl	3m- cosbk	10YR8/2 fppr caf	3vft 1ft	3vf ir 1f+m dt	sl		
Bk1	12-22	aw	10YR6/3	10YR4/4	vgrsl	2f-msbk	10YR8/2 cpr caf	3vf+fc 2mt 1cot	3vf+ft ir* 2m ir* 1vf dt	st	10YR8/ 1 vfli arf can	many fungi, root mats,
Bk2	22-34	cw	10YR6/3	10YR4/4	vgrls	sgr	10YR8/2 cp-dpr caf	3vfc 2fc 1mc	3vf+ft ir* 1m ir* 3vf+ft	st		many fungi, root mats
Bk3	34-44	cw	10YR6/3	10YR4/4	vgrls	sgr	10YR8/2 cpr caf	2vf+fc	3vf+ft ir*	st		many fungi, root mats, salt crystals
BC	44-54+		10YR6/3	10YR4/4	xgrls	sgr	10YR8/2 fppr caf	1fc	3vf+ft ir*	ve		many fungi, root mats, some salt crystals

Table 4.2 (continued)

Horizon ^a	Depth (cm)	Bndy ^b	Munsell color		Txtr ^c	Stret ^d	Ped/Void ^e surf feat	Roots ^f	Pores ^g	Efv ^h	CaCO ₃ ⁱ morph	Comments
			dry	moist								
Desert pavement (1DPIN): Durinodic Haplocalcid												
P	2-0	vs					10YR8/1 fp-cpr caf					dense clast cover, some fungal hyphae under clast and CaCO ₃ precipitate some fungi
Av	0-7	vs	10YR7/4	10YR4/4	sil	3c-vcpr	10YR7/4 fed sif	1vfc	3vf-m ve	ve		
Btk	7-16	cw	10YR6/4	10YR4/4	l	2f-msbk	10YR6/6 cpdb+i clif 10YR8/1	3vft 2ft 2mt	3vfir 1fir	ve	10YR8/1 fl mat cam	many fungi
Bk1	16-29	cw	10YR7/4	10YR4/4	vgrsl	2f-msbk	vfpr caf 10YR8/1 cdpr caf	3vf+ft 1mt	3vfir 1fir	ve		many fungi
Bk2	29-38	aw	10YR7/3	10YR5/6	vgrsl	1mgr/ sbk	10YR8/1 cdpr caf	1ct 2vf+ft 2mt	1m ir 1vfir 1m ir	ve	10YR8/1 vf1 can	
Bkkq1	38-49	aw	10YR7/3	10YR5/4	vgrsl	ma	10YR8/1 cdpr caf	1ft	1vfir	ve	10YR8/1 m4 cam	
Bkkq2	49-57	aw	10YR7/3	10YR5/4	xgrsl	ma	10YR8/1 cdpr caf	1fr	1vfir	ve		fungal hyphae in few cracks, durinodes
BC	57-65+		10YR6/4	10YR4/6	vgrsl	ma	10YR8/1 fdpr caf	1vfc	2vfir	sl		

Table 4.2 (continued)

Horizon ^a	Depth (cm)	Bndy ^b	Munsell color		T _{xtr} ^c	Strct ^d	Ped/Void ^e surf feat	Roots ^f	Pores ^g	Efv ^h	CaCO ₃ ⁱ morph	Comments
			dry	moist								
Shrub zone (1SZIN): Durinodic Haplocambid												
A	0-7	as	10YR6/3	10YR4/4	ls	2mgr 2tnpl	10YR8/1 cdpr caf	1vft	3vf-fir	ve		many fungi, dark algal crust, cyanolichen crust many fungi, root mats
B	7-16	cs	10YR6/3	10YR4/4	sl	2mgr 2f-msbk	10YR8/1 vfdpr caf	3vf+ft 1mt	3vf+ir 1fte 2m ir	ve		many fungi
Bw	16-29	cs	10YR6/3	10YR4/6	grsl	2mgr 2f-msbk	10YR8/1 fdpr caf	3vf+ft 3m-ct	3vf+fir 3f+m te	st		some fungi
Bk	29-38	gw	10YR6/3	10YR4/6	vgrsl	2mgr	10YR8/1 mdpr caf	3vf+f +ct	3vf+fir 2fir 2fte	ve		some fungi
Bkq1	38-49		10YR6/3	10YR4/4	xgrsl	ma	10YR8/1 mdpr caf	2f+ct	2f-m ir	ve		some fungi, sgr if durinodes get disturbed

^a horizon designations follow USDA-NRCS definitions, except for P (= pavement horizon) and Av (= vesicular horizon).

^b Bndy = horizon boundary, v = very abrupt, a = abrupt, c = clear, g = gradual, s = smooth, w = wavy.

^c T_{xtr} = rock fragments, gr = gravelly, vgr = very gravelly, xgr = extremely gravelly, soil texture determined by the hydrometer method, ls = loamy sand, sl = sandy loam, sil = silt loam, l = loam

^d Strct = soil structure, 1 = weak, 2 = moderate, 3 = strong; vf = very fine, f = fine, m = medium, co = coarse, tn = thin, tk = thick; pl = platy, sbk = subangular blocky, pr = prismatic, sgr = single grain, ma = massive.

^e Ped/Void surf feat = ped and void surface features, color is given for dry features; vf = very few, f = few, c = common, m = many; p = patchy, d = discontinuous, c = continuous; p = prominent; r = on rock fragments; clf = clay films, sil = silans, caf = carbonate coats.

^f Roots = root distribution, 1 = few, 2 = common, 3 = many; vf = very fine, f = fine, m = medium, c = coarse; c = in cracks, t = throughout

^g Pores = pore voids, 1 = few, 2 = common, 3 = many; vf = very fine, f = fine, m = medium; dt = dentritic tubular, ve = vesicular, ir = interstitial, * = in cracks.

^h efv = effervescence, sl = slightly, st = strongly, ve = violently.

ⁱ CaCO₃^h morph = calcium carbonate morphology, vf = very few, f = few, c = common, m = many, 1 = fine, 2 = medium, 3 = coarse, 4 = very coarse; cam = carbonate masses, can = carbonate nodules.

Table 4.3 Soil taxonomic classification among the seven landform units on a lower piedmont in the Mojave Desert. X's represent occurrence out of 3 replicate soils: X = 1/3 occurrences; XX = 2/3 occurrences; XXX = 3/3 occurrences.

Soil morphology	Young surface		Intermediate surface			Old surface	
	BR ^a	SW ^b	FB ^c	FS ^d	BT ^e	DP ^f	SZ ^g
Entisols							
Orthents	X	XX	X	XX	X		
Fluents	XX	X					
Aridisols							
Cambids							XX
Calcids		X	XX	X	XX	XXX	X

^a BR = bar

^b SW = swale

^c FB = flattened bar

^d FS = flattened swale

^e BT = bioturbated

^f DP = desert pavement

^g SZ = shrub zone

Table 4.4 Best age-estimation of the three geomorphic surfaces located on the Clark Mountain fan skirt.

Locale PM ^c	Soda Mountain ^a plutonic and metavolcanic			Providence Mountain ^b limestone			Clark Mountain dolomite		
Geol Time ^d	Fan surf ^e	Carb Morph ^f	¹⁴ C ^g	Fan surf ^e	Carb Morph ^f	Mult. dat. meth. best estimate ^h	Fan skirt surf ⁱ	Carb Morph ^f	Best age estimate
Holo- cene	Qf6	0		Qf8	0				
	Qf5			Qf7	I	500	Qf3	I	500 – 1,000
	Qf4	I	3,400±60	Qf6	I-II	4,000	Qf2	I-I+	4,000
	Qf3	I							
	Qf2	II	83,50±300 - 13,670±550	Qf5	II-III	10,000			
Pleisto- cene	Qf1	II-III	14,660±260 – 20,320±740	Qf 4	III+	50,000	Qf1	II-III+	10,000 - 50,000
				Qf3	IV	130,000			
				Qf2	IV-V	650,000			

^a Source: Wells et al. 1987

^b Source: McDonald 1994

^c PM = parent material

^d Geol Time = geologic time

^e Fan surf = fan surfaces

^f Carb Morph = calcium carbonate morphology of the B horizon after Gile et al. 1966

^g ¹⁴C = radiocarbon dating reported in McDonald 1994

^h Mult. dat. meth. best estimate = best age estimate using multiple dating methods after McDonald 1994

ⁱ Fanskirt surf = fanskirt surfaces

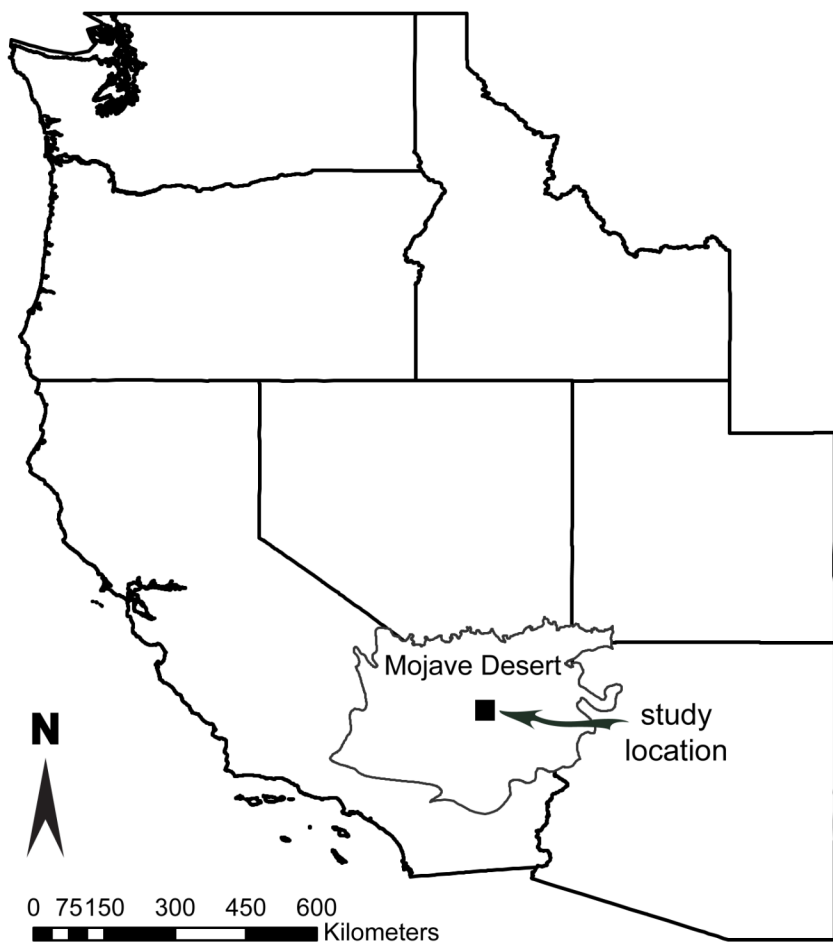


Figure 4.1 Map of the study location within the western U.S.

