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MICROTOPOGRAPHY OF MICROBIOTIC CRUSTS ON THE COLORADO PLATEAU, AND DISTRIBUTION OF COMPONENT ORGANISMS

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ABSTRACT.—We analyzed the microtopography of microbiotic soil crusts at 3 sites on the Colorado Plateau of southern Utah and investigated distributions of cyanobacteria and several lichens in distinctive microhabitats created by this topography. At all 3 sites the long axes of linear soil mounds were oriented nonrandomly in a NNW–SSE direction. The conspicuous and consistent orientation of soil mounds may result from a combination of physical and biotic processes. Subtle differences across sites in mound orientation and organismal distribution suggest that these variables may be useful in comparing disturbance histories of crusts retrospectively.

Differences in colonization frequencies, abundances, and distributions of microorganisms comprising the crusts, as a function of mound aspect or exposure, suggest that these organisms are associated with particular aspects due to distinctive and favorable microhabitats on these exposures. Polysaccharide sheath material, deposited by cyanobacteria, and associated filaments occurred in greater quantities on ENE than WSW mound exposures, and cover by *Collema* spp. lichens exhibited the same pattern. Colonization of mounds by common lichen species occurred significantly more frequently on ENE than WSW mound aspects at 2 of 3 sites. In contrast, the 3 most common lichen species, aside from *Collema* spp., did not exhibit a tendency for greater cover on ENE than WSW mound aspects. Physiological differences between gelatinous cyanolichens and green-algal lichens may explain the different distributional patterns of *Collema* spp. and the 3 other lichens.

Key words: microbiotic crusts, cryptobiotic soil, colonization, microtopography, nonrandom orientation, exposure, *Collema*, lichen, cyanobacteria, disturbance history.

Microbiotic crusts (or cryptogamic, cryptobiotic, and microphytic crusts), consisting of cyanobacteria, algae, lichens, fungi, and mosses growing on soil surfaces, provide the predominant cover for many semiarid and arid regions throughout the world (Fig. 1a). Several researchers have reported on ecological services provided by these crusts: substrate stabilization, nutrient enhancement, and, perhaps, increased moisture availability (Harper and Marble 1988, Isichei 1990, West 1990, Metting 1991, Johansen 1993, Eldridge and Greene 1994, Evans and Johansen 1999). The importance of these effects has been highlighted by increasing levels of anthropogenic disturbances which disrupt microbiotic crusts, reduce services provided, and potentially lead to desertification of some semiarid ecosystems (Johansen et al. 1984, Schlesinger et al. 1990, Belnap 1993, Evans and Ehleringer 1993, Johansen 1993).

Estimated recovery times for disturbed crusts in arid and semiarid regions of the Great Basin (Andersen et al. 1982, Johansen et

al. 1984, Johansen and St. Clair 1986) and the Colorado Plateau (Cole 1990, Belnap 1993) vary in relation to soil type, climate, and component organisms, but full recovery of ecosystem services provided by the crusts is generally conceded to be slow. Recovery rates for cyanobacteria (including the widely distributed *Microcoleus vaginatus*), lichens, and mosses have been estimated at 40 yr, 45–85 yr, and 250 yr, respectively (Belnap 1993). Factors prolonging crust recovery remain poorly explored, and elucidation of these factors may require considering both physical and biological processes.

One possible requisite for crust recolonization by particular species may be the creation of new microhabitats by naturally and gradually occurring changes in the microtopography of crusts and underlying soils. On the Colorado Plateau, well-developed microbiotic crusts often exhibit a consistent and distinctive microtopography composed of elliptically shaped pedicellations (mounds) with short and long axes (Fig. 1a). Pedicellated mounds are small,

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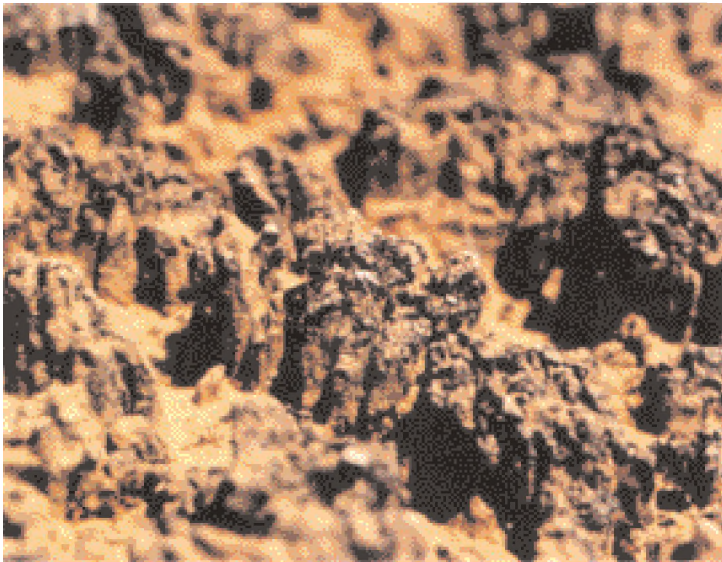


