

EVIDENCE FOR MICRONUTRIENT LIMITATION OF BIOLOGICAL SOIL CRUSTS: IMPORTANCE TO ARID-LANDS RESTORATION

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Abstract. Desertification is a global problem, costly to national economies and human societies. Restoration of biological soil crusts (BSCs) may have an important role to play in the reversal of desertification due to their ability to decrease erosion and enhance soil fertility. To determine if there is evidence that lower fertility may hinder BSC recolonization, we investigated the hypothesis that BSC abundance is driven by soil nutrient concentrations. At a regional scale (north and central Colorado Plateau, USA), moss and lichen cover and richness are correlated with a complex water–nutrient availability gradient and have approximately six-fold higher cover and approximately two-fold higher species richness on sandy soils than on shale-derived soils. At a microscale, mosses and lichens are overrepresented in microhabitats under the north sides of shrub canopies, where water and nutrients are more available. At two spatial scales, and at the individual species and community levels, our data are consistent with the hypothesis that distributions of BSC organisms are determined largely by soil fertility. The micronutrients Mn and Zn figured prominently and consistently in the various analyses, strongly suggesting that these elements are previously unstudied limiting factors in BSC development. Structural-equation modeling of our data is most consistent with the hypothesis of causal relationships between the availability of micronutrients and the abundance of the two major nitrogen (N) fixers of BSCs. Specifically, higher Mn availability may determine greater *Collema tenax* abundance, and both Mn and Zn may limit *Collema coccophorum*; alternative causal hypotheses were less consistent with the data. We propose experimental trials of micronutrient addition to promote the restoration of BSC function on disturbed lands. Arid lands, where BSCs are most prevalent, cover ~40% of the terrestrial surface of the earth; thus the information gathered in this study is potentially useful in many places worldwide.

Key words: *Collema*; cryptobiotic soils; desertification; lichens; manganese; micronutrient limitation; mosses; restoration; semi-arid desert; soil crusts and arid-land restoration; soil nutrients; zinc.

INTRODUCTION

Biological soil crusts (BSCs) are communities of sessile organisms (bryophytes, lichens, eukaryotic algae, cyanobacteria, free-living fungi, and bacteria) occupying the surfaces of mineral soils and performing key ecosystem functions in numerous habitats worldwide (Alexander and Calvo 1990, Belnap et al. 1994, Mazor et al. 1996, Grettarsdottir et al. 2004). Elements of these crusts both arrest soil erosion (Belnap and Gardner 1993, Mazor et al. 1996) and contribute to carbon and nitrogen fixation (Beymer and Klopatek 1991, Evans and Ehleringer 1993), in addition to affecting soil moisture and nutrient levels (Alexander and Calvo 1990, Reynolds et al. 2001). Therefore, BSCs can be considered ecosystem engineers, i.e., organisms that physically modify, maintain, or create habitat for other organisms by causing physical-state changes in biotic

or abiotic materials (Jones et al. 1997). This is especially true for arid and semi-arid lands, where BSCs are most prevalent, and that cover ~40% of the earth's terrestrial surface. A reduction in BSC-mediated ecosystem services under anthropogenic disturbance is both a component and accelerator of desertification (Belnap et al. 1994).

Broadly defined, “desertification” is degradation of marginal habitats, including but not limited to arid lands, and resulting in both reduced productivity and the formation of deserts or barren desert-like land (Arnalds 2000). Desertification of rangelands is costly, accounting for ~\$23 billion/yr (1990 \$US) in foregone income, displacing human populations (Dregne and Chou 1992), and negatively impacting the livelihoods of ~1 billion people (Arnalds 2000). Although desertification can be strictly climate driven, many causes of desertification are directly or indirectly anthropogenic, including surface disturbances, overgrazing, overharvesting of fuelwood, and extreme climate events linked to the greenhouse effect (Schlesinger et al. 1990, Archer and Stokes 2000). In arid regions of

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the world, desertification is associated with either a net loss of soil fertility (Havstad et al. 2000, Sparrow et al. 2003) or a redistribution of soil nutrients from plant interspaces to "shrub islands" (Schlesinger et al. 1990). Desertification-linked soil-fertility losses could potentially hinder reestablishment of BSCs to disturbed lands.

Land managers are concerned about widespread land degradation and have requested better information on the potential occurrence and abundance of BSCs, and methods to hasten BSC recovery. To address both of these needs, we sought to determine which specific components of soil fertility or other environmental factors are best correlated with BSC abundance in relatively undisturbed systems. Nonquantitative biogeographical studies of BSCs have addressed floristics of major land masses (Büdel 2003), and BSC distribution along moisture availability–seasonality gradients (Rosentreter and Belnap 2003). In more quantitative studies, water availability, as influenced by both precipitation and slope aspect, appears to influence distributions of BSC organisms in arid lands at regional scales (Nash et al. 1977, Eldridge and Tozer 1997, Ullmann and Büdel 2003). Vascular-plant community structure, manifest as total cover, species composition, or influence of plant canopies on microsites, can affect BSC cover and composition as well (Eldridge and Tozer 1997, Ponzetti and McCune 2001, Maestre and Cortina 2002). Soil properties (e.g., texture, pH, salinity, etc.) can be very influential in determining the distributions of BSC organisms (Ponzetti and McCune 2001, Ullmann and Büdel 2003). However, the role of soil fertility remains largely unexplored. Two studies investigated the relationship between BSC distribution and two soil nutrients (Ca in Rogers [1972], Ca and S in Ullmann and Büdel [2003]) at local and continental scales—although in the case of the local-scale studies (Ullmann and Büdel 2003), the results were as strongly influenced by salinity gradients as by fertility. Additional soil nutrients (e.g., N, P, K, Mg, Fe, Mn, Zn, Cu, and others) are likely to affect BSC abundance and/or composition, but studies on that topic are lacking.