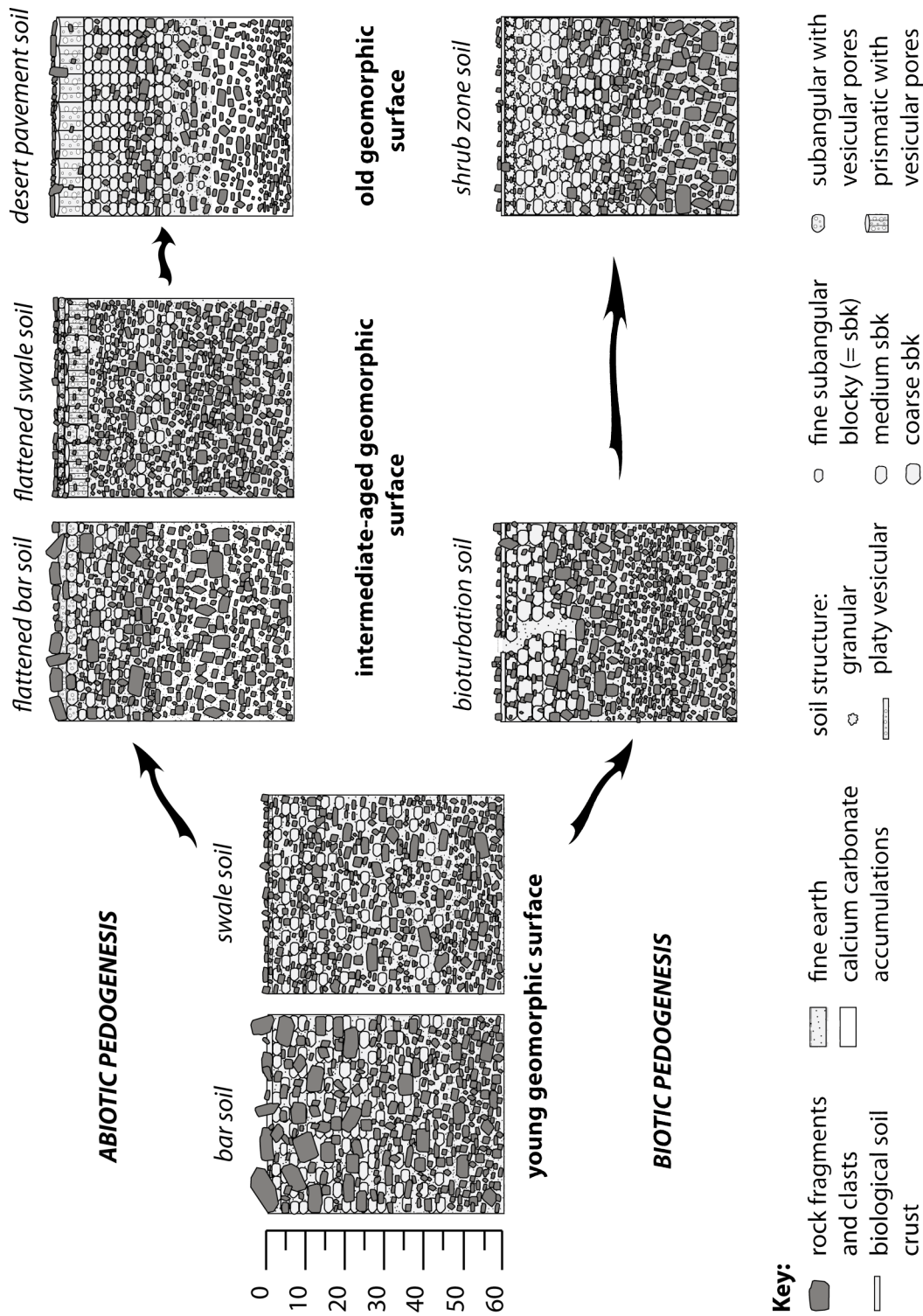


Figure 4.2 Scheme of hypothesized pedogenesis. Soils are drawn to scale using soil profile descriptions and soil physical data from a representative soil of each landform.

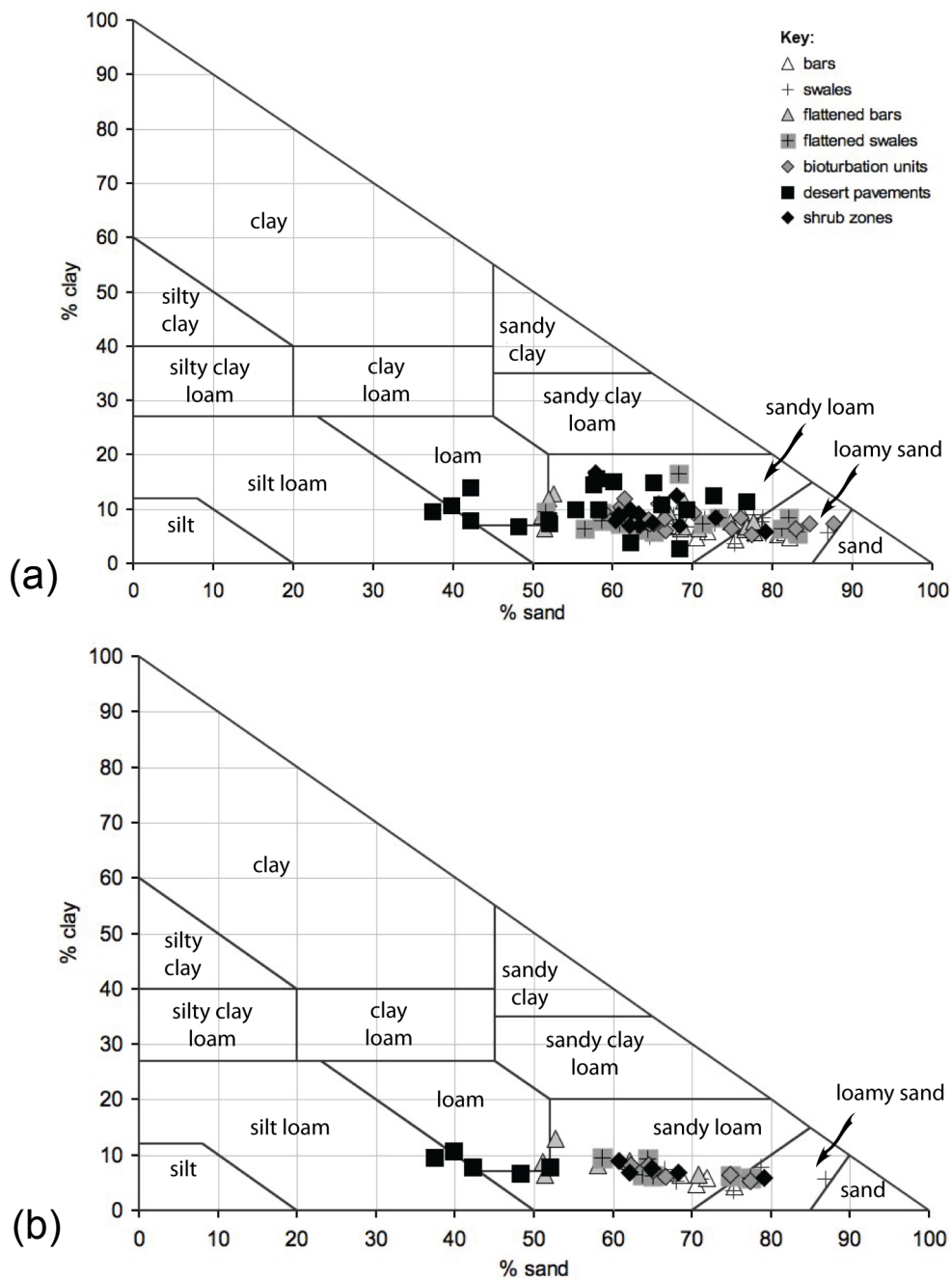


Figure 4.3 Soil texture plots for the fine-earth fraction (< 2 mm) collected from the soil horizons among the seven fan skirt landform type. Depicted are (a) all horizons sampled and (b) all A horizons.

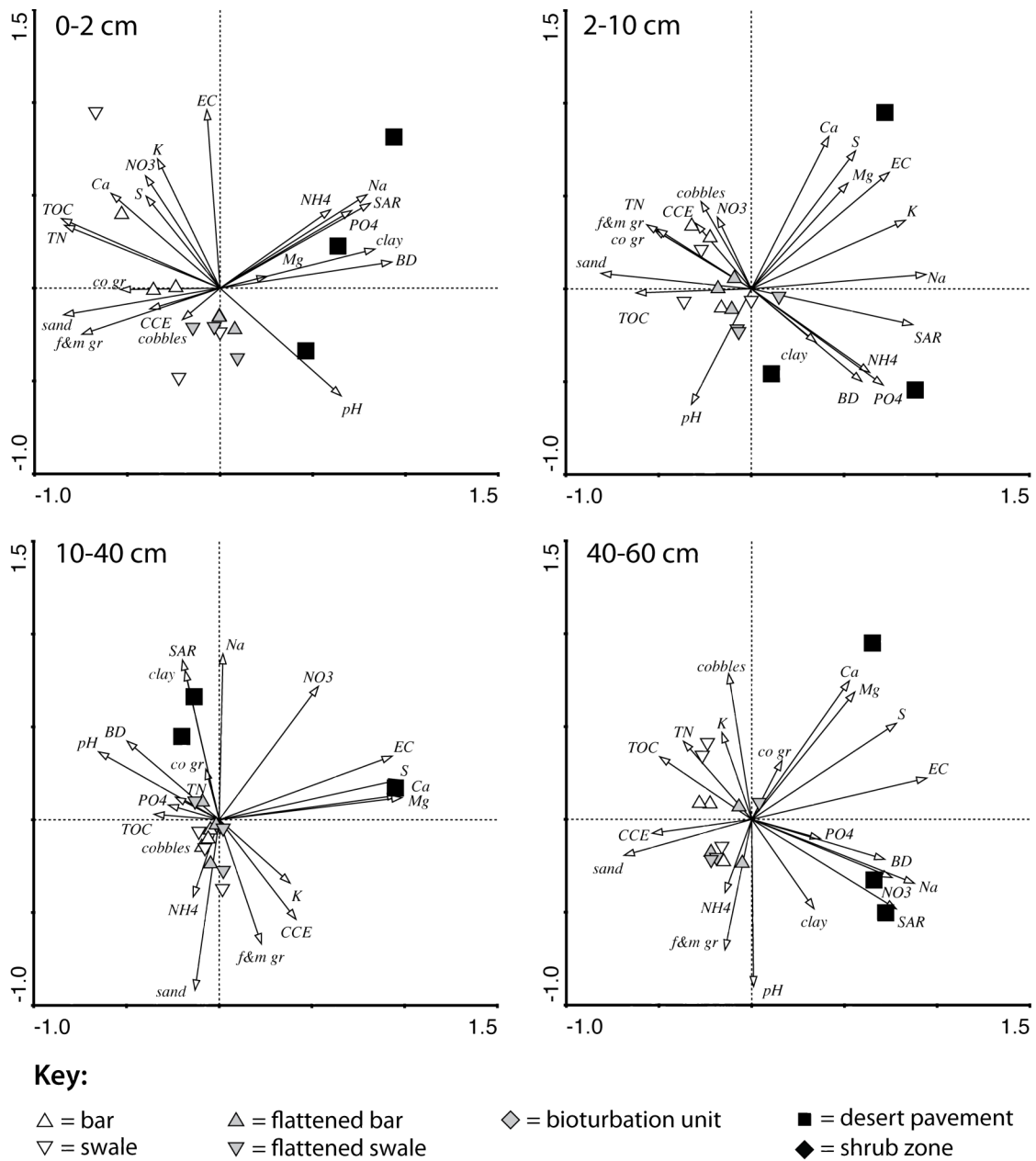


Figure 4.4 PCA scatterplots for abiotic structured soils showing the four soil depths analyzed. Symbols represent study plots classified after landform unit type. Vectors represent soil chemical and physical variable studied as dependent variables.