Fig. 1. a, High percent cover by linear crusts on shallow soils in the Needles District of Canyonlands National Park on the Colorado Plateau (note elliptical mounds); b, close-up view of a pedicellated soil mound.

typically 5–15 cm long and up to 7 cm tall from base to crown (Fig. 1b). Although mounds form perhaps the most visually striking of all soil crusts, the processes producing them remain poorly understood (J. Johansen personal communication). Traditionally, their origins have been attributed to a combination of frost-heaving during freeze-thaw cycles in cooler seasons (West 1990) and selective erosion (Metting 1991, Johansen 1993, and see

below), but such causality has yet to be tested explicitly with empirical evidence. As the microtopography of crusts develops through time, microtopographic heterogeneity increases (Cole 1990). The degree of microtopographic heterogeneity may affect both quality and quantity of microhabitats found on resultant mounds. The gradual development of microtopography could therefore result in new microhabitats that afford “safe sites” for colonization

and establishment of early-arriving species (e.g., van der Valk 1992).

In addition, early-arriving species may somehow modify the environment in ways that favor colonization by species that recruit later in the successional sequence. For example, some of the first colonists in succession on crusts of the Colorado Plateau are nitrogen-fixing species, cyanolichens in the genus *Collema* and epiphytic diazotrophic bacteria associated with *M. vaginatus* (Steppe et al. 1996). Such species may affect both absolute and relative availabilities of nutrients to microorganisms. Moreover, several cyanobacteria, particularly the predominant *M. vaginatus* on the Colorado Plateau (Belnap and Gardner 1993), tend to arrive long before *Collema* lichens (Johansen et al. 1984, Belnap 1993), and they secrete polysaccharide sheaths that are left behind as dry, fibrous remains as the organisms continue growing. By binding strongly to soil particles (Belnap and Gardner 1993), this sheath material may impose structure and stability on mounds, contribute to changes in crust microtopography, and even affect moisture penetration and retention (Harper and Marble 1988, Metting 1991, Johansen 1993, Eldridge and Greene 1994, Williams et al. 1999). A better understanding of successional changes in conditions favoring colonization and growth of soil microorganisms may suggest ways in which assisted natural regeneration could enhance recovery rates of disturbed crusts.

The purpose of our study is to characterize the microtopography of crust-covered mounds on shallow soils of the Colorado Plateau and to examine how this microtopography correlates with recruitment, abundance, and distribution of the microorganisms comprising microbiotic crusts. Toward this end, we first examined whether linear mounds exhibit nonrandom compass directions. After confirming directionality, we then determined whether abundances and/or distributions of microorganisms vary in relation to mound aspect.

METHODS

Data were taken at sites established (1) near Pothole Point in the Needles District of Canyonlands National Park (109°48'W, 38°10'N, 1585 m elev), (2) at Behind-the-Rocks (BTR) area, approximately 12 miles south of Moab (109°30'W, 38°25'N, 1675 m), and (3) on the

southern lip of White Canyon, near Cheesebox Butte (16 miles west of the junction of route 95 and the turnoff to Natural Bridges National Monument, 110°10'W, 37°40'N, 1525 m). At each of the 3 sites, pinyon-juniper communities with sparse densities of herbs formed the dominant higher plant cover on shallow, sandy substrates, dissected by exposed bedrock. Data were taken on 4 April 1997 and 1 May 1998 at Pothole, 12 October 1997 at BTR, and 26 March and 1 May 1998 at Cheesebox.

Four kinds of data were taken: (1) compass orientations of linear mounds, (2) amounts of cyanobacterial sheath material on opposing long sides of mounds, (3) relative cover of *Collema* spp. (all sites) and 3 other lichen species (Pothole Point only) on opposing long faces of mounds, and (4) numbers of colonization events of lichens on opposing long and short sides of mounds.