The northern and central portions of the Colorado Plateau ecoregion (USA) include a diversity of habitats across which to investigate abiotic and biotic determinants of the natural distributions of BSCs and component organisms. Within this 80 000-km² area, we investigated the hypothesis that higher soil-nutrient concentrations positively drive the regional and small-scale distributions of BSC bryophytes and lichens. This was a two-phase study. In the first phase, we asked two questions: (1) At a regional scale, which environmental gradients or combinations of gradients (climate, physiography, shrub cover, plant spacing, soil nutrients, chemistry, and texture) correlate most consistently with the community composition of BSC bryophytes and lichens? (2) Do BSC community composition and soil properties differ in relation to orientation around vas-

cular plants? We initiated the second phase of the study because our data suggested that micronutrients were particularly important correlates with cover of BSC organisms, and we sought to elucidate the relationships between micronutrients and the two major N-fixing soil lichens of the Colorado Plateau (*Collema tenax* and *C. coccophorum*). Thus, in phase two we investigated three competing hypotheses at the regional scale: (1) Greater availability of micronutrients determines greater abundance of *Collema*, (2) Greater abundance of *Collema* lichens leads to greater micronutrient availability, and (3) Abundance of *Collema* is correlated with micronutrient availability as a result of their shared correlation with some third variable. Both phases of our study are designed to help identify which environmental variables may be manipulated to restore cover of soil mosses and lichens to desertified regions.

METHODS

Site selection

Eighty-five sites were selected and surveyed in clusters at several locations around the northern and central Colorado Plateau (USA) (see Plate 1), including Glen Canyon National Recreation Area, Canyonlands National Park, Arches National Park, and Hovenweep, Dinosaur, and Natural Bridges National Monuments (Appendix A). We conducted our sampling in portions of national parks where livestock grazing impacts are nonexistent or low (due to either inaccessibility or long rest periods) so that the effect of disturbance could be minimized to the greatest extent possible. These localities span a precipitation gradient ranging from 135 mm to 320 mm/yr. Sites were selected to represent all possible combinations of the following site attributes: (1) flat (slope $\leq 5^\circ$), north-sloping (slope $> 5^\circ$, aspect $315\text{--}45^\circ$ N) and south-sloping physiography (slope $> 5^\circ$, aspect $135\text{--}225^\circ$ N); (2) shallow (> 1 m) and deep (≤ 1 m) soils; (3) widely spaced (> 1.5 m) and closely spaced (≤ 1.5 m) vascular plant canopies; and (4) fine bentonitic shale-derived and coarse sandstone-derived soils. Cutoff values for soil depth and plant spacing were based upon natural breaks in these parameters.

Survey methods

Each site was represented by a single point-intercept transect. A measuring tape was laid out in a random direction from a haphazardly selected starting point across the area to be surveyed. Each intersected shrub or bunchgrass greater than 20 cm tall or wide comprised a sampling station ($n = 30$ stations), as did the corresponding point on the line equidistant between that plant and the next ($n = 30$ stations). Due to differing plant spacing among sites, transect length was also variable. Plant canopy sampling stations were alternated so that half represented the southern sides, and half the northern sides ($n = 15$ stations for each aspect). This microscale positioning of the sampling station is ab-



PLATE 1. Biological soil crusts, visible as darkened bumpy soil, occupy most of the available soil surface in undisturbed semi-arid ecosystems of the Colorado Plateau. Photo credit: Charlie Schelz.

breviated as follows: SCN = shrub canopy north side, SCS = shrub canopy south side, IS = interspace.

Each position was sampled using quadrats of varying sizes, wherein percent cover of all lichen and moss species was estimated visually by a single investigator (M. A. Bowker) to the nearest 5%; an additional category specified trace counts (recorded as 2.5%). Litter and rock cover was also estimated to the nearest 5%. Soil depth was measured once with a metal probe in each quadrat and in <60-cm-deep soils only. Finally, we registered distance between shrubs and on sloping sites, and distance to nearest plant or other erosion-reducing barrier uphill. Cover was computed as percentage of available habitat, excluding litter and rock, which are not inhabited by biological soil crusts (BSCs). This calculation controls for variance caused solely by differing availability of habitat from site to site. Quadrat size differed by size of shrub or bunchgrass: 7×14 cm for small plants (≤ 30 cm tall or wide, mostly *Hilaria* and dwarf *Atriplex* spp.), 20×20 cm for medium-sized plants (≤ 30 – 200 cm tall or wide, mostly *Coleogyne*, *Atriplex*, and *Stipa* spp.) and all interspaces, and 50×50 cm for large shrubs or small trees (≤ 200 cm tall or wide, mostly *Pinus*, *Juniperus*, and *Artemisia*).

At each station within sites, a small amount (~ 10 g) of soil was collected to a depth of ~ 1 cm and composited into a shrub canopy (SC) composite soil sample ($n = 30$ stations; including both SCN and SCS soil or an IS soil sample $n = 30$ stations). Composite soil samples collected during the survey were sieved in a 2-mm sieve and the removed material was discarded.