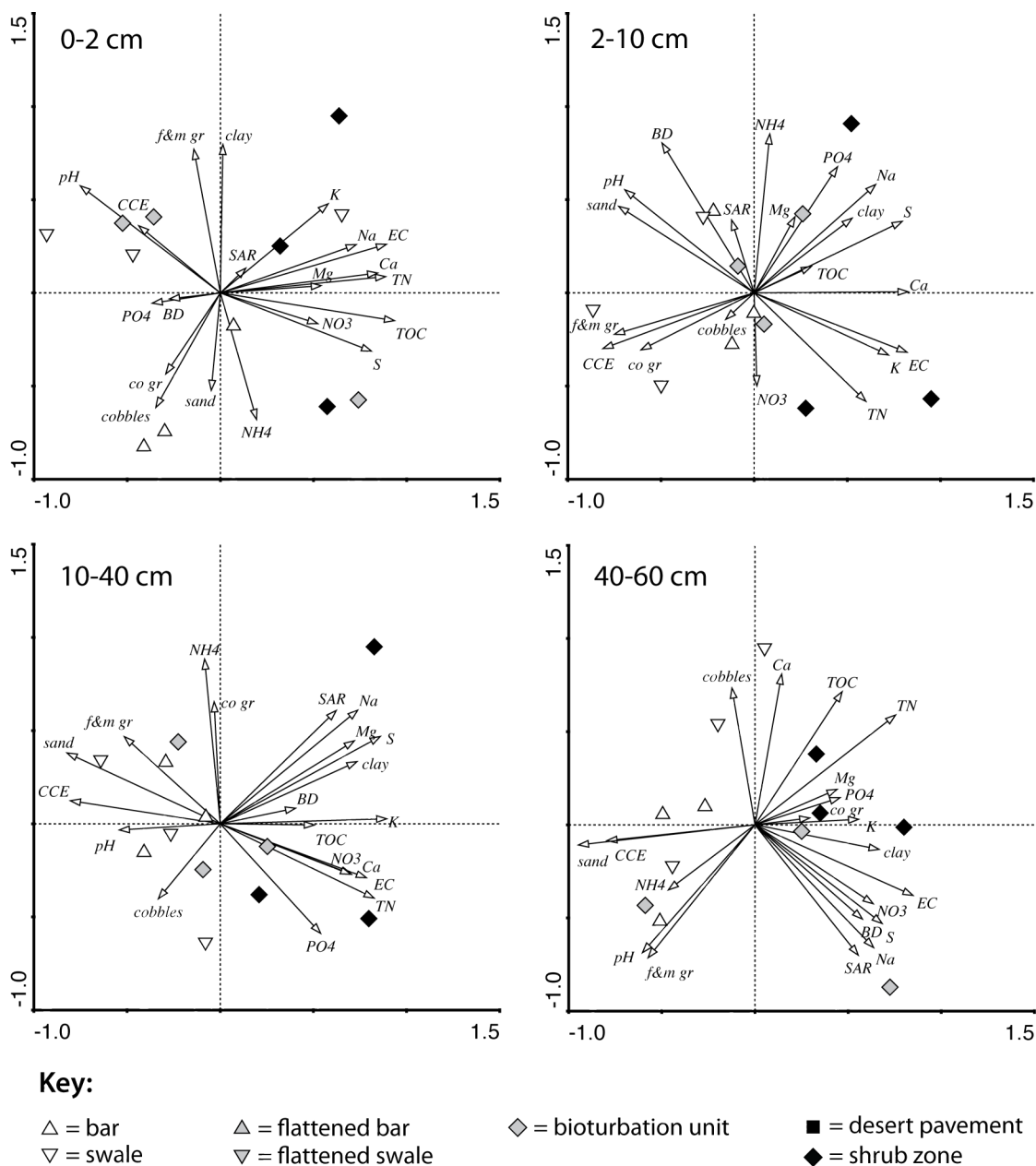


Figure 4.5 PCA scatterplots for biotic structured soils showing the four soil depths analyzed. Symbols represent study plots classified after landform unit type. Vectors represent soil chemical and physical variable studied as dependent variables.

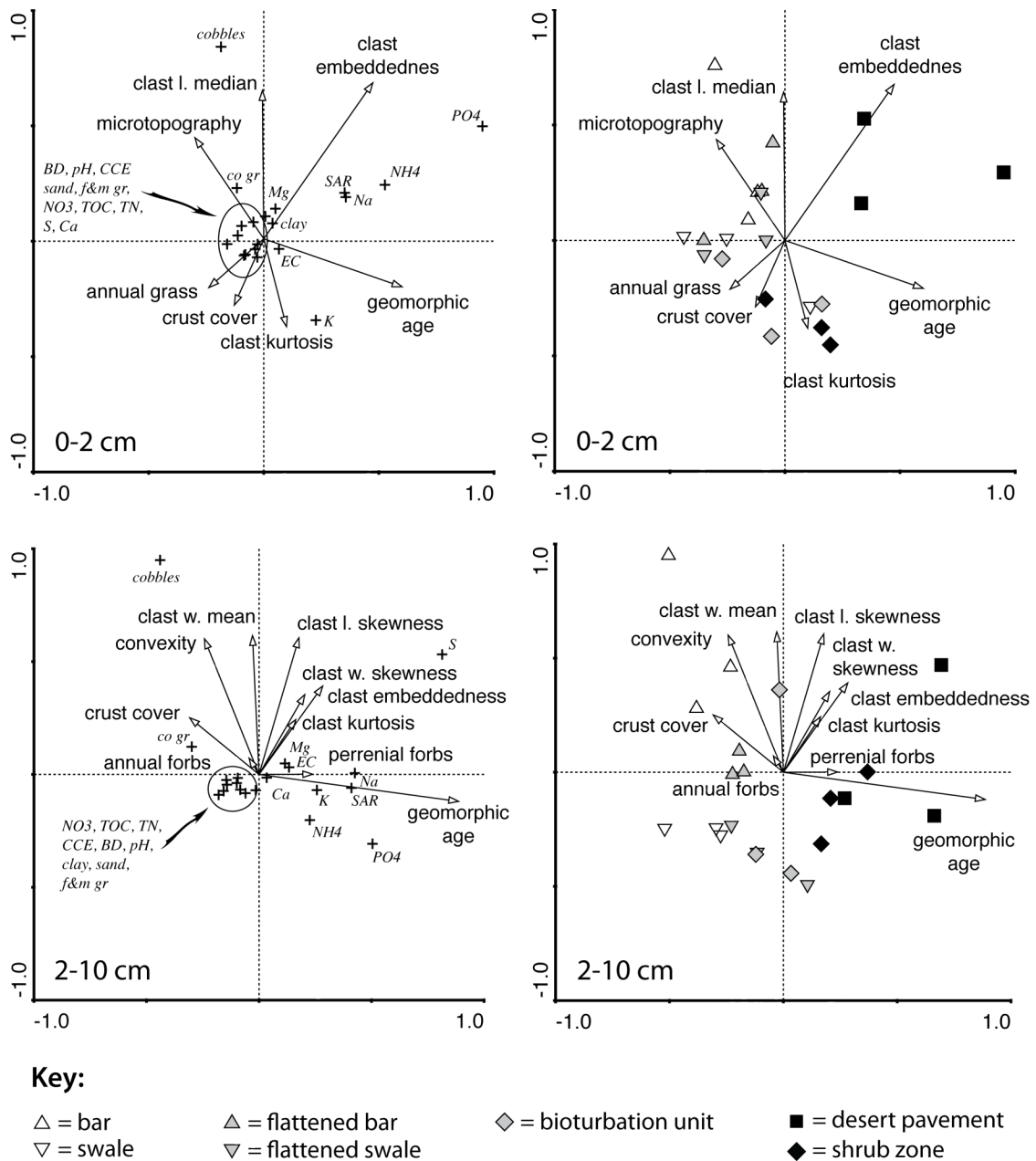


Figure 4.6 CCA bi-plots showing the two surface soil depths analyzed. Left plots depict dependent chemical and physical soil characteristics as crosses and environmental land surface properties as vectors. The right plots show spatial separation of study plots. Symbols represent study plots classified after landform unit type.

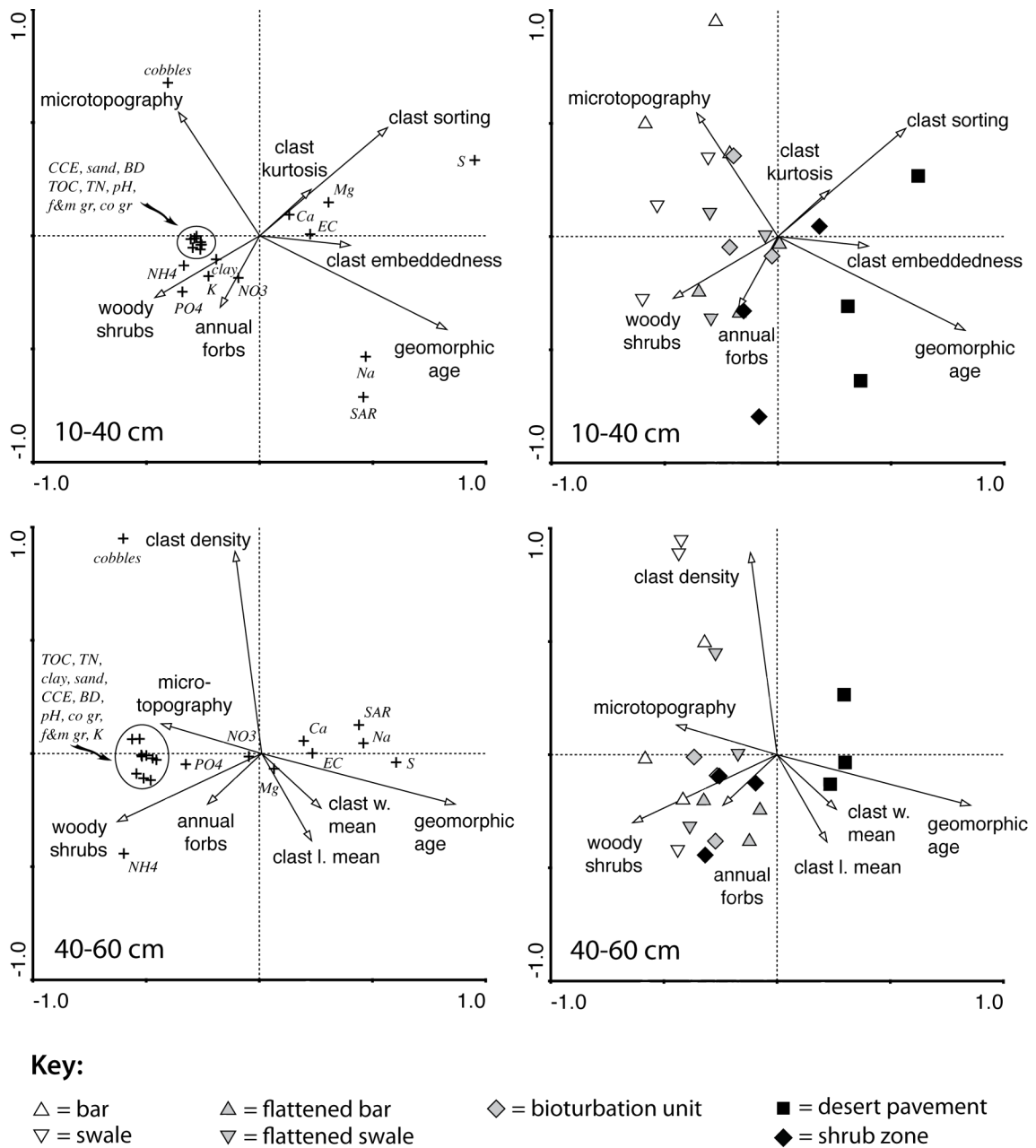


Figure 4.7 CCA bi-plots showing the two sub-surface soil depths analyzed. Left plots depict dependent chemical and physical soil characteristics as crosses and environmental land surface properties as vectors. The right plots show spatial separation of study plots. Symbols represent study plots classified after landform unit type.

5. CONCLUSIONS

The linkages and feedbacks of land surface properties to the biota were investigated in this work. The study encompassed vascular plants, biological soil crusts, ecological functions related to biological soil crusts, and soil development. All relationships studied were incorporated in a geomorphic framework of a lower piedmont fan skirt landscape in the Mojave Desert.

My work showed that unique combinations of abiotic and biotic land surface attributes can be used to describe and statistically predict seven mesoscale landform mosaics in the fan skirt landscape occurring on three geomorphic surfaces of different ages. The landform mosaics distinguished in this study included: young bars and swales; intermediate-aged flattened bars, swales, and bioturbation units; and old desert pavements and shrub zones. Two landform evolutionary trajectories, described as abiogenic and biogenic, were hypothesized. These tracks explained the formation and change of each landform unit on the three geomorphic surfaces through time. In the abiogenic trajectory abiotic processes prevail. It describes the development from a young alluvial deposit with high-relief bar and swale microtopography, rock crevices with bare soil, abundant plants and biological soil crusts to a flat and barren desert pavement devoid of biota. The biogenic trajectory explained a trajectory that was dominated by biotic processes and biological activity. The young bar and swale deposit undergoes bioturbation and over time, due to biological interactions and feedbacks with the soil environment, develops into a plant-rich shrub zone.

Pedogenesis and soil property changes were also linked to these two contrasting trajectories. Surface and subsurface morphology varied greatly between the two trajectories. Surface horizons of the abiogenic landform evolution developed from weakly structured soils under bars and swales to a well-developed, thick vesicular horizon under desert pavements. In addition, these horizons became finer in texture, more alkaline and salty. This was associated with the continued accumulation of dust over time. An increase in bulk density was linked to shrink-and-swell processes of clays and silts derived mostly from dust inputs. The subsurface horizon changed from weak B-horizon development with thick carbonate coatings under bars and swales to a well-developed thick calcic horizon under desert pavements.

Strongly developed vesicular or calcic horizons were not found in the biotic-dominated track that included a change from young bars and swales to intermediate bioturbation units to old shrub zones. During biogenic landform evolution an increase of organic carbon and total nitrogen was observed in surface and subsurface horizons. Soil texture did not change, rather a coarse texture was maintained through time. Bulk density increased initially due to the development from single-grained soils to a structured soil, but remained moderate through further development. Bulk density maintenance and persistence of coarse texture was related to the continued mixing of soil material by the burrowing of small mammal, which inhibited vesicular horizon formation. These soils also were less salty due to enhanced leaching below the 50 cm depth. The coarse soil texture and lack of vesicular horizon allowed more effective infiltration and leaching. The soil properties resulting from biogenic landform evolution contrast with those

produced by abiotic evolution and may explain the higher abundance of plants recorded in the old shrub zone units.