Mound Orientation

At each site mound orientation was determined for 20 cyanobacterial mounds (mounds without lichens) and 20 lichen mounds (mounds dominated by *Collema* spp. lichen cover). Mounds were located in areas with a mixture of exposed bedrock and sandy soils, including depressions commonly referred to as potholes. We worked within relatively homogeneous, intershrub habitats where direct sunlight would not have been obscured by trees, shrubs, or topographic features. We chose the first 20 mounds of each type haphazardly, with the following qualifications: First, we avoided mounds that had been trampled by livestock, wildlife, and humans. Second, we required mounds to be lichen-free (cyanobacterial mounds) or predominantly *Collema*-covered (lichen mounds), depending on the type of mound being investigated. Third, we used no more than 2 mounds per pothole or soil outcrop. In addition, we worked within arm's length of slickrock, where we could stand without damaging the crust.

Compass measurements were taken along the long mound axes, and orientations in degrees from North (0°) were recorded for axes present between 0° and 180° (Fig. 2). Declination adjustments corrected compass measurements to true North. Since data sets for both cyanobacterial and lichen mounds met the assumptions of parametric statistics, we used an ANOVA to test continuous compass measurements in each of the 2 data sets for site

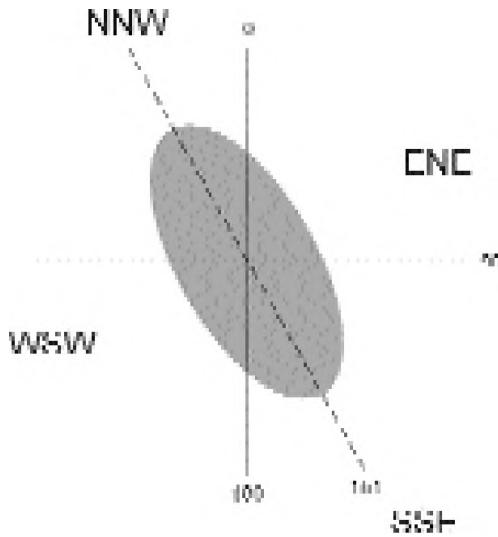


Fig. 2. Diagram demonstrating how microtopographic orientation was determined for elliptical soil mounds (shaded) of microbiotic crusts on the Colorado Plateau.

differences in mean mound orientations. Where significant differences were observed, we employed Tukey pairwise tests to determine which comparisons were responsible for such disparities. Differences in orientations of cyanobacterial and lichen mounds were tested with t tests independently for each site. Multiple comparisons were taken into account by correcting α to a tablewise value of 0.05 (Rice 1989).

Subsequently, compass measurements were grouped into a categorical variable with 4 levels (0–45°, 46–90°, 91–135°, 136–180°). A chi-square analysis was used to compare numbers of observations across levels to the expectation, under random orientation, of equal observations per level. Cyanobacterial and lichen mounds were treated separately and for each site independently in these analyses. Multiple comparisons for each mound type required adjustment of critical levels of α to a tablewise value of $\alpha = 0.05$ (Rice 1989).

Cyanobacterial Sheath Material

Cyanobacterial mounds sampled for mound orientation were subsequently divided in half along their discernible lengthwise axes with a straight edge. After removal of litter, each mound half (substrate and dead and live organic matter) was collected separately until level with the surrounding soil surface. Samples were

placed in appropriately labeled coin envelopes and returned to the lab, where they were dried for approximately 1 wk at 42°C in a Precision oven. Dried filaments and associated sheath material were separated from soil particles (substrate) using progressively finer USA Standard Testing Sieves (1 mm, 710 μm , 600 μm , 500 μm). Filamentous material that remained after each level of sieving was removed and considered to be cyanobacterial sheath. Material passing completely through all sieves and found in the collection pan was considered to be substrate. (While the substrate fraction assuredly contained some organic matter in addition to substrate, this minor contamination would not have biased our comparisons of mound exposures, and the method's resolution was appropriate to the question we were asking.) Substrate and cyanobacterial material were weighed separately to the nearest 0.01 g for each side of each mound and expressed as a sheath-to-substrate ratio (g of sheath material / g of substrate).

Sheath-to-substrate ratios were analyzed by split-plot ANOVA (to account for paired data) to identify effects of site, exposure, and site-by-exposure interactions. Subsequent multiple pairwise comparisons by the Tukey method determined which sites contributed most strongly to the significant effect of mound exposure. Paired t tests were used to identify which sites accounted for the significant site-by-exposure interaction. For multiple paired t tests, α was corrected to a tablewise value of 0.05 (Rice 1989).