Subsamples of ~ 200 g were sent to the Brigham Young University Soils Testing Laboratory (Provo, Utah, USA) for chemical and textural analyses: percentage sand, silt, and clay by hydrometer; acid-neutralizing potential (ANP; a measure of carbonates and other acid-neutralizing compounds based upon effervescence of CO_2 under acid addition and reported as percentage CaCO_3 equivalent); DTPA-extractable Zn, Mn, Fe, and Cu; NaHCO_3 -extractable (also known as available) P and K; NH_4OAc -extractable Mg, K, Ca, and Na (e.g., exchangeable cations); saturated paste extracted pH and electrical conductivity (EC; a measure of all salts more soluble than gypsum). Precipitation data were obtained from the Western Regional Climate Center (Reno, Nevada, USA; data *available online*),⁴ and several other climate variables were modeled by Alan Flint (U.S. Geological Survey, *personal communication*): potential evapotranspiration (PET), solar radiation, net radiation (corrected for slope and aspect), and average temperature minimum and maximum. Precipitation deficit was calculated as $|\text{precipitation} - \text{PET}|$.

Statistical analyses

Community-level hypotheses were tested using several techniques reviewed by McCune and Grace (2002). These methods are used because they are designed for multivariate analyses and allowed us to avoid one or more of the following problems: (1) unrealistic assumptions about community data distribution, (2) exclusive reliance on metric distance measures regardless

⁴ (<http://www.wrcc@dri.edu>)

of data properties, (3) assumption of linear relationships between correlated variables, and (4) unreliable results due to numerous zero values, typical in most community datasets.

First, at the regional scale, a Mantel test (a multivariate correlation procedure based upon randomization) was used to determine whether a distance matrix of environmental variables had explanatory power for a community-composition distance matrix. Individual environmental and community variables were rescaled from 0 to 1 (McCune and Grace 2002). We used the Bray–Curtis distance measure to construct the community distance matrix, and Euclidean distance to construct the environmental distance matrix.

To detect patterns in species distributions, nonmetric multidimensional scaling (NMDS) was used to ordinate lichen and bryophyte species. NMDS ordination creates the best possible multi-dimensional configuration based upon community data alone. Rare species that occurred only once were deleted from analyses because their positions in the ordination were erratic and not generally repeatable. To determine which environmental variables best correlated with the community data, a joint plot of environmental variables was fitted to the species ordination.

Because >50% of the sites on shale-derived soils had no moss and lichen cover, they could not be used in the NMDS ordination. Because of this drawback of the ordination, a subset of the data was used in a *t* test to better determine the effect of shale-derived soils on moss and lichen cover. The subsample consisted of all of the shale-derived sites ($n = 22$) and the nearest sandy-soil site to each of these. Only data from IS microsites were used, because many of the shale-derived sites were unvegetated. Data were log transformed to equalize variance.

The hypothesis that communities and environmental variables differ across microsites (IS vs. SCS vs. SCN for the former, and IS vs. SC for the latter) was tested using the blocked multi-response permutation procedure (MRBP; Mielke 1991). MRBP tests the hypothesis of no difference in multiple variables between groups of sampling units in a blocked design. Chance-corrected within-group agreement, represented by *A*, ranges from 1 (identical within-group data) through 0 (agreement expected by chance) to <0 (less than chance agreement) in this test. Prior to the test, all variables were relativized to a common scale, a prerequisite for this method. For the community data, post hoc indicator-species analysis was performed to determine which individual species differed between groups (Dufrene and Legendre 1997). Indicator-species analysis uses abundance and frequency data to calculate a percentage of perfect indication value for each variable-group combination, and tests for significance. Because indicator-species analysis is not appropriate for environmental data (McCune and Grace 2002), direct discriminant analysis was used as an alternative post

hoc test after significance was detected in the environmental model. This test provides the Fisher's standardized discriminant-function coefficient for each variable indicating that variable's relative contribution to a function discriminating between groups of samples, along with tests of significance for each individual variable. Prior to discriminant analysis, two transformations were used to convert the data to a similar format as that used in MRBP: (1) All variables were relativized to a common scale (0–1) to standardize their influence upon the analysis. (2) The medians of each pair of values were standardized to zero to preserve the blocking effect. Statistical significance in MRBP and indicator-species analysis was determined at $\alpha = 0.05$. All Mantel tests, MRBP, indicator-species analysis, and NMDS were conducted in PC-ORD version 4 (MJM Software Design 1999). Discriminant analysis was performed using SPSS 10.0 (2000 SPSS Inc.).

To test a posteriori causal hypotheses regarding micronutrient metals and *Collema* spp., we used structural-equation modeling (SEM). As Bollen (1989:38) states, the purpose of SEM is "to determine if the causal inference of the researcher is consistent with the data." Structural-equation modeling derives from a synthesis of path analysis and factor analysis, and has the unique ability to falsify causal hypotheses using observational nonexperimental data (Grace and Pugesek 1998). Although the strength of SEM-generated causal inferences is weaker than that of a properly implemented randomized experiment (Shipley 2000), the researcher is able to formulate one or more causal hypotheses that may underlie a correlation, and confront them with the data. By comparing the covariance structure of data that is *implied* by the model with the *actual* covariance structure of the data, we can test whether a model fits the data. Because SEM is too complex to fully describe here, we refer readers to chapters (McCune and Grace 2002) and books (Bollen 1989, Shipley 2000) on the subject.

We used the following protocol: (1) We created an a priori conceptual model of causal relationships between our variables of interest. (2) We developed a measurement model consistent with the conceptual model. A measurement model describes the hypothesized relationship between one or more measured variables and underlying unmeasured factors (termed "latent variables"). This stage of modeling is analogous to factor analysis. Our measurement model was tested iteratively and modified until a satisfactory fit with the data was achieved using the bootstrap goodness-of-fit test (Bollen and Stine 1992). (3) Full structural models, each representing a different hypothesis, were created by mapping the hypothesized causal relationships between the measurement model and each *Collema* species independently. A total of 18 specific models were tested (9 models per *Collema* species), all of which are variations on our three broad hypotheses stated in the *Introduction*, above (Table 1). For example, the hy-

TABLE 1. Specific causal hypotheses regarding the relationship between *Collema* spp. and the micronutrients Mn and Zn, and relative and absolute goodness-of-fit measures for the associated models.