The seven landforms also differed significantly in functional group diversity of vascular plants and biological soil crusts. Abiotic land surface properties drive the abundance and diversity patterns. Specifically, microhabitat conditions affect biological soil crusts and may impact vascular plant seeds. Roughened landforms with large surface rocks offering rock crevices are preferentially found in young bars. And these landforms had the greatest diversity of biological soil crust community types and some of the highest abundance of total biological soil crusts. In contrast, plants were most abundant in old shrub zone units with greater cover of exposed soil and smaller surface rock dimensions. Other landforms were almost devoid of biological soil crusts and plants due to a dense interlocking surface rock layer. This difference in diversity and abundance of biological soil crust produces significant differences in ecological function that are associated with these communities. I investigated three important ecological functions of biological soil crusts: nitrogen fixation, photosynthetic carbon fixation, and soil aggregate stability. My results showed that different functional groups of biological soil crust performed differently among the three functions. I integrated these findings by developing an index that incorporated all three functions including a qualitative descriptor for the hydrological impact of these communities. The index can be used to assess a site according to its diversity of crust community types. It has the potential to be a powerful tool for land management. The index could be used to evaluate the quality of

biological soil crusts according to their most important ecological functions and is based on the coverage by each community type within an area.

This dissertation demonstrated that landform mosaics with defined land surface characteristics are tightly linked to biological soil crust community diversity, ecosystem functions, and pedogenesis. Overall, it shows how finer-scaled geomorphological studies with an ecological focus can make profound contributions to the understanding of desert landscape evolution, ecology, and pedogenesis.

APPENDIX A
SOIL PROFILE DESCRIPTIONS

Table A Soil profile descriptions for fourteen additional soils described.

Horizon ^a	Depth (cm)	Bndy ^b	Munsell color dry	moist	Txtr ^c	Strct ^d	Ped/Void ^e surf feat	Roots ^f	Pores ^g	Efv ^h	CaCO ₃ ⁱ morph	Comments
Bar (2BRIN): Typic Torriorthent												
P	2-0	aw					10YR 8/3 fpr caf					high in lichen crust
A	0-7	aw	10YR5/3	10YR4/4	sl	2m- cosbk 2tkpl	10YR 8/2 fp-dpr caf	2vft	3vf+fir 2m ir 2m te			algal crust creates structure, many fungi
Bk1	7-20	aw	10YR6/3	10YR4/4	grsl	3m- cosbk	10YR 8/3 cdpr caf	3vf+f+ mt lcot	3vf+f +m ir 1vfte		10YR8/1 fl/d arf/rpo cam	many fungi, rootmats on peds and clasts
Bk2	20-32	cw	10YR6/4	10YR4/4	grsl	sgr	10YR 8/2 cd-cpr caf	3vf+f+ m+coc	3vf+f+ m ir			many fungi, root mats
Bk3	32-47	cw	10YR6/4	10YR4/4	vgrsl	sgr	10YR 8/2 cd-cpr caf	3vf+fc lmc	3vf+fir			many fungi, root mats, salts
BC	47-54+		10YR6/4	10YR4/4	vgrls	sgr	10YR 8/2 fdpr caf	2ft	3vf+fir			root mats, salts

Table A (continued)

Horizon ^a	Depth (cm)	Bndy ^b	Munsell color dry moist	Txtr ^c	Strct ^d	Ped/Void ^e surf feat	Roots ^f	Pores ^g	Efv ^h	CaCO ₃ ⁱ morph	Comments
Bar (3BRIN): Typic Torrifuvent											
P	5-0	cw				10YR 8/3 vfpr caf					big embedded clasts
A	0-6	cw	10YR6/4 10YR4/4	vgrsl	3tk-vkpl 2msbk	10YR 8/3 vfpr caf	3vft+ft	3vf+fir 3vfdt 2m dt	vs		1-1.5 cm crust but due to rocks not a separate horizon, many fungi many fungi, root mats – associated with calcium carbonate
Bk1	6-28	gw	10YR6/3 10YR4/4	vgrsl	sgr	10YR 8/1 cp-dpr caf	2vf+f+ mt	3vf+f+ m ir*	sl		many fungi, root mats, salts fungi rare, root mats, salts
Bk2	28-46	gw	10YR6/3 10YR4/4	vgrls	1fsbk	10YR 8/1 cppr caf	3vf+ft lmt	3vf+fir	sl		
BC	46-52+		10YR6/3 10YR4/6	vgrls	sgr	10YR 8/1 fpr caf	1vf+ft	3vf+fir	st		

Table A (continued)

Horizon ^a	Depth (cm)	Bndy ^b	Munsell color dry	moist	Txtr ^c	Strct ^d	Ped/Void ^e surf feat	Roots ^f	Pores ^g	Efv ^h	CaCO ₃ ⁱ morph	Comments
Swale (2SWIN): Typic Torriorthent												
P	1-0	vs					10YR8/3 fpr caf					lose fine gravel pavement
Av	0-1	vs	10YR6/3	10YR4/4	xgrls	1tprl	10YR8/3 fpr caf		3vf+fir			many fungi, incipient algal crust
A	1-13	cw	10YR6/3	10YR4/4	vgrls	sgr	10YR8/3 fp-dpr caf	1vf+ft	1 fve 3vf+fir			no fungi
Bw	13-24	gw	10YR6/3	10YR4/4	xgrsl	2f-msbk	10YR8/3 cpr caf	1vft 3ft	1 m ir 3vf+f ir*			many fungi, root mats
									2m ir* 2fte			
Bk1	24-39	cw	10YR6/3	10YR4/4	xgrsl	1fsbk	10YR8/2 cp-dpr caf	3vf+ft 1m+cot	1m te 3vf+f+			many fungi, root mats
Bk2	39-54+		10YR6/3	10YR4/4	vgrsl	1fsbk	10YR8/2 cd-cpr caf	2ft	m ir* 3vf+f ir*			some fungi

Table A (continued)

Horizon ^a	Depth (cm)	Bndy ^b	Munsell color		Txtr ^c	Stret ^d	Ped/Void ^e surf feat	Roots ^f	Pores ^g	Efv ^h	CaCO ₃ ⁱ morph	Comments
			dry	moist								
Swale (3SWIN): Typic Torriorthent												
P	1-0	as					10YR8/2 fpr caf					fine gravel
A1	0-1	as	10YR5/3	10YR4/4	vgrsl	1fsbk	10YR8/2 vfpr caf	2vft	3vf+fir if dt	sl		many fungi
A2	1-10	gw	10YR6/3	10YR4/3	vgrls	sgr	10YR8/3 vfpr caf	3vf+ft	3vf+fir	sl		many fungi, root mats on clasts
Bk1	10-25	gw	10YR6/3	10YR4/4	vgrsl	3m- cosbk	10YR8/1 fp-dpr caf	3vf+ft lmt	3vf+ft m ir 3f dt 2vf+m dt	sl		some fungi, root mats on clasts
Bk2	25-39	cw	10YR6/3	10YR4/4	grsl	1fsbk	10YR8/1 cp-dpr caf	2vf+ft mt	3vf+fir 1f dt	st	10YR8/1 fll arf can	many fungi, root mats on clasts
BCk	39-51+		10YR6/3	10YR4/4	vgrsl	sgr	10YR8/1 cdpr caf	2vft 1ft	3vf+fir	st		some fungi, root mats

Table A (continued)

Horizon ^a	Depth (cm)	Bndy ^b	Munsell color		Txtr ^c	Strct ^d	Ped/Void ^e surf feat	Roots ^f	Pores ^g	Efv ^h	CaCO ₃ ⁱ morph	Comments
			dry	moist								
Flattened bar (2FBIN): Typic Haplocalcid												
P	1-0	as					10YR8/1 fppr caf					
A	0-5	aw	10YR6/3	10YR4/4	sl	1m- cosbk	10YR8/2 vfppr caf	1vft	3vf+fir 1vfve	sl		some fungi
ABk	5-20	gw	10YR6/3	10YR4/4	sl	2msbk	10YR8/3 fp-dpr caf	3vft 1ft	3vf+fir 2vf+fte	sl	10YR 8/1 fld rpo cam 10YR 8/1 f3s mat can	many fungi, root mats on peds and clasts
Bk1	20-29	cw	10YR6/3	10YR4/4	sl	1co-vc gr	10YR8/1 fp-dpr caf	3vf+ft 2ct	3vf+ft m ir*	sl	10YR 8/1 f3i arf can can	many fungi, root mats
Bk2	29-52	cw	10YR6/3	10YR4/4	grsl	1f-msbk	10YR8/1 cp-dpr caf	3vf+fc	3vf+f ir*	st		many fungi, root mats
BC	52-66+		10YR6/3	10YR4/6	vgrsl	sgr	10YR8/1 cdpr caf		3vf+f ir*	st		some root mats

Table A (continued)

Horizon ^a	Depth (cm)	Bndy ^b	Munsell color		Txtr ^c	Stret ^d	Ped/Void ^e surf feat	Roots ^f	Pores ^g	Efv ^h	CaCO ₃ ⁱ morph	Comments
			dry	moist								
Flattened bar (3FBIN): Typic Haplocalcid												
P	2-0	as					10YR8/3 fpr caf					fungi at the interface to Av
A1	0-6	as	10YR6/3	10YR4/4	grl	3msbk	10YR8/2 fpr caf	2vft	3vf+fir if dt	sl		some fungi, Av in sbk broken
A2	6-13	aw	10YR6/3	10YR4/4	grsl	2msbk	10YR8/2 cpr caf	3vft 2ft	3vf+fir	st		many fungi, root mats on clasts and peds
Bk1	13-18	cw	10YR6/3	10YR5/4	vgrl	1msbk	10YR8/1 cp-dpr caf	3vf+ft	3vf+ft m ir 3f dt 2vf+m dt	st	10YR8/1 fli arf can 10YR8/1 fli mat can	many fungi, root mats
Bk2	18-39	gw	10YR7/3	10YR5/4	vgrsl	ma	10YR8/1 cdpr caf	1vf+ft	3vf+fir 1f dt	ve	10YR8/1 c3i mat can	root mats on clasts
Bck	39-52+		10YR7/3	10YR4/6	vgrsl	sgr	10YR8/1 fd-cpr caf	1vf+ft	3vf+fir	ve		salts

Table A (continued)

Horizon ^a	Depth (cm)	Bndy ^b	Munsell color		Txtr ^c	Strct ^d	Ped/Void ^e surf feat	Roots ^f	Pores ^g	Efv ^h	CaCO ₃ ⁱ morph	Comments
			dry	moist								
Flattened swale (2FSIN): Typic Haplocalcid												
P	1-0	as					10YR8/2 vfpr caf					fungi at the interface to Av some fungi
A	0-3	as	10YR6/3	10YR4/4	grsl	sgr	10YR8/3 vfpr caf	1vft	3vfir	sl		
Av	3-9	aw	10YR6/3	10YR4/6	grsl	3m- cosbk	10YR8/3 vfpr caf	2vft	3vfir 3vfve 2fve	st		some fungi on bottom side, no silt lining in ve many fungi, root mats, salts
Bk1	9-16	cw	10YR6/4	10YR4/6	grsl	1msbk	10YR8/2 fdpr caf	2vf+fc 2mt	3vf+fir	st	10YR8/2 vf2i arf can	
Bk2	16-25	gw	10YR6/4	10YR4/4	grsl	1f-m sbk	10YR8/1 cdpr caf	2f+mc	3vf+fm ir*	st	10YR8/2 vf2i arf can 10YR8/1 flt arf cam	root mats
Bk3	25-40	cw	10YR6/3	10YR4/4	vgrsl	sgr	10YR8/1 cp-dpr caf	2fc 1mc	3vf+f ir*	st		salts
BC	40-55+		10YR6/3	10YR4/4	vgrls	sgr	10YR8/1 fppr caf		3vf+f ir*	st		salts

Table A (continued)