Lichen Cover Versus Mound Aspect

The commonness of *Collema* spp., *Placidium squamulosum*, *Psora decipiens*, and *Squammarina lentigera* in preliminary censuses led us to focus on these species in our comparisons of lichen cover in relation to mound aspect. Except for *Collema* spp., which were examined at all 3 sites ($N = 20$ mounds per site, or 60 mounds in total), these comparisons were made just at Pothole Point ($N = 20$ mounds per non-*Collema* spp.).

For each of the 4 lichen species independently, we determined visually whether relative cover was greater on either of the opposing long sides. Sampling was restricted to homogeneous intershrub habitat in areas with a mixture of exposed bedrock and shallow,

sandy soils including potholes. We used only mounds oriented in the naturally prevailing compass direction (verified by compass measurements), worked from slickrock on the edges of crusts, and scored a maximum of 2 mounds per pothole or soil outcrop. Mounds were rejected if the species of interest was absent. With these exceptions, we chose the first 20 mounds haphazardly. Excluding mounds used to sample the relative cover of *Collema* spp., those sampled for relative cover were unique and independent of mounds used in other analyses. Mounds sampled for relative cover of *Collema* spp. were scored concurrently for lichen colonization events (see below).

We scored cover as higher on either the ENE or WSW aspect and, depending on sample sizes, analyzed the data by 1 of 2 methods. To determine whether data on *Collema* spp. could be lumped across sites, we compared numbers of mounds with greater *Collema* lichen cover on ENE versus WSW mound exposures across 3 sites using a Fisher's exact test. (Some cell counts were too low for a contingency test.) Site differences were not significant ($P = 0.835$), and we therefore pooled data across sites ($N = 60$ mounds in total) and used a nonparametric binomial test to evaluate the hypothesis that cover did not differ between the 2 mound exposures. If the numbers of mounds with higher cover on ENE and WSW exposures were equal, then the expected frequency or probability of each outcome under the binomial distribution would be 0.50. We used a z approximation of the binomial distribution to assess departure of these dichotomous data from expected frequencies of 0.50.

Sample sizes were smaller for non-*Collema* lichens. We therefore used a chi-square test to compare numbers of mounds with greater cover on ENE versus WSW mound faces against the assumption of equal cover on the 2 mound aspects. To correct for multiple comparisons, we adjusted the critical level of α to a tablewise value of 0.05 (Rice 1989).

Lichen Colonization Events

At all 3 sites, lichen colonization events were examined relative to mound aspects for all lichen species encountered. For this study a colonization event was defined as the initialization of growth by lichen on a particular

mound aspect. Because lichens typically grow outward radially from a central point, colonization events could be recognized when thallus surfaces covered a single exposure. When a lichen thallus extended over multiple aspects, it was not evident which exposure had been colonized first. By our definition, colonization might be confused with cases of retracting lichens. However, the observation of radial growth outward from a central point and the absence of senescent thalli consistently indicated colonization rather than retraction.

Twenty mounds were sampled within relatively homogeneous intershrub areas on shallow soils dissected by exposed bedrock. We worked from bedrock at the edges of crusts and imposed 3 additional conditions during selection of mounds. First, no more than 2 mounds were sampled per pothole or soil outcrop. Second, mounds were rejected unless they were aligned in the typical direction (see Results below). Third, in all but the BTR site, where we did not reject any mound, we rejected mounds lacking lichens. Otherwise, we again sampled 20 mounds haphazardly during each site visit (1 visit to BTR and 2 visits to the other sites; see above). To bolster our sample sizes, we pooled all non-*Collema* lichens, which included *Psora decipiens*, *Psora tuckermanii*, *Fulgensia* spp., *Placidium squamulosum*, *Diplochistes* sp., *Toninia* sp., *Squamarina lentigera*, and *Heppia* sp., as well as the moss *Tortula ruralis*. A chi-square test was used to test for equality of observed colonization events between exposures with similar total surface areas (NNW vs. SSE, and ENE vs. WSW).