Hypothesis†	Mean discrepancy	AIC	<i>P</i>	χ^2/df	GFI
<i>C. tenax</i> models					
Mn → <i>C. tenax</i>	33.4	37.2	0.41	1.2	0.990
Zn → <i>C. tenax</i>	95.9	97.9	<0.0001	11.3	0.921
Zn, Mn ↔ <i>C. tenax</i>	84.0	87.2	<0.0001	9.5	0.928
Mn, Zn → <i>C. tenax</i>	35.9	39.2	0.24	1.4	0.990
<i>C. tenax</i> → Mn	53.8	57.5	0.003	4.6	0.960
<i>C. tenax</i> → Zn	98.1	100.9	<0.0001	11.8	0.915
<i>C. tenax</i> → Mn, Zn	54.6	58.2	0.001	5.2	0.961
Mn → <i>C. tenax</i> → Zn	35.7	39.2	0.26	1.4	0.990
Zn → <i>C. tenax</i> → Mn	53.8	56.5	0.001	4.9	0.965
<i>C. coccophorum</i> models					
Mn → <i>C. coccophorum</i>	44.9	48.4	0.018	3.1	0.975
Zn → <i>C. coccophorum</i>	50.5	52.7	0.004	3.8	0.970
Zn, Mn ↔ <i>C. coccophorum</i>	51.3	54.7	0.003	4.1	0.964
Mn, Zn → <i>C. coccophorum</i>	35.6	38.9	0.31	1.4	0.990
<i>C. coccophorum</i> → Mn	53.3	56.9	0.003	4.5	0.961
<i>C. coccophorum</i> → Zn	58.7	61.0	<0.0001	5.2	0.958
<i>C. coccophorum</i> → Mn, Zn	49.0	52.2	0.006	4.0	0.970
Mn → <i>C. coccophorum</i> → Zn	37.4	40.5	0.17	1.7	0.987
Zn → <i>C. coccophorum</i> → Mn	37.5	40.7	0.18	1.7	0.987

Notes: Best model selection was based upon lowest mean discrepancy; Akaike's information criterion (AIC) is presented as an alternative model-selection criterion and confirms our selection. Absolute fit was assessed by the bootstrap goodness-of-fit test ($P > 0.05$); additional fit criteria (χ^2/df and Joreskog's goodness-of-fit index, GFI [Joreskog and Sorbom 1984]) are presented as confirmation of this test. Lowest relative-fit criteria, and acceptable absolute-fit criteria are indicated in bold ($P > 0.05$, $\chi^2/df < 2.0$, and GFI > 0.95).

† Single-headed arrows indicate a direct causal relationship pointing from hypothesized cause to effect; double-headed arrows indicate correlation due to shared causes.

pothesis that Mn influences *C. tenax* had a causal pathway from Mn to *C. tenax*, and the opposite hypothesis had a causal pathway from *C. tenax* to Mn. (4) To select a "best model" we assessed the relative fit of the models. We used the mean discrepancy between the implied and actual covariance matrices of 5000 bootstrapped samples of our data (Linhart and Zucchini 1986); models with the lowest mean discrepancy were considered best models. (5) In addition to assessing relative fit, we also tested absolute fit of our best models using the Bollen and Stine (1992) bootstrap test. This test compares the researcher's model with a perfect model to detect lack of fit, whereas relative-fit criteria (above) merely allow the comparison of a set of alternative models to one another. It is important to note that in this test $P < 0.05$ indicates a significant lack of fit, and is therefore contrary to most statistical tests, where $P > 0.05$ is considered desirable.

RESULTS

Regional community-level analyses

A Mantel test determined that many environmental variables (Appendix B) were significantly correlated with species abundance data ($P = 0.001$, $r = 0.37$). To determine which specific environmental variables were correlated with the species-abundance data, we performed a three-dimensional NMDS (nonmetric multidimensional scaling) ordination. This analysis ex-

plained 73% of the total variance in the data: 31%, 25%, and 18% for each of three axes, respectively. Most species were positively correlated with Axis 1 (Appendix C). A joint plot overlay was created to add the significantly correlated environmental variables to the ordination (Fig. 1). A complex gradient consisting of precipitation deficit and sand on the negative pole, and several soil nutrients and silt on the other pole, was well correlated with Axis 1 (Appendix B). The majority of species were correlated with the wetter, more fertile end of this gradient. The best correlate with Axis 2 was Mn (Fig. 1). Most species were positively correlated with this axis, and therefore higher Mn (Fig. 1). The third axis (not shown) was best correlated with soil depth on the negative pole and with average minimum temperature on the positive pole (Appendix B). There were only a few moderately strong correlations between species and this axis, some with higher minimum temperature and some with deeper soils (Appendix C).

A comparison of sites with shale-derived soils and nearest-neighbor sandy-soil sites (using the independent *t* test) revealed that percent cover and species richness were dramatically lower in shale-derived soils. Moss cover ($P = 0.002$), lichen cover ($P < 0.0001$), and moss + lichen cover (summed totals for each category; $P = 0.0002$) were all approximately six-fold greater in sandy soils (Fig. 2). The most common spe-

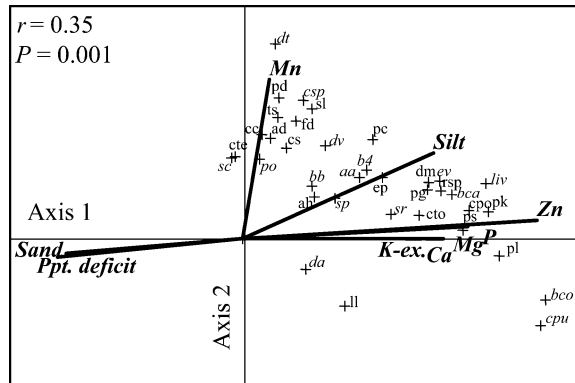


FIG. 1. Plot of species in nonmetric multidimensional scaling (NMDS) ordination space with an overlay of environmental variables. Each point (+) represents a species, each line an environmental variable, and the length of the line is proportional to its r (correlation coefficient; presented in Appendix B). Whole-model Mantel test results appear in the upper left corner and represent multivariate correlation between all environmental data and all species-abundance data. Bryophyte codes are italicized, and lichen codes are not.