Horizon ^a	Depth (cm)	Bndy ^b	Munsell color		Txtr ^c	Stret ^d	Ped/Void ^e surf feat	Roots ^f	Pores ^g	Efv ^h	CaCO ₃ ⁱ morph	Comments
			dry	moist								
Flattened swale (3FSIN): Typic Haplocalcid												
P	1-0	vs					10YR8/4 vfpr caf					fungi at the interface to Av
Av	0-4	as	10YR6/4	10YR4/4	grsl	2m- cosbk	10YR8/2 vfpr caf	1vft	3vf ir 1vf ve	sl		some fungi, incipient crust
A	4-14	cw	10YR6/4	10YR4/4	grsl	3cosbk	10YR8/2 vfpr caf	2vft 1ft	3vf ir 2f+1m dt	st		Some fungi
Bk1	14-29	cw	10YR6/3	10YR4/6	grsl	3cosbk	10YR8/2 fd-p-dpr caf	3vf+ft 2mt	3vf ir 3vf dt 2f+m dt	st		many fungi, root mats on clasts and peds
Bk2	29-37	cw	10YR6/3	10YR3/3	vgrsl	2m- cosbk	10YR8/2 cdpr caf	3vfc 2fc 1m+coc	3vf+f ir	st	10YR8/2 vfi arf can	many fungi, root mats on clasts
Bk3	37-51+		10YR5/4	10YR4/6	vgrsl	1fsbk	10YR8/1 cd-cpr caf	3vft 1ft	3vf+f ir	st	10YR8/2 cli arf can	root mats

Table A (continued)

Horizon ^a	Depth (cm)	Bndy ^b	Munsell color		Txtr ^c	Strct ^d	Ped/Void ^e surf feat	Roots ^f	Pores ^g	Efv ^h	CaCO ₃ ⁱ morph	Comments
			dry	moist								
Bioturbation unit (2FDIN): Typic Haplocalcid												
A1	0-5	as	10YR6/3	10YR4/4	grsl	1mpl	10YR8/2 fp-dpr caf	3vft	3vf+fir 1vfte	sl		many fungi, crust builds structure
A2	5-12	aw	10YR6/3	10YR4/4	grsl	3m- cosbk 2mpr	10YR8/2 fppr caf	2vft	3vfir 1mte	sl		some fungi, root mats on clasts and peds
Bk	12-27	cw	10YR6/4	10YR4/4	sl	3co- vcsbk	10YR8/2 cdpr caf	2vf+ft 2mt	2f+m+ co te	st	10YR8/2 clt/d ppo arf cam	some fungi, root mats on clasts and peds
Bkk1	27-38	cw	10YR6/4	10YR4/4	vgrsl	1msbk	10YR8/1 cdpr caf	3vf+fc	3fir 3vf+f+ mir*	st		many fungi, root mats on clasts
Bkk2	38-54	gw	10YR6/3	10YR4/4	grsl	sgr	10YR8/1 cd-cpr caf	3vf+fc	3vf+f+ mir*	st		many fungi, root mats
BC	54-67+		10YR6/3	10YR4/4	vgrsl	sgr	10YR8/1 vfp-dpr caf	3vf+fir		st		root mats, salts

Table A (continued)

Horizon ^a	Depth (cm)	Bndy ^b	Munsell color		Txtr ^c	Strct ^d	Ped/Void ^e surf feat	Roots ^f	Pores ^g	Efv ^h	CaCO ₃ ⁱ morph	Comments
			dry	moist								
Bioturbation unit (3FDIN): Typic Haplocalcid												
Av	0-5	as	10YR6/3	10YR4/4	vgrsl	1fsbk	10YR8/2 fp-cpr caf	2vft	3vf+fir 1vft dt 1vf+f ve	sl		many fungi, crust builds structure
A	5-20	cw	10YR6/4	10YR4/4	grsl	3cosbk	10YR8/2 fp-cpr caf	3vft 2ft	3vf+fir 2ft+dt	sl		many fungi, burrows, root mats on clasts and peds
Bk	20-36	aw	10YR7/4	10YR4/6	grsl	3m- cosbk	10YR8/2 cp-dpr caf	3vft 2ft	3vf+fir 2ft+dt	st	10YR8/1 vfi arf can	many fungi, burrows, root mats on clasts
Bkk1	36-48	cw	10YR7/3	10YR4/6	xgrsl	3m- cosbk	10YR8/1 mp-dpr caf	3vft	3vf+f ir*	ve	10YR8/1 m3i mat can	many fungi, root mats on clasts
Bkk2	48-55+		10YR7/3	10YR4/6	vgrsl	ma	10YR8/1 mcpr caf	1vft	1vf ir*	ve	10YR8/1 m4i mat can	many fungi, root mats

Table A (continued)

Horizon ^a	Depth (cm)	Bndy ^b	Munsell color		Txtr ^c	Struct ^d	Ped/Void ^e surf feat	Roots ^f	Pores ^g	Efv ^h	CaCO ₃ ⁱ morph	Comments
			dry	moist								
Desert Pavement (2DPIN): Typic Haplocalcid												
P	1-0	vs					10YR7/4 cpr caf					Hypolithic crust, some fungi under clast, 7.5YR4/4 desert varnish clast have vesicular horizon attached to it tightly
Av	0-4	as	10YR6/3	10YR4/4	sil	3f-mpr 1 tnp1	10YR7/4 fprr caf 10YR6/3 cd-cf sp slf	3vf+f+ m ve 2vf ir	vs			
Av/Bt	4-10	cs	10YR6/4	10YR4/6	l	3cosbk 2tkpl	10YR8/2 vfpr caf	2vfc	3vf+f ir 1f te	sl	10YR8/1 cfd cam	cam associated with dendritic roots, collapsed ve, clay films
Bk1	10-25	gw	10YR6/4	10YR4/4	sl	3cosbk	10YR8/1 cdpr caf	3vf+ft 2mt	3vf+f+ m ir 1m te	st	10YR8/1 cfd cam, 10YR8/2 f5m mat can	some fungi, some root mats
Bk2	25-41	gw	10YR6/3	10YR4/4	grsl	2m- cosbk	10YR8/1 cd-cpr caf	3vf+ft 2mt	3vf+f ir 2vf te	st	10YR8/1 cfd cam	some fungi, root mats on clasts
Bk3	41-53	gw	10YR6/3	10YR4/6	sl	2msbk	10YR8/1 cd-cpr caf	2vf+ft	3vf ir 1vf te	st	10YR8/1 cfd cam	some fungi
BC	53-65+		10YR6/3	10YR4/6	vgrsl	sgr	10YR8/1 fprr caf	3vf t		st		

Table A (continued)

Horizon ^a	Depth (cm)	Bndy ^b	Munsell color		Txtr ^c	Strct ^d	Ped/Void ^e surf feat	Roots ^f	Pores ^g	Efv ^h	CaCO ₃ ⁱ morph	Comments
			dry	moist								
Desert Pavement (3DPIN): Durinodic Haplocalcid												
P	2-0	vs					10YR7/2 fppr caf					Some fungi at the interface to Av, desert varnish silt coatings in vesicular pores
Avt	0-5	as	10YR6/3	10YR4/4	grsil	1tmp1 3co- vcsbk 3m-co pr	10YR7/2 vfppr caf 10YR4/4 fpp bf clf	1vf	3vf+f+ m ve 1co ve	sl		
Avb	5-13	cw	10YR6/4	10YR4/4	grsl	2m- cosbk 3cosbk	10YR8/2 fppr caf	2vft	3vf+f ir 1vf ve	sl	10YR8/1 fl t arf cam 10YR8/1 fl i brf cam	some fungi, salts
Bk1	13-21	cw	10YR6/4	10YR4/6	grsl	1msbk	10YR8/2 cppr caf	2vft 1ft	3vf+f ir	st	10YR8/1 fl t brf + arf cam	many fungi, root mats, salt
Bkq2	21-32	cw	10YR6/3	10YR4/6	vgrsl	1msbk	10YR8/2 cp-dpr caf	3vf+ft 2mt	3vf+f ir 2m ir	st	10YR8/1 fl t arf cam	many fungi, root mats, salts, durinodes
Bkkq	32-38	aw	10YR6/3	10YR4/4	grsl	1msbk	10YR8/2 cd-cpr caf	3vf+ft	3vf+f ir	st	10YR8/1 c2t arf cam	many fungi, root mats, durinodes
BCq	38-51+		10YR6/3	10YR4/4	vgrsl	sgr	10YR8/2 fdpr caf	3vf+ft	3vf+f ir	st	10YR8/1 vfl t arf cam	some fungi, root mats, durinodes

Table A (continued)

Horizon ^a	Depth (cm)	Bndy ^b	Munsell color dry	moist	Txtr ^c	Strct ^d	Ped/Void ^e surf feat	Roots ^f	Pores ^g	Efv ^h	CaCO ₃ ⁱ morph	Comments
Shrub zone (2SZIN): Typic Haplocambid												
A1	0-8	as	10YR6/3	10YR4/4	grsl	1tnpl 3m-co sbk	10YR7/1 fp-dpr caf	3vft	3vf+ir 2vf+te	sl		many fungi, algal crust produce pl structure
A2	8-28	gw	10YR6/3	10YR4/4	grsl	3co-vc sbk	10YR8/2 fp-dpr caf	2vf+ft 1mc	3vf+ir 1m+ir 1f+te	st		many fungi, root mats on clasts
Bk1	28-52	gw	10YR6/3	10YR4/6	grsl	1m-co sbk	10YR8/2 cdpr caf	3vf+f+ mt	2m+te 3vf+f+ vc+ir 3f-co+te	st	10YR8/1 fld pro cam	many fungi, root mats on clasts, 25% of volume is taken by burrows many root mats
Bk2	52-62+		10YR6/3	10YR4/6	grsl	1msbk	10YR8/2 cd-cpr caf	3vft	3vf+f+ir	st		

Table A (continued)

Horizon	Depth (cm)	Bndy ^a	Munsell color		Txtr ^b	Strct ^c	Ped/Void ^d surf feat	Roots ^e	Pores ^f	Efv ^g	CaCO ₃ ^h morph	Comments
			dry	moist								
Shrub zone (3SZIN): Typic Haplocalcid												
A1	0-4	as	10YR6/3	10YR4/4	vgrsl	2f-msbk 3m-tkpl	10YR8/1 f-cpr caf	3vft	3vf+fir 2f dt	vs		many fungi, algal crusts
A2	4-19	cw	10YR6/3	10YR4/4	grsl	3co- vcsbk	10YR8/1 fprr caf	3vft 1ft	3vf+f ir*	sl		many fungi, root mats on clasts, burrows
ABk	19-33	cw	10YR6/3	10YR4/4	grsl	3m- cosbk	10YR8/1 feprr caf	3vft 2f-mt	3vf+f ir*	sl		many fungi, root mats on clasts
Bk1	33-43	cw	10YR6/3	10YR4/4	grsl	3m- cosbk	10YR8/1 cd-cpr caf	2vf+ft 1m+cot	3vf+fir 2fir*	st	10YR8/1 c1 arf can	some fungi, root mats on clasts
Bk2	43-52+		10YR6/3	10YR4/4	vgrsl	3f-msbk	10YR8/1 cepr caf	2vft 1m+cot	3vf+f ir*	st	10YR8/1 c3i arf can	some fungi, root mats on clasts, salts

^a horizon designations follow USDA-NRCS definitions, except for P (= pavement horizon) and Av (= vesicular horizon).

^b Bndy = horizon boundary, v = very abrupt, a = abrupt, c = clear, g = gradual, s = smooth, w = wavy.

^c Txtr = rock fragments, gr = gravelly, vgr = very gravelly, xgr = extremely gravelly, soil texture determined by the hydrometer method, ls = loamy sand, sl = sandy loam, sil = silt loam, l = loam

^d Strct = soil structure, 1 = weak, 2 = moderate, 3 = strong; vf = very fine, f = fine, m = medium, co = coarse, tn = thin, tk = thick; pl = platy, sbk = subangular blocky, pr = prismatic, sgr = single grain, ma = massive.

^e Ped/Void surf feat = ped and void surface features, color is given for dry features; vf = very few, f = few, c = common, m = many; p = patchy, d = discontinuous, c = continuous; p = prominent; r = on rock fragments; clf = clay films, sil = silans, caf = carbonate coats.

^f Roots = root distribution, 1 = few, 2 = common, 3 = many; vf = very fine, f = fine, m = medium, c = coarse; c = in cracks, t = throughout

^g Pores = pore voids, 1 = few, 2 = common, 3 = many; vf = very fine, f = fine, m = medium; dt = detritic tubular, ve = vesicular, ir = interstitial, * = in cracks.

^h efv = effervescence, sl = slightly, st = strongly, ve = violently.