RESULTS

Mound Orientation

ANOVAs demonstrated highly significant differences in mound orientations among the 3 sites for cyanobacterial mounds ($F_{2,57} = 5.692$, $P = 0.006$) but not for lichen mounds ($F_{2,57} = 0.009$, $P = 0.991$; Fig. 3). For the former, subsequent Tukey pairwise comparisons indicated a significant difference between orientations at Cheesebox and BTR, and a marginal difference between Cheesebox and Pothole Point (Table 1). Long axes of cyanobacterial mounds at Cheesebox are oriented more closely to the E-W axis, on average, than are those at BTR and Pothole (by 17° and 12° ,

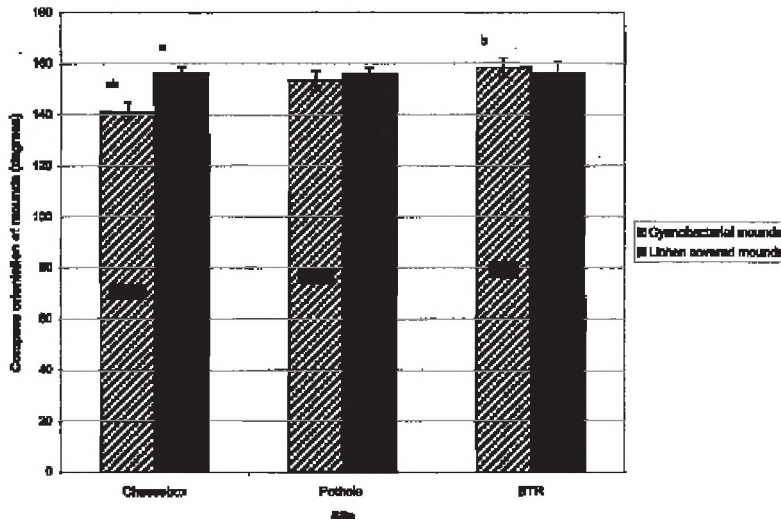


Fig. 3. Mean orientations (degrees from North) of elliptical soil mounds in microbiotic crusts at 3 sites on the Colorado Plateau in southeastern Utah. Data compare cyanobacterial crusts lacking lichen and mounds with abundant *Collema* spp. lichen. Each column represents data from 20 mounds. Vertical bars represent standard error of the mean orientation. The same letter above 2 columns indicates a statistically significant difference.

respectively). They are also farther from mean orientations of lichen mounds at all sites, and they face more toward the east than do the long axes of lichen mounds at Cheesebox ($t = -3.295$, $df = 38$, $P = 0.001$), but not at the other sites (Pothole Point: $t = -.459$, $df = 38$, $P = .324$; BTR: $t = -.384$, $df = 38$, $P = .351$; Fig. 3).

In chi-square analyses at each of the 3 sites, orientations of both cyanobacterial and lichen mounds were highly directional (Fig. 4a, cyanobacterial mounds: Cheesebox: $\chi^2 = 23.6$, $df = 3$, $P = 3.03E-5$; Pothole Point: $\chi^2 = 45.6$, $df = 3$, $P = 6.9E-10$; BTR: $\chi^2 = 52.4$, $df = 3$, $P = 2.46E-11$; Fig. 4b, lichen mounds: Cheesebox: $\chi^2 = 52.4$, $df = 3$, $P = 2.46E-11$; Pothole Point: $\chi^2 = 52.4$, $df = 3$, $P = 2.46E-11$; BTR: $\chi^2 = 39.6$, $df = 3$, $P = 1.3E-8$). For both types of mounds, the 4th level (136° – 180°) received the overwhelming majority of observations at each of the 3 sites.

Cyanobacterial Sheath Material

In the split-plot ANOVA, mean sheath-to-substrate ratios differed significantly among the 3 sites ($F_{2,57} = 78.51$, $P < 0.000$). ENE exposure exhibited a significantly higher ratio than did WSW exposure ($F_{2,57} = 18.48$, $P <$

0.000). The interaction between site and exposure was significant ($F_{2,57} = 2.40$, $P = 0.037$; Fig. 5). Subsequent paired t tests demonstrated that average cyanobacterial sheath-to-substrate ratio was greater on the ENE than WSW aspect for 2 of 3 sites (Table 2). The comparison was not significant at the 3rd site, Cheesebox, though the difference lay in the same direction.