Notes: Species codes (taxonomic authority is provided in Appendix C): aa, *Anomobryum argenteum*; bco, *Brachythecium collinum*; bca, *Bryum caespiticium*; bb, *Bryum bicolor*; b4, *Bryum sp.*; cpu, *Ceratodon purpureus*; csp, *Crossidium sp.*; da, *Didymodon australaesia*; dt, *Didymodon trifarius*; dv, *Didymodon vinealis*; ev, *Encalypta sp.*; po, *Pterygoneurum ovatum*; sc, *Syntrichia caninervis*; sp, *Syntrichia papillosissima*; sr, *Syntrichia ruralis*; liv, unknown liverwort; ah, *Aspicilia hispida*; ad, *Aspicilia desertorum*; cto, *Caloplaca tominii*; cs, *Catapyrenium spp.*; cpo, *Cladonia pocillum*; cc, *Collema coccophorum*; cte, *Collema tenax*; dm, *Diploschistes muscorum*; ep, *Endocarpon pusillum*; fd, *Fulgensia desertorum*; ll, *Leptogium lichenoides*; pk, *Peltigera kristinsonii*; ps, *Phaeorrriza saepeptana*; pc, *Psora cerebriformis*; pd, *Psora decipiens*; pg, *Psora globifera*; pl, *Psora luridella*; rsp, *Rinodina sp.*; sl, *Squamarina lentigera*; ts, *Toninia sedifolia*.

cies and almost all other individual species were more abundant on the sandy soils. Species richness was two-fold greater in sandy soils ($P = 0.002$).

Microsite associations

Across all sites, crust community composition differed significantly among microsites (Fig. 3). Calculated A (chance-corrected within-group agreement; see *Methods: Statistical analyses*, above) for the three positions as a whole was 0.09 ($P < 0.0001$), suggesting a moderate effect size (an $A \geq 0.3$ is considered very strong, and ≈ 0.0 very weak). Subsequent testing of all pair-wise combinations of microsites determined that SCN (shrub cover north side) microsites differed significantly from interspace (IS) ($A = 0.12$, $P < 0.0001$) and SCS (shrub cover south side) microsites ($A = 0.08$, $P < 0.0001$) in community composition. Interspace and SCS microsites were statistically different from each other, but this effect was rather weak ($A = 0.02$, $P = 0.002$). Indicator-species analysis determined that two mosses and one lichen were significant indicators of SCN microsites: *Syntrichia caninervis* (Indicator value

= 45, $P = 0.002$), *Syntrichia ruralis* (Indicator value = 41, $P = 0.001$), and *Fulgensia desertorum* (Indicator value = 21, $P = 0.01$). There were no significant indicators of SCS or IS microsites.

The substrate parameters of IS and shrub canopy microsites (SC, composites of SCN and SCS), were characterized using blocked multi-response permutation procedure (MRBP) and discriminant analysis. Significant grouping was detected between IS and the grouped SC microsites (Fig. 3). Highly significant associates of SC microsites included soil depth, litter, sand, electrical conductivity (EC), ratio of phosphorus to acid-neutralizing potential (P:ANP), and most nutrients. Rock, silt, and Cu were the only variables significantly higher in IS habitats. Higher K (exchangeable), Mg, and Mn were especially useful for distinguishing SC from IS microsites as indicated by the Fisher's canonical discriminant-function coefficient (Appendix B).

Species-level analyses

Our structural-equation models all shared the following characteristics (Fig. 4): (1) the measured variables P, Mn, Zn, and Fe (all immobile nutrients) are interpreted as being caused by an underlying unmeasured latent variable, "nutrient mobility"; (2) *Collema* spp. and nutrient mobility share $\text{CaCO}_3\text{:P}$ as a hypothesized causal influence; and (3) in addition to sharing the cause "nutrient mobility," Mn and Fe, and Zn and Fe are specified to covary because they are measured simultaneously in the same extraction and Fe may reduce mobility of Mn and Zn.

In our set of models we varied only the position, number, and direction of causal arrows between *Collema* spp., Mn, Zn, or nutrient mobility to be consistent with various specific hypotheses (listed in Table 1). Based upon relative-fit criteria (lowest mean discrepancy), we selected a best structural-equation model (SEM) for each *Collema* species (Table 1). We selected the model with a single causal pathway from Mn to *Collema tenax* (mean discrepancy = 33.4, presented in

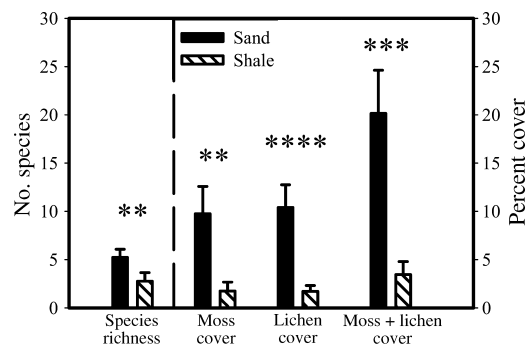


FIG. 2. BSC (biological soil crust) moss and lichen diversity and cover on shale-derived sites ($n = 22$) and their nearest neighbor sandy-soil sites ($n = 22$). Data are means and SE. ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