ⁱ CaCO₃^h morph = calcium carbonate morphology, vf = very few, f = few, c = common, m = many, 1 = fine, 2 = medium, 3 = coarse, 4 = very coarse; can = carbonate masses, can = carbonate nodules.

APPENDIX B
SOIL CHEMICAL AND PHYSICAL CHARACTERISTICS

Table B1 Soil chemical properties.

LFU ^a	ID	Horizon	Depth cm	NO ₃ ⁻ N ^b ppm	NH ₄ ⁺ -N ^b ppm	PO ₄ -P ^b ppm	pH ^b	EC ^b µS/cm	Ca mmol/l	Mg mmol/l	Na mmol/l	SAR	S mmol/l	K mmol/l
BR ^c	1BRIN	A	0-1	3.26	3.99	0.46	8.0	257.1	0.72	0.15	0.11	0.114	0.08	0.17
		AB	1-25	1.67	3.59	0.48	8.7	138.1	0.66	0.42	0.11	0.102	0.07	0.22
		BC	25-46	1.42	3.35	0.08	8.8	159.2	0.27	0.19	0.15	0.217	0.04	0.07
		Bck	46-57+	1.11	3.46	0.04	9.0	153.1	0.27	0.27	0.33	0.451	0.05	0.08
2BRIN	A	0-7	2.47	1.29	0.69	8.2	175.1	0.93	0.16	0.11	0.109	0.08	0.16	
	Bk1	7-20	2.11	1.10	0.21	8.4	148.4	1.36	0.21	0.11	0.085	0.07	0.14	
	Bk2	20-32	1.07	1.12	0.12	8.5	139.1	1.17	0.26	0.12	0.103	0.07	0.13	
	Bk3	32-47	0.64	0.96	0.13	8.7	142.5	0.85	0.30	0.13	0.121	0.06	0.10	
	BC	47-54+	2.17	1.21	0.06	8.9	151.3	0.35	0.39	0.18	0.208	0.06	0.15	
3BRIN	A	0-6	5.00	0.55	0.71	8.3	210.9	0.84	0.25	0.12	0.115	0.12	0.22	
	Bk1	6-28	1.52	0.48	0.16	8.7	134.5	0.46	0.20	0.10	0.129	0.04	0.16	
	Bk2	28-46	0.77	0.37	0.09	9.0	135.3	0.38	0.31	0.12	0.143	0.04	0.11	
	BC	46-52+	1.95	0.35	0.05	8.9	157.3	0.37	0.37	0.16	0.188	0.06	0.13	

Table B1 (continued)

LFU ^a	ID	Horizon	Depth cm	NO ₃ ⁻ N ^b ppm	NH ₄ ⁺ -N ^b ppm	PO ₄ -P ^b ppm	pH ^b	EC ^b µS/cm	Ca mmol/l	Mg mmol/l	Na mmol/l	SAR mmol/l	S mmol/l	K mmol/l
SW ^d	1SWIN	Av	0-1	1.71	2.77	0.56	8.4	161.2	0.63	0.13	0.10	0.118	0.05	0.14
		A	1-8	2.09	2.79	0.64	8.6	131.8	1.13	0.72	0.11	0.084	0.07	0.35
		B	8-16	0.74	3.01	0.55	8.9	122.2	0.47	0.15	0.09	0.111	0.04	0.15
		Bk1	16-36	0.41	2.84	0.07	8.9	132.1	0.59	0.33	0.10	0.106	0.05	0.19
		Bk2	36-47	1.65	3.40	0.05	8.8	147.1	0.40	0.22	0.14	0.182	0.05	0.09
		Bk3	47-57	1.51	2.88	0.03	8.9	141.1	0.40	0.23	0.19	0.233	0.04	0.05
		Bck	57-69+	1.88	2.94	0.03	8.9	139.1	0.34	0.25	0.23	0.298	0.04	0.04
2SWIN		Av	0-1	1.84	0.74	0.49	8.5	156.6	0.73	0.11	0.09	0.098	0.06	0.09
		A	1-13	1.56	0.77	0.29	8.7	121.3	0.53	0.09	0.09	0.120	0.04	0.08
		Bk1	13-24	0.82	0.83	0.55	8.6	116.2	1.18	0.18	0.10	0.090	0.06	0.09
		Bk2	24-39	0.57	0.59	0.45	8.6	127.2	1.28	0.24	0.10	0.081	0.06	0.10
		Bk3	39-54+	0.40	0.52	0.11	8.6	138.9	1.24	0.28	0.11	0.090	0.07	0.09
3SWIN		A1	0-2	2.91	0.57	0.34	8.2	389.8	1.36	0.24	0.15	0.119	0.09	5.02
		A2	2-10	3.23	0.24	0.3	8.6	167.8	0.71	0.13	0.09	0.103	0.07	0.33
		Bk1	10-25	1.42	0.32	0.97	8.6	133.6	0.88	0.18	0.07	0.073	0.05	0.24
		Bk2	25-39	0.56	0.33	0.08	8.6	145.2	0.80	0.20	0.09	0.085	0.04	0.24
		Bck	39-51+	0.73	0.67	0.04	8.7	146.5	0.61	0.21	0.10	0.110	0.04	0.19

Table B1 (continued)

LFU ^a	ID	Horizon	Depth cm	NO ₃ ⁻ N ^b ppm	NH ₄ ⁺ -N ^b ppm	PO ₄ -P ^b ppm	pH ^b	EC ^b µS/cm	Ca mmol/l	Mg mmol/l	Na mmol/l	SAR mmol/l	S mmol/l	K mmol/l
FB ^c	1FBIN	Av	0-6	1.85	2.79	0.85	8.6	158.6	0.94	0.96	0.14	0.102	0.06	0.44
		AB	6-15	1.33	3.15	0.11	8.8	149.2	0.41	0.26	0.13	0.154	0.04	0.19
		Bk1	15-25	0.54	2.36	0.05	8.7	150.2	0.34	0.29	0.11	0.143	0.04	0.16
		Bk2	25-33	0.49	2.12	0.04	8.8	143.5	0.30	0.30	0.12	0.153	0.03	0.11
		Bk3	33-44	1.43	2.59	0.04	8.8	156.5	0.35	0.38	0.22	0.255	0.06	0.08
	BC	44-56+	2.02	2.50	0.06	8.9	162.9	N/A	N/A	N/A	N/A	N/A	N/A	
2FBIN		Av	0-5	1.77	1.20	N/A	8.6	158.8	0.48	0.31	0.12	0.135	0.07	0.16
		ABk	5-20	2.94	0.80	1.28	8.7	165.9	0.64	0.22	0.22	0.235	0.09	0.27
		Bk1	20-29	0.59	0.29	1.04	8.8	144.8	0.44	0.23	0.13	0.157	0.06	0.27
		Bk2	29-52	1.41	0.34	1.00	8.9	151.4	0.39	0.31	0.14	0.167	0.08	0.31
		BC	52-66+	1.80	0.24	0.06	9.0	168.9	0.53	0.34	0.31	0.331	0.06	0.22
3FBIN		Av	0-6	2.62	0.43	2.91	8.6	163.5	0.70	0.19	0.13	0.141	0.07	0.17
		ABk	6-13	2.39	0.23	0.47	8.6	154.8	0.62	0.23	0.14	0.156	0.05	0.10
		Bk1	13-18	0.89	0.18	0.11	8.6	150.3	0.53	0.26	0.18	0.200	0.05	0.06
		Bk2	18-39	1.45	0.17	0.08	8.8	146.7	0.43	0.27	0.22	0.265	0.07	0.05
		Bck	39-52+	8.00	0.21	0.1	9.2	289.1	0.21	0.15	2.48	4.118	0.05	0.02

Table B1 (continued)

LFU ^a	ID	Horizon	Depth cm	NO ₃ ⁻ N ^b ppm	NH ₄ ⁺ -N ^b ppm	PO ₄ -P ^b ppm	pH ^b	EC ^b µS/cm	Ca mmol/l	Mg mmol/l	Na mmol/l	SAR	S mmol/l	K mmol/l
FS ^f	1FSIN	Av1	0-2	1.37	4.66	1.03	8.5	159.9	0.56	0.18	0.15	0.171	0.05	0.27
		Av2	2-9	2.67	4.66	5.07	8.6	157.4	1.01	0.67	0.16	0.124	0.08	0.41
		Bk1	9-20	1.46	2.87	0.99	8.8	143.7	0.45	0.27	0.12	0.137	0.32	0.24
		Bk2	20-31	2.23	2.42	0.05	8.8	216.1	0.29	0.27	0.11	0.148	0.04	0.15
		Bck1	31-48	0.66	2.03	0.03	9.0	150.5	0.28	0.34	0.15	0.190	0.05	0.13
		Bck2	48-58+	1.05	2.72	0.04	9.1	139.8	0.21	0.36	0.43	0.571	0.02	0.07
2FSIN	A		0-3	1.37	0.63	3.09	8.6	162.1	0.94	0.18	0.11	0.048	0.07	0.24
		Av	3-9	2.41	0.94	3.79	8.8	138.4	0.63	0.21	0.12	0.058	0.06	0.21
		Bk1	9-16	1.77	0.33	0.50	8.8	142.9	0.41	0.23	0.12	0.065	0.05	0.21
		Bk2	16-25	0.57	0.38	0.18	8.9	139.5	0.41	0.29	0.14	0.076	0.05	0.18
		Bk3	25-40	1.75	0.27	0.13	8.8	356.7	0.80	1.04	0.25	0.084	1.33	0.16
		BC	40-55+	7.55	0.28	0.11	9.2	219.4	0.28	0.56	0.43	0.209	0.08	0.15
3FSIN	Av		0-4	1.42	0.23	0.59	8.5	132.7	0.54	0.10	0.10	0.130	0.05	0.20
		A	4-14	2.06	0.18	0.42	8.6	134.1	0.55	0.13	0.10	0.124	0.05	0.15
		Bk	14-29	0.65	0.15	0.2	8.6	125.9	0.53	0.15	0.11	0.135	0.03	0.12
		Bk2	29-37	0.48	0.21	0.02	8.7	140.1	0.47	0.21	0.17	0.205	0.05	0.09
		Bk3	37-51+	2.94	0.26	0.07	8.6	161.5	0.52	0.28	0.32	0.358	0.08	0.05

Table B1 (continued)

LFU ^a	ID	Horizon	Depth cm	NO ₃ ⁻ -N ^b ppm	NH ₄ ⁺ -N ^b ppm	PO ₄ -P ^b ppm	pH ^b	EC ^b μS/cm	Ca mmol/l	Mg mmol/l	Na mmol/l	SAR	S mmol/l	K mmol/l
FD ^g	1FDIN	A1	0-4	3.72	4.05	0.70	8.0	271.9	1.58	0.41	0.12	0.088	0.17	0.50
		A2	4-12	2.20	2.92	1.17	8.5	169.2	0.81	0.15	0.13	0.134	0.09	0.40
		Bk1	12-22	0.72	3.41	0.32	8.6	134.9	0.67	0.17	0.14	0.147	0.07	0.32
		Bk2	22-34	0.81	2.54	0.09	8.7	136.2	0.46	0.19	0.15	0.186	0.08	0.27
		Bk3	34-44	2.43	2.35	0.04	8.7	157.8	0.37	0.24	0.18	0.233	0.11	0.24
		BC	44-54+	1.70	2.63	0.03	9.0	143.2	0.31	0.21	0.17	0.234	0.06	0.19
2FDIN		A1	0-5	1.74	0.62	0.86	8.6	175.8	0.80	0.15	0.14	0.148	0.08	0.29
		A2	5-12	2.32	0.28	0.42	8.8	147.7	0.61	0.12	0.11	0.128	0.06	0.23
		Bk1	12-27	1.45	0.46	1.02	8.9	132.7	0.84	0.17	0.10	0.099	0.05	0.26
		Bk2	27-38	0.76	0.38	0.13	8.9	147.1	0.40	0.17	0.15	0.196	0.06	0.28
		Bk3	38-54	4.01	0.32	0.05	8.8	180.1	0.40	0.34	0.25	0.286	0.07	0.19
		BC	54-67+	2.28	0.29	0.06	9.0	156.8	0.29	0.30	0.38	0.491	0.08	0.14
3FDIN		Av	0-5	3.09	0.29	1.6	8.5	187.1	0.93	0.17	0.09	0.088	0.08	0.23
		A	5-20	3.88	0.49	0.78	8.6	181.2	0.92	0.18	0.09	0.089	0.09	0.27
		Bk	20-36	1.74	0.47	0.39	8.7	162.4	0.58	0.17	0.12	0.138	0.07	0.28
		Bkk	36-48	6.37	0.29	0.21	8.8	203.5	0.35	0.20	0.91	1.238	0.15	0.16
		Bkk	48-55+	3.57	0.18	0.06	8.8	244.5	0.32	0.24	1.11	1.480	0.42	0.07