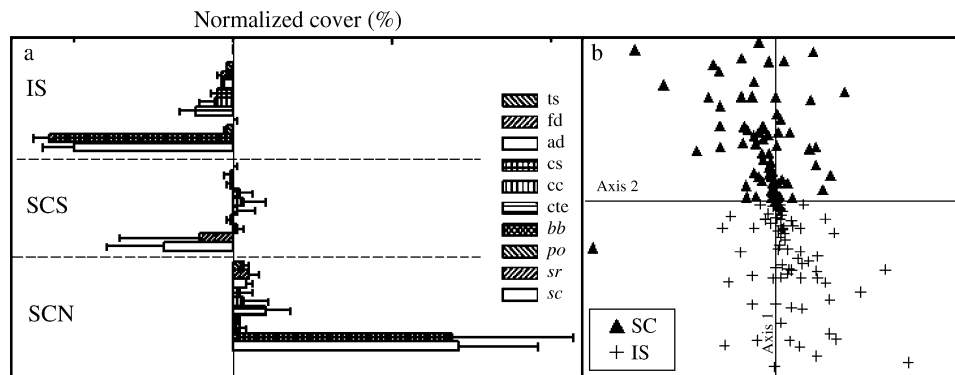


FIG. 3. Comparisons between different microsite types: SCN, shrub canopy north; SCS, shrub canopy south; SC, shrub canopy (north and south pooled); IS, interspace. (a) Community composition compared among SCN, SCS, and IS microsites (blocked multi-response permutation procedure [MRBP]; $A = 0.09$, $P \leq 0.0001$). The percent cover values of the 10 most common species are shown; cover within a block is normalized (centered on zero). See Fig. 1 for key to species codes. (b) Soil properties compared between SC and IS microsites in nonmetric multidimensional scaling (NMDS) ordination space (MRBP; $A = 0.19$, $P < 0.0001$).

Fig. 4), and the model consistent with Mn and Zn limitation of *C. coccophorum* (mean discrepancy = 35.6). Both best models achieved a satisfactory absolute fit ($P = 0.41$ and $P = 0.31$, respectively). The best model for *Collema tenax* is presented in Fig. 4, accounting for about one third of the variance in the abundance of this species. In both cases, there were two alternative models with slightly greater mean discrepancy, but a satisfactory absolute fit. In the case of *C. tenax*, all of

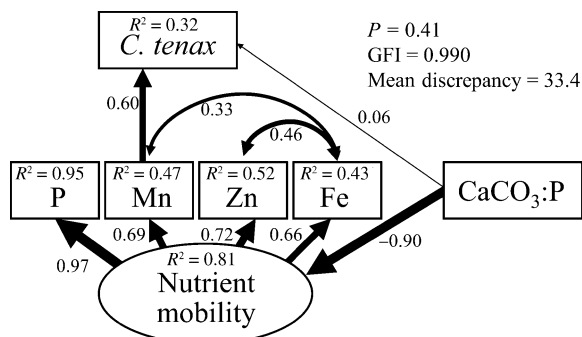


FIG. 4. An example of a structural-equation model specifying the hypothesis that Mn limits *Collema tenax*. This model was selected as our best model for this species, based upon the lowest mean discrepancy between the actual covariance structure of our data and that implied by the model. Measured variables appear in rectangles, while a latent (or unmeasured) variable appears in an oval. Proportions within rectangles or ovals indicate R^2 for that variable. Arrows indicate a unidirectional causal relationship pointing from cause to effect. Proportions next to arrows indicate path coefficients (equivalent to correlation coefficients), and the width of the arrows is proportional to the path coefficients.

Note that the latent variable “nutrient mobility” is a hypothesized underlying cause of the four measured nutrients; it is equivalent to a factor in factor analysis. GIF is the goodness-of-fit index (Joreskog and Sorbom 1984); the discrepancy function (mean discrepancy) measures the incongruence between the covariance structure implied by the model and that derived from the bivariate covariance matrix of the data.

the satisfactorily fitting models were consistent with a Mn limitation of *C. tenax*. Two of these models had negligibly weak pathways between Zn and *C. tenax*. Therefore the simpler model “Mn \rightarrow *C. tenax*,” with the arrow (\rightarrow) representing a unidirectional causal pathway from hypothesized cause to effect, is clearly the better model based upon both fit and parsimony. The best model for *C. coccophorum* stated that both Mn and Zn have a causal influence upon the lichen. In the case of *C. coccophorum*, one alternative model was of the form Mn \rightarrow *C. coccophorum* \rightarrow Zn, while the other took the form Zn \rightarrow *C. coccophorum* \rightarrow Mn, thus considerable uncertainty remains about the direction of the relationships between this lichen and the micronutrients. The best model for *Collema coccophorum*, and the two alternatives appear in Appendix D. These three models had less explanatory power than the *Collema tenax* best model ($R^2 \leq 0.14$). The remainder of the models for both species had little support, using either relative or absolute criteria.

DISCUSSION

This study is the first to relate the distribution of biological soil crusts (BSCs) to an extensive suite of soil nutrients (and other environmental parameters) at both very large and very small spatial scales. The prominent and repeated positive correlations between micronutrients (Mn and Zn) and moss and lichen abundance were particularly novel and unexpected. Structural-equation modeling suggested that micronutrient limitation of lichens was the explanatory causal hypothesis most consistent with the data. Because Zn (and likely Mn) limitation occurs in several arid and semi-arid regions of the globe (Hacisalihoglu and Kochian 2003), these findings may be useful in developing restoration methods in many regions worldwide.

Drivers of community composition at the regional scale

Two complex factors explained much of the variance in moss and lichen distribution in the north and central Colorado Plateau (USA). One factor was a gradient involving coarse texture and aridity at one end and fertility (primarily Zn, P, Mg, Ca, and K) and silt at the other. At the moist end of the gradient there is likely to be more weathering of soils and more vegetative cover, both of which could enhance nutrient status and silt (and therefore cation exchange capacity, CEC) at the soil surface. In our present study, no taxon was most abundant in the driest portions of the study area, and the majority were negatively correlated with aridity to some degree. Overall, this interpretation is consistent with the observations of Rosentreter and Belnap (2003) that moss and lichen cover and diversity are negatively correlated with a potential evapotranspiration (PET) gradient across the western United States. Axis 2 (Fig. 1) of the ordination is driven by Mn, adding another parameter to the positive correlation between BSC mosses and lichens and soil fertility.

Because half of the data from the barren shale sites were not included in the ordination, due to the complete absence of BSC cover, we believe that the relative importance of the negative effect of shales on BSC was not adequately captured in the nonmetric multi-dimensional scaling (NMDS) ordination. The magnitude of this effect is well illustrated by the comparison of shale sites to their nearest sandy-soil neighbors (Fig. 2), wherein BSC cover and richness are six-fold and two-fold greater, respectively, on sandstone-derived soils than shale-derived soils. Furthermore, on a regional scale, sandstone-derived and shale-derived soils are the most widespread soil types on the Colorado Plateau (>50% and ~10–15%, respectively). Although the shale soils in this study tend to be high in base cations (Ca, Mg, K, Mg), they may be unfavorable habitats due to a high proportion of unstable shrinking–swelling clays and low availability of immobile nutrients (P, Mn, Zn)

Community composition in relation to microhabitat

We found that BSC moss and lichen communities were significantly different in all three microsite types (SCN, SCS, IS). Shrub canopy north (SCN) microsites can represent a more shaded and cooler environment than do surrounding SCS and IS (interspace) microsites and the soil surface retains moisture longer (Bowker et al. 2000; Maestre et al. 2001). At a still smaller scale, on ~5-cm-tall linear ridges in the BSC, several BSC organisms also are most abundant on the more mesic micro-aspects (George et al. 2000; M. A. Bowker, J. Belnap, D. W. Davidson, and H. Goldstein, *unpublished manuscript*). Thus, the BSC organisms that are capable of light harvesting in shadier conditions are likely able to remain hydrated and active longer when growing in

SCN habitats, resulting in greater percent cover (this study) and larger sizes of individuals (Bowker et al. 2000).

Additionally, shrub canopy (SC) microsites may act as fertility islands in nutrient-poor arid regions (Schlesinger et al. 1990). Interestingly, most of the nutrients that were significantly associated with SC microsites are also strong drivers of Axis 1 (P, K, Zn, Fe, Mg) and Axis 2 (Mn) in the regional-scale analysis. Thus, BSC organisms seem to be responding to a similar fertility–effective moisture gradient at two very different scales. This pattern was conservative because our study design did not differentiate SCN and SCS microsites in soil analyses; had it done so, the distance between SCN and IS microsites might have been even greater.

Species-level distribution

The strong correlations between the BSC moss and lichen community and micronutrients suggested three competing a posteriori hypotheses regarding the distribution of N-fixing *Collema* lichens: (1) *Collema* spp. are micronutrient limited, and therefore are most abundant where these nutrients are more available; (2) due to either micronutrients adhering to lichen surfaces or modification of the soil environment by lichens, *Collema* determines greater micronutrient availability; and (3) *Collema* and micronutrients are correlated because both are causally dependent upon the same additional variables. Using structural-equation modeling (SEM), we formulated and tested models consistent with these hypotheses, eliminating most variations of hypotheses 2 and 3 above. Our best models suggested that Mn limits *C. tenax*, both Mn and Zn limit *C. coccophorum*, and that Mn values of at least ~8 ppm and Zn values of at least ~0.4 ppm may result in greater *Collema* cover. Nitrogen fixation in two terrestrial cultures of *Nostoc* (the photobiont genus of *Collema* lichens) was generally stimulated by supplemental addition of heavy metals (As, Cd, Pb, Ni, Pd, and Zn) at low levels, with variable effects at higher concentrations (Henriksson and DaSilva 1978). An experimental P and K addition to transplanted *Collema* lichens failed to consistently enhance growth or physiological response (Davidson et al. 2002), but the treatment did not amend the sub-optimal (as inferred from the present data) Zn and Mn concentrations.

Conclusions and future research

In this study we have determined that BSC lichen and moss abundance is positively correlated with greater moisture and nutrient availability at two very different scales—specifically the nutrients Mn and Zn. Most importantly, we determined the following using SEM: (1) our data are most consistent with the hypothesis that Mn limits *Collema tenax* and are less consistent with alternative explanations, and (2) our data are most consistent with the hypothesis that *both*

Mn and Zn limit *Collema coccophorum* and are less consistent with alternative models.

In the federal lands of the arid western United States, BSCs are currently addressed in all environmental assessments and impact statements. These documents outline the expected impacts of proposed federal actions (such as road construction, or changes in resource-extraction policy) upon the environment, including BSCs. They are used to aid in choosing among multiple action alternatives. Often, regarding BSCs, these treatments are vague or simply inaccurate because too little is known about the potential development and importance of BSCs in any given locality. The findings in the present study will help ameliorate this paucity of information. For example, our results suggest that BSCs are likely not a management concern on bentonitic shales, however they may be exceptionally important on sandy soils in relatively mesic areas.