Table B1 (continued)

LFU ^a	ID	Horizon	Depth cm	NO ₃ ⁻ -N ^b ppm	NH ₄ ⁺ -N ^b ppm	PO ₄ -P ^b ppm	pH ^b	EC ^b μS/cm	Ca mmol/l	Mg mmol/l	Na mmol/l	SAR	S mmol/l	K mmol/l
DP ^h	1DPIN	Av	0-7	2.52	15.11	25.81	8.5	319.1	0.71	0.30	0.65	0.643	0.05	0.73
		Btk	7-16	1.18	2.33	0.27	8.5	209.7	0.35	0.17	1.35	1.875	0.09	0.14
		Bk1	16-29	3.33	0.72	0.23	9.3	341.5	0.17	0.11	3.74	7.082	0.24	0.04
		Bk2	29-38	2.32	2.33	0.28	9.2	471.1	0.61	0.14	4.86	5.595	0.83	0.05
		Bkkq1	38-49	3.41	2.13	0.22	9.1	1128.0	0.25	0.17	11.04	17.095	3.23	0.05
		Bkkq2	49-57	7.21	2.41	0.36	8.9	2266.0	0.58	0.68	23.43	20.854	8.54	0.09
		Bck	57	14.80	2.28	0.33	8.4	4462.0	7.46	4.64	36.91	10.609	23.36	0.24
2DPIN	Av1	0-4	1.24	2.45	9.90	8.8	130.3	0.62	0.31	0.23	0.236	0.05	0.23	
	Av/Bt	4-10	1.93	0.62	0.65	8.7	143.4	0.29	0.11	0.18	0.284	0.03	0.11	
	Bk1	10-25	0.68	0.38	0.20	9.1	157.5	0.30	0.15	1.29	1.925	0.05	0.05	
	Bk2	25-41	2.80	0.28	0.38	9.7	398.8	0.36	0.10	4.35	6.468	0.55	0.02	
	Bk3	41-53	15.68	0.37	0.29	9.9	1494.0	0.19	0.06	15.62	31.376	2.87	0.02	
	BC	53-65+	25.80	0.36	0.23	9.2	2721.0	0.49	0.59	26.83	25.906	8.37	0.05	
		Av	0-5	2.01	0.41	1.38	8.7	203.9	0.48	0.54	0.66	0.657	0.10	0.58
3DPIN	Avb	5-13	2.33	0.66	0.07	8.2	737.8	2.55	1.33	0.75	0.383	4.24	0.66	
	Bk1	13-21	1.52	0.20	0.05	8.4	581.2	1.34	1.60	0.81	0.474	3.11	0.24	
	Bk2	21-32	2.76	0.22	0.08	8.2	1719.0	6.89	5.22	1.20	0.345	12.93	0.18	
	Bkkq	32-38	3.30	0.21	0.07	8.1	2485.0	13.18	5.03	1.37	0.320	19.82	0.13	
	BCq	38-51+	7.68	0.24	0.12	8.1	2835.0	13.51	5.55	5.35	1.225	21.09	0.16	
		Av	0-5	2.01	0.41	1.38	8.7	203.9	0.48	0.54	0.66	0.657	0.10	0.58

Table B1 (continued)

LFU ^a	ID	Horizon	Depth cm	NO ₃ ⁻ -N ^b ppm	NH ₄ ⁺ -N ^b ppm	PO ₄ -P ^b ppm	pH ^b	EC ^b µS/cm	Ca mmol/l	Mg mmol/l	Na mmol/l	SAR	S mmol/l	K mmol/l
SZ ⁱ	1SZIN	A	0-3	2.76	3.18	0.54	7.9	272.8	1.01	0.24	0.15	0.136	0.17	0.47
		AB	3-12	1.45	2.98	1.54	8.4	158.8	1.03	0.29	0.14	0.123	0.13	0.35
		Bw	12-29	1.96	3.54	0.19	8.5	140.0	0.81	0.20	0.19	0.184	0.07	0.20
		Bk	29-37	1.25	3.33	0.04	8.6	178.9	1.97	1.76	1.54	0.798	0.51	1.51
		Bkq	37+	0.49	3.32	0.03	8.7	194.2	0.26	0.44	0.28	0.335	0.07	0.36
2SZIN	A1		0-8	2.89	0.66	0.17	8.4	353.4	1.25	0.40	0.17	0.133	0.11	3.04
	A2		8-28	2.50	0.75	1.81	8.6	209.9	2.76	0.56	0.15	0.081	0.14	0.69
	Bk1		28-52	6.33	0.45	0.04	8.7	233.7	0.57	0.43	0.29	0.285	0.11	0.65
	Bk2		52-62+	8.46	0.69	0.08	8.6	282.9	0.53	0.51	0.62	0.602	0.20	0.59
3SZIN	A1		0-4	3.36	0.41	0.6	8.4	257.0	1.31	0.26	0.11	0.088	0.12	0.59
	A2		4-19	2.51	0.35	0.37	8.7	180.2	1.04	0.19	0.12	0.106	0.08	0.45
	ABk		19-33	0.61	0.27	0.41	8.7	164.4	1.03	0.25	0.13	0.115	0.08	0.36
	Bk1		33-43	1.04	0.33	0.06	8.7	169.1	0.60	0.26	0.18	0.190	0.09	0.25
	Bk2		43-52+	1.25	0.28	0.13	8.6	160.4	0.67	0.28	0.20	0.210	0.07	0.10

^a landform unit.^b 1:1 soil extract.^c BR = bar.^d SW = swale.^e FB = flattened bar.^f FS = flattened swale.^g FD = bioturbation unit.^h = desert pavement.ⁱ = shrub zone.

Table B2 Soil physical properties and total nitrogen, carbon, inorganic carbon and calcium carbonate equivalent.

LFU ^a	ID	Horizon	Depth cm	BD ^b g/cm ³	f&m gr ^c %	co gr ^d %	cobbles ^e %	fine ^f %	sand %	silt %	clay %	TN ^g g/kg	TIC ^h %	TOC ⁱ %	CCE ^j %
BR ^k	1BRIN	A	0-1	1.1	23	32	1	44	75	20	4	0.50	2.33	0.60	19.41
		AB	1-25	1.2	38	17	11	34	69	25	6	0.21	3.01	0.72	25.11
		BC	25-46	1.2	52	22	3	23	81	14	5	0.18	5.19	0.30	43.24
		Bck	46-57+	1.2	52	12	1	35	81	14	5	0.16	5.87	0.43	48.92
2BRIN	A	0-7	1.1	28	26	13	33	71	25	25	5	0.45	3.34	0.54	27.83
	Bk1	7-20	1.3	30	25	9	36	66	25	25	8	0.40	4.02	0.59	33.47
	Bk2	20-32	0.8	31	29	17	23	70	22	8	8	0.42	4.47	0.75	37.28
	Bk3	32-47	0.8	42	29	11	19	76	15	9	9	0.35	5.93	0.44	49.41
	BC	47-54+	0.8	40	29	5	26	78	14	7	7	0.26	6.71	0.40	55.88
3BRIN	A	0-6	1.1	42	19	5	34	72	22	22	6	0.64	3.70	0.65	30.80
	Bk1	6-28	1.2	21	24	46	9	67	26	7	7	0.32	4.18	0.41	34.81
	Bk2	28-46	1.0*	43	15	11	31	82	13	6	6	0.30	6.89	0.32	57.38
	BC	46-52+	0.8*	41	10	32	16	82	13	5	5	0.21	6.87	0.39	57.28

Table B2 (continued)

LFU ^a	ID	Horizon	Depth cm	BD ^b g/cm ³	f&m gr ^c %	co gr ^d %	cobbles ^e %	fine ^f %	sand %	silt %	clay %	TN ^g g/kg	TIC ^h %	TOC ⁱ %	CCE ^j %
SW ¹	1SWIN	Av	0-1	1.0	44	1	0	55	66	26	7	0.32	3.10	0.43	25.83
		A	1-8	1.4	39	4	0	57	68	27	5	0.22	3.49	0.35	29.08
		B	8-16	1.1	63	5	0	32	77	16	6	0.21	5.37	0.28	44.78
		Bk1	16-36	0.9	54	19	2	26	79	15	6	0.23	5.81	0.24	48.41
		Bk2	36-47	0.9	49	19	2	29	77	18	5	0.26	4.53	0.28	37.79
		Bk3	47-57	0.9*	50	16	1	33	78	14	9	0.26	4.83	0.39	40.21
		BCK	57-69+	0.9*	57	10	0	32	79	13	8	0.26	5.25	0.34	43.75
2SWIN	Av		0-1	1.0*	55	10	4	31	79	14	8	0.34	6.73	0.48	56.12
	A		1-13	1.2*	45	27	0	28	87	7	6	0.26	6.32	0.42	52.64
	Bk1		13-24	1.2	46	13	0	40	71	20	8	0.31	4.70	0.42	39.18
	Bk2		24-39	1.1	47	18	0	34	73	20	7	0.32	4.99	0.49	41.60
	Bk3		39-54+	0.9	27	18	32	23	71	21	7	0.41	5.02	0.67	41.82
3SWIN	A1		0-2	1.0	45	19	0	36	71	23	6	0.60	3.58	0.87	29.82
	A2		2-10	1.2	45	23	2	30	75	21	4	0.38	4.87	0.36	40.62
	Bk1		10-25	1.2	36	13	10	41	65	31	5	0.38	3.13	0.48	26.11
	Bk2		25-39	1.0	24	8	51	17	68	23	9	0.45	4.15	0.80	34.56
	BCK		39-51+	0.9*	34	10	35	21	72	21	7	0.38	5.29	0.56	44.11

Table B2 (continued)

LFU ^a	ID	Horizon	Depth cm	BD ^b g/cm ³	f&m gf ^c %	co gr ^d %	cobbles ^e %	fine ^f %	sand %	silt %	clay %	TN ^g g/kg	TIC ^h %	TOC ⁱ %	CCE ^j %
FB ^m	1FBIN	Av	0-6	1.2	36	22	5	38	51	42	6	0.29	3.13	0.48	26.10
		AB	6-15	1.0	47	16	4	33	71	23	6	0.28	5.31	0.32	44.26
		Bk1	15-25	1.2	43	28	7	22	76	17	6	0.25	4.79	0.34	39.89
		Bk2	25-33	0.9*	62	11	0	27	78	16	6	0.29	5.28	0.41	44.03
		Bk3	33-44	0.9*	48	29	0	23	77	16	7	0.32	4.66	0.44	38.84
		BC	44-56+	0.9*	69	13	0	18	78	15	8	0.31	6.31	0.34	52.56
2FBIN		Av	0-5	1.3	17	25	6	52	58	34	8	0.39	2.41	0.49	20.12
		ABk	5-20	1.2	28	42	0	30	62	29	9	0.39	3.49	0.47	29.07
		Bk1	20-29	1.1	36	33	2	29	69	25	7	0.34	5.13	0.43	42.76
		Bk2	29-52	0.9	43	20	6	32	67	23	10	0.31	5.15	0.44	42.95
		BC	52-66+	1.0	50	16	0	34	75	17	8	0.23	6.26	0.51	52.14
		3FBIN		Av	0-6	1.1	42	20	0	38	51	40	9	0.40	2.83
ABk	6-13			1.0	38	14	5	44	53	34	13	0.41	3.21	0.49	26.72
Bk1	13-18			1.1	48	22	0	31	52	36	12	0.50	2.97	0.95	24.75
Bk2	18-39			0.8	64	12	0	24	67	24	10	0.32	5.25	0.43	43.76
Bck	39-52+			0.7	56	8	0	36	69	20	12	0.31	4.95	0.47	41.24

Table B2 (continued)

LFU ^a	ID	Horizon	Depth cm	BD ^b g/cm ³	f&m gr ^c %	co gr ^d %	cobbles ^e %	fine ^f %	sand %	silt %	clay %	TN ^g g/kg	TIC ^h %	TOC ⁱ %	CCE ^j %
FS ⁿ	1FSIN	Av1	0-2	1.2	44	18	0	38	56	37	6	0.4	2.86	0.55	23.87
		Av2	2-9	1.4	44	5	0	51	52	39	10	0.3	3.40	0.36	28.33
		Bk1	9-20	0.9	58	15	0	27	73	18	8	0.22	5.52	0.33	46.03
		Bk2	20-31	1.2	55	17	0	28	83	11	6	0.26	5.79	0.28	48.25
		Bck1	31-48	0.9*	51	24	0	24	81	12	6	0.22	5.71	0.27	47.58
		Bck2	48-58+	0.9*	54	20	0	26	82	10	8	0.22	6.22	0.24	51.79
2FSIN	A		0-3	1.2	39	24	0	37	64	30	6	0.40	3.24	0.42	26.97
		Av	3-9	1.3	31	9	0	59	59	32	9	0.31	2.82	0.39	23.49
		Bk1	9-16	1.1	36	32	0	32	63	30	7	0.34	4.06	0.43	33.87
		Bk2	16-25	1.1	48	18	0	33	59	33	8	0.38	3.99	0.43	33.29
		Bk3	25-40	0.9*	44	29	6	21	71	21	7	0.33	5.92	0.41	49.32
		BC	40-55+	0.9*	64	10	0	27	83	11	6	0.26	7.04	0.35	58.64
3FSIN	Av		0-4	1.4	35	7	0	58	65	29	6	0.31	2.06	0.34	17.16
		A	4-14	1.3	31	6	0	64	64	29	6	0.29	1.69	0.37	14.09
		Bk	14-29	1.2	18	23	15	43	61	32	7	0.31	2.31	0.29	19.25
		Bk2	29-37	1.1	30	12	31	27	61	30	9	0.33	3.89	0.47	32.38
		Bk3	37-51+	1.0	35	34	7	24	68	15	17	0.35	4.26	0.37	35.50

Table B2 (continued)

LFU ^a	ID	Horizon	Depth cm	BD ^b g/cm ³	f&m gr ^c %	co gr ^d %	cobbles ^e %	fine ^f %	sand %	silt %	clay %	TN ^g g/kg	TIC ^h %	TOC ⁱ %	CCE ^j %
FD ^o	1FDIN	A1	0-4	1.0	38	9	0	54	77	17	5	0.64	3.25	0.85	27.10
		A2	4-12	1.3	30	9	0	61	75	19	6	0.31	2.97	0.42	24.74
		Bk1	12-22	1.1	34	26	14	26	76	16	8	0.32	4.09	0.52	34.09
		Bk2	22-34	1.3	46	28	0	27	83	11	6	0.29	5.50	0.47	45.83
		Bk3	34-44	1.2	60	9	0	31	85	8	7	0.24	6.41	0.45	53.39
		BC	44-54+	1.0*	52	18	0	30	88	5	7	0.23	7.13	0.28	59.42
2FDIN	A1		0-5	1.1	41	6	0	53	67	27	6	0.44	2.96	0.53	24.68
	A2		5-12	1.3	37	5	0	58	65	28	7	0.35	2.90	0.43	24.20
	Bk1		12-27	1.2	38	5	0	57	65	28	7	0.32	3.11	0.40	25.88
	Bk2		27-38	1.1	41	25	7	27	66	25	8	0.35	4.90	0.39	40.87
	Bk3		38-54	1.3	19	37	20	24	61	29	10	0.35	4.35	0.47	36.28
	BC		54-67+	1.0*	53	14	0	33	70	21	9	0.35	5.52	0.45	45.98
3FDIN	Av		0-5	1.1	40	14	0	45	64	27	8	0.41	3.09	0.44	25.76
	A		5-20	1.2	29	19	11	41	62	30	8	0.33	3.11	0.28	25.90
	Bk		20-36	1.1	32	14	0	54	66	23	11	0.36	3.09	0.33	25.79
	Bkk		36-48	1.2	43	16	0	40	59	32	10	0.35	3.90	0.41	32.51
	Bkk		48-55+	1.2	40	16	8	36	61	27	12	0.26	4.17	0.29	34.74

Table B2 (continued)

LFU ^a	ID	Horizon	Depth cm	BD ^b g/cm ³	f&m gr ^c %	co gr ^d %	cobbles ^e %	fine ^f %	sand %	silt %	clay %	TN ^g g/kg	TIC ^h %	TOC ⁱ %	CCE ^j %
DP ^p	1DPIN	Av	0-7	1.6	8	11	0	82	40	50	11	0.17	2.59	0.28	21.55
		Btk	7-16	1.0	10	0	0	90	42	44	14	0.28	2.90	0.31	24.15
		Bk1	16-29	1.2	31	40	0	29	58	26	16	0.29	3.78	0.41	31.51
		Bk2	29-38	1.3	31	16	0	53	58	28	15	0.26	4.51	0.41	37.59
		Bkkq1	38-49	1.5	41	26	0	33	60	25	15	0.19	4.28	0.39	35.64
		Bkkq2	49-57	1.5	67	4	0	29	73	15	13	0.17	4.97	0.29	41.38
		BCK	57	1.5	67*	4*	0*	29*	77	12	12	0.17	5.01	0.31	41.72
2DPIN	Av1	Av1	0-4	1.4	22	11	8	58	42	50	8	0.21	2.62	0.24	21.85
		Av/Bt	4-10	1.4	11	3	0	87	52	40	8	0.27	3.73	0.27	31.10
		Bk1	10-25	1.2	27	8	0	65	55	35	10	0.33	3.84	0.45	31.98
		Bk2	25-41	1.1	23	32	7	37	58	32	10	0.28	4.12	0.34	34.30
		Bk3	41-53	1.2	42	11	0	47	65	20	15	0.23	4.30	0.28	35.82
		BC	53-65+	1.2	43	26	5	25	69	21	10	0.27	5.78	0.17	48.15
		3DPIN	Av	Av	0-5	1.5	21	9	0	70	37	53	10	0.26	3.03
Avb	5-13	1.1		36	17	10	37	48	45	7	0.23	4.63	0.20	38.62	
Bk1	13-21	1.0		54	8	0	38	52	41	7	0.26	4.89	0.38	40.72	
Bk2	21-32	0.7		40	16	21	23	66	23	11	0.27	5.82	0.29	48.51	
Bkkq	32-38	1.2		37	38	0	26	62	34	4	0.27	5.34	0.26	44.47	
BCq	38-51+	1.1		32	25	26	18	68	29	3	0.25	5.05	0.28	42.06	

Table B2 (continued)

LFU ^a	ID	Horizon	Depth cm	BD ^b g/cm ³	f&m gr ^c %	co gr ^d %	cobbles ^e %	fine ^f %	sand %	silt %	clay %	TN ^g g/kg	TIC ^h %	TOC ⁱ %	CCE ^j %
SZ ^a	1SZIN	A	0-3	1.2	31	8	0	61	79	15	6	0.59	2.03	0.84	16.92
		AB	3-12	1.3	15	4	0	81	73	19	8	0.30	1.80	0.43	15.03
		Bw	12-29	1.1	26	23	0	51	62	28	10	0.46	2.37	0.64	19.79
		Bk	29-37	1.3	58	16	0	26	58	25	17	0.46	3.37	0.62	28.12
		Bkq	37+	1.1	34	56	0	10	68	19	13	0.38	4.62	0.66	38.52
2SZIN	A1		0-8	1.2	41	8	0	51	61	30	9	0.69	3.74	0.76	31.17
	A2		8-28	1.2	34	14	0	52	62	31	7	0.56	3.39	0.54	28.21
	Bk1		28-52	1.1	37	17	4	42	60	32	8	0.47	4.06	0.56	33.87
	Bk2		52-62+	1.2	41	18	0	41	63	30	7	0.53	4.57	0.66	38.05
3SZIN	A1		0-4	0.9	39	6	0	55	68	25	7	0.64	3.02	0.78	25.18
	A2		4-19	1.3	35	5	0	60	65	27	8	0.47	3.09	0.54	25.79
	ABk		19-33	1.1	31	7	0	62	63	28	9	0.44	3.03	0.43	25.25
	Bk1		33-43	1.1	22	25	12	40	61	31	9	0.43	3.01	0.47	25.11
	Bk2		43-52+	1.1	30	17	13	40	62	28	10	0.42	3.53	0.47	29.41

^a LFU = landform unit.^b BD = bulk density.^c f&m gr = fine and medium gravel.^d co gr = coarse gravel.^e cobbles = cobble sized fragments.^f fine = fine earth fraction.^g TN = total nitrogen.^h TIC = total inorganic carbon.ⁱ TOC = total organic carbon.^j CCE = calcium carbonate equivalent.^k BR = bar.^l SW = swale.^m FB = flattened bar.ⁿ FS = flattened swale.^o FD = bioturbation unit.^p P = desert pavement.^q q = shrub zone.

* = estimated value from actually determined bulk density values of morphologic similar horizons

APPENDIX C

GPS COORDINATES OF LANDFORM UNITS

Table C GPS coordinates of all landform units studied in this work. Coordinates are given in degree.minute.second format.

LFU ID ^a	Latitude	Longitude
1BR1*	35.30.18.9	115.41.58.7
1BR2	35.30.16.3	115.41.55.2
1BR3	35.30.16.2	115.41.57.3
2BR1*	35.29.56.6	115.41.35.6
2BR2	35.30.00.3	115.41.29.0
2BR3	35.29.54.6	115.41.32.0
3BR1*	35.30.14.9	115.41.32.6
3BR2	35.30.15.3	115.41.32.1
3BR3	35.30.14.3	115.41.32.1
1SW1*	35.30.18.8	115.41.58.3
1SW2	35.30.14.9	115.41.54.8
1SW3	35.30.13.5	115.42.05.2
2SW1*	35.29.56.6	115.41.35.7
2SW2	35.29.56.2	115.41.37.7
2SW3	35.30.00.0	115.41.26.8
3SW1*	35.30.15.0	115.41.32.4
3SW2	35.30.14.2	115.41.32.6
3SW3	35.30.15.9	115.41.33.0
1FB1*	35.30.17.8	115.41.57.8
1FB2	35.30.18.2	115.41.59.9
1FB3	35.30.17.6	115.42.03.3
2FB1*	35.29.59.9	115.41.34.9
2FB2	35.29.58.2	115.41.34.6
2FB3	35.30.00.5	115.41.26.4
3FB1*	35.30.11.4	115.41.33.7
3FB2	35.30.13.5	115.41.32.9
3FB3	35.30.12.4	115.41.34.0
1FS1*	35.30.18.0	115.41.57.9
1FS2	35.30.19.1	115.42.00.1
1FS3	35.30.16.0	115.42.06.2
2FS1*	35.29.59.8	115.41.34.9
2FS2	35.30.00.5	115.41.26.4
2FS3	35.29.57.7	115.41.26.9
3FS1*	35.30.11.4	115.41.33.8
3FS2	35.30.12.9	115.41.35.5
3FS3	35.30.11.8	115.41.38.0
1FD1*	35.30.18.1	115.41.57.8
1FD2	35.30.19.1	115.42.00.1
1FD3	35.30.15.4	115.41.57.3
2FD1*	35.30.00.2	115.41.34.9
2FD2	35.29.58.2	115.41.30.5
2FD3	35.29.55.6	115.41.29.5
3FD1*	35.30.11.5	115.41.33.9
3FD2	35.30.12.7	115.41.32.2
3FD3	35.30.13.4	115.41.31.0

Table C1 (continued)

LFU ID ^a	Latitude	Longitude
1DP1*	35.30.12.5	115.42.05.6
1DP2	35.30.09.9	115.42.03.3
1DP3	35.30.06.9	115.41.50.5
2DP1*	35.29.53.7	115.41.33.1
2DP2	35.29.54.5	115.41.35.8
2DP3	35.29.52.9	115.41.32.4
3DP1*	35.30.09.9	115.41.30.3
3DP2	35.30.09.5	115.41.33.8
3DP3	35.30.10.9	115.41.29.7
1SP1*	35.30.12.0	115.42.05.6
1SP2	35.30.11.5	115.42.02.3
1SP3	35.30.11.1	115.42.03.9
2SP1*	35.29.53.3	115.41.33.2
2SP2	35.29.55.0	115.41.40.4
2SP3	35.29.54.2	115.41.36.7
3SP1*	35.30.10.1	115.41.31.2
3SP2	35.30.10.9	115.41.29.7
3SP3	35.30.07.3	115.41.27.3

^aLFU ID = landform unit identification code, BR = bar, SW = swale, FB = flattened bar, FS = flattened swale, FD = bioturbation unit, DP = desert pavement, SZ = shrub zone.
 * = landforms chosen for soil investigations (Chapter 4, Appendix A).