Further research should focus on refining our ability to predictively model BSC abundance and composition, so that appropriate reference conditions are known. Reference conditions are used in the related fields of range management and ecological restoration and consist of a set of parameters and their natural variance describing an undisturbed or desired state of the ecosystem being managed (Moore et al. 1999). These reference conditions (e.g., potential cover of various crust types, or species richness) will be useful in monitoring the condition of rangelands, setting appropriate restoration goals, and determining when restoration efforts have been successful.

Because of the high cost of desertification and large number of people affected (Dregne and Chou 1992), there is a clear need for arid-land restoration tools that are widely applicable on large scales to curb some of these losses. The finding that micronutrients may limit *Collema* species is a "first step" toward developing a potentially useful restoration method to be used in arid-lands restoration ecology. We believe this for four reasons. (1) BSC mosses and lichens are cosmopolitan components of arid-land ecosystems, and many ecosystem processes are strongly tied to their presence. We would argue that restoration of many arid ecosystems is not complete, and in some cases probably not possible, without restoration of these organisms. (2) Zinc deficiency is widespread in arid lands (for example North American, Middle Eastern, Australian, and Chinese deserts, among other areas; Hacisalihoglu and Kochian 2003), and it is reasonable to assume that Mn deficiency may occur in the same areas because it is caused by many of the same edaphic factors (Marschner 1995). (3) In addition to inherent nutrient deficiencies, surface disturbance in arid lands is often associated with erosion-mediated net losses in soil fertility (for example, Zn in Havstad et al. [2000]) or a redistribution of nutrients out of plant interspaces where most BSC cover is present overall (Schlesinger et al. 1990). We would expect that in areas where nu-

trients are already limiting, surface disturbance is likely to exacerbate the problem due to the loss of organic matter and previously assimilated eolian dust. (4) Fertilization-based restoration methods are a potential option to overcome soil-fertility losses because they are relatively inexpensive, applicable on a large scale, and are effective in restoring mosses and lichens, at least in devastated cool mesic systems (Grettarsdottir et al. 2004). This type of restoration method has scarcely been investigated in arid lands (but see Davidson et al. [2002]), and has not specifically focused on micronutrients.

We must further explore the degree to which micronutrients may limit *Collema*, and the usefulness of this finding in restoration applications. In the data-analysis philosophy of SEM, greater confidence in results is obtained via repeatability, and confirmation with alternative approaches. Micronutrient limitation of *Collema* should be investigated as an a priori hypothesis using SEM methods on additional data sets. This may give us greater confidence that Mn limits *Collema tenax*, and Mn and Zn limit *C. coccophorum*, and would allow us to extend our hypotheses to new study areas. Consideration of the two alternative models for *C. coccophorum* (those with bootstrap goodness-of-fit $P > 0.05$) is advisable as well, because much uncertainty remains about the direction of the relationships between this lichen and the micronutrients. Experiments should also be used as a confirmatory alternative approach.

Experimental work should be designed to ascertain how applicable our findings are to restoration. Perhaps the broadest question that experiments can answer is whether micronutrient fertilization can significantly speed the recovery of mosses and lichens compared to passive restoration, i.e., removal of the stressor. Mosses and lichens of BSCs are generally thought of as slow growing (although this could be due partially to degraded site conditions), thus it is reasonable to consider whether they can be restored on the temporal scales used in restoration. This may be an especially important consideration in hot deserts where unaided recovery time may span several decades (Belnap and Warren 1998). A recently published restoration project involving soil stabilization in a cold desert does suggest that active restoration methods can markedly enhance the recovery of the BSC community compared to no action (Li et al. 2004).

Targeted experiments can be used to develop and refine methodology. Our results suggest that available concentrations of Mn and Zn should be above ~8.0 ppm and ~0.4 ppm, respectively, but also that soil characteristics such as CaCO_3 content impact mobility. Trials of various application rates on soils representing a CaCO_3 gradient would be quite useful in determining how much fertilizer must be added to attain the desired conditions. Because degraded lands may be depleted in many soil nutrients, experiments must determine

whether micronutrient addition alone can enhance BSC recovery, or whether simultaneous addition of other nutrients is also necessary. We must also determine, using experiments and observational studies, whether the micronutrient-limitation hypothesis can be extended to the other major component of BSCs, the cyanobacteria. It would be informative to conduct a factorial experiment comparing the effects of micronutrient fertilization on cyanobacterial crust development with other proposed restoration techniques such as cyanobacterial inoculation (Buttars et al. 1998). As mentioned above, we have inferred that because micronutrient deficiency is common (Hacisalihoglu and Kochian 2003), techniques aimed at reversing this condition may be a widely applicable restoration technique for BSCs. This assertion should be tested in multiple regions using experiments like those described here, and SEM of observational data sets. As a precaution, we must also complete similar research on the response of exotic plants to micronutrients, to ensure that fertilization will not simply promote problem species such as *Bromus tectorum*, a frequent component of plant communities on the Colorado Plateau (Belnap and Phillips 2001).

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APPENDIX A

A map showing the study region (north and central Colorado Plateau, USA) and the distribution of sampling sites in the National Park units used in this study is available in ESA's Electronic Data Archive: *Ecological Archives* A015-058-A1.

APPENDIX B

A table showing the correlations with ordination axes and discriminant analysis results of environmental variables is available in ESA's Electronic Data Archive: *Ecological Archives* A015-058-A2.

APPENDIX C

A table showing the correlations with ordination axes, indicator-species analysis results, and frequency of occurrence of BSC moss and lichen species is available in ESA's Electronic Data Archive: *Ecological Archives* A015-058-A3.

APPENDIX D

The best structural-equation model for *Collema coccophorum* and two alternative models are available in ESA's Electronic Data Archive: *Ecological Archives* A015-058-A4.