Lichen Cover Versus Mound Aspect

As determined by the binomial test, the ENE exposure exhibited greater *Collema* cover than did the WSW exposure (Table 3). We were unable to reject the null hypothesis of equal cover on the 2 opposing aspects for any of the 3 other species examined at Pothole Point (*Psora decipiens*: $\chi^2 = 0.059$, $df = 1$, $P = 0.808$; *Squamarina lentigera*: $\chi^2 = 1.143$, $df = 1$, $P = 0.285$; *Placidium squamulosum*: $\chi^2 = 0.692$, $df = 1$, $P = 0.405$).

Lichen Colonization Events

For pooled non-*Collema* lichens and moss (listed above) at 2 sites, chi-square analysis of colonization events detected significantly more events on the ENE than WSW aspect (BTR: $\chi^2 = 2.37$, $df = 1$, $P = 0.002$; Pothole Point: χ^2

TABLE 1. Differences in mean orientation of cyanobacterial mounds at 3 sites in southeastern Utah. Twenty mounds were sampled at each site.^a

Site 1	Site 2	Mean difference between sites (Site 1–Site 2)	Standard error ^b	P	95% confidence interval	
					Lower bound	Upper bound
BTR	Cheesebox	17.2	5.2	.005	4.6	29.7
BTR	Pothole	5.1	5.2	.601	-7.5	17.6
Pothole	Cheesebox	12.1	5.2	.062	-5	24.7

^aMultiple pairwise comparisons using the Tukey procedure

^bPooled standard error of the mean difference

= 11.21, $df = 1$, $P = 0.0008$). Although the comparison for Cheesebox was in the same direction, the result was not significant ($\chi^2 = 3.07$, $df = 1$, $P = 0.080$). Comparison of the NNW against SSE aspect revealed no significant differences at any site. Our ability to detect strong patterns in the NNW versus SSE comparison may have been reduced due to the very small surface areas of these exposures (Fig. 2).

DISCUSSION

Mound Formation and Directionality

Pedicellation of soil mounds in microbiotic crusts of southeastern Utah appears to produce distinctive microhabitats to which components of these crusts respond. What factors might account for mound formation and directionality and for variation in microhabitat favorability? To date, no specific studies have focused on the formation of crust-covered mounds, but it is commonly held that both physical and biological forces play a role in the development of mound microtopography (Harper and Marble 1988, West 1990, Metting 1991, Belnap and Gardner 1993, Johansen 1993). West (1990) highlights the physical forces of needle ice and frost-heaving for areas that receive much of their precipitation during cold seasons. Physical forces like wind erosion and deposition may also shape the microtopography of crusts. For example, on the Colorado Plateau, where predominant winds are from the west (NW in cooler seasons and SW in warmer months), we noted that our soil mounds often gave the appearance of being heavily eroded or “sand-blasted” on their west-ern exposures.

These physical factors may interact with biotic factors to influence substrate microtopography and microhabitat differentiation, as illustrated, e.g., by soil hummocking beneath

some desert vascular plants. Biotic effects on the microtopography of soil crusts are perhaps best documented by Belnap’s (1993) study of the recovery of intentionally scalped crusts in southeastern Utah. There, plots inoculated with scalped material developed greater pedicellation more quickly than did plots receiving no inoculum. Substrate binding properties of the predominant cyanobacterium, *M. vaginatus*, almost certainly play a major role in determining microtopography of crusts (Harper and Marble 1988, Metting 1991, Belnap 1993, Belnap and Gardner 1993, Johansen 1993, etc.). Using electron microscopy, Belnap and Gardner (1993) demonstrated the effectiveness with which soil is bound by *M. vaginatus*. By growing prolifically inside an envelope of secreted polysaccharide and leaving this material behind as dry sheath, *M. vaginatus* cements the upper mound surface into less erodible aggregates of substrate (Harper and Marble 1988, Belnap and Gardner 1993, Johansen 1993). Cementation, coupled with physical processes like erosion (see above), substrate deposition, and frost-heaving (e.g., Cole 1990), has been suggested as the reason for the rugose microtopography of soil crusts (Metting 1991, Johansen 1993).

Interactive effects of physical and biological factors in mound formation likely vary with mound aspect, due to a combination of wind directionality and microhabitat effects on the growth of microorganisms (see below). Winds may deposit sediments differentially on the windward (westerly) exposures, possibly covering slow-growing lichens (D. Davidson and colleagues unpublished data). Alternatively, or in addition, they may erode lichens or prevent their colonization and establishment. If such moisture differentials exist, they could contribute to better performances of *M. vaginatus* and *Collema* on ENE than WSW exposures of soil mounds. We discuss determinants for these performance differences below and note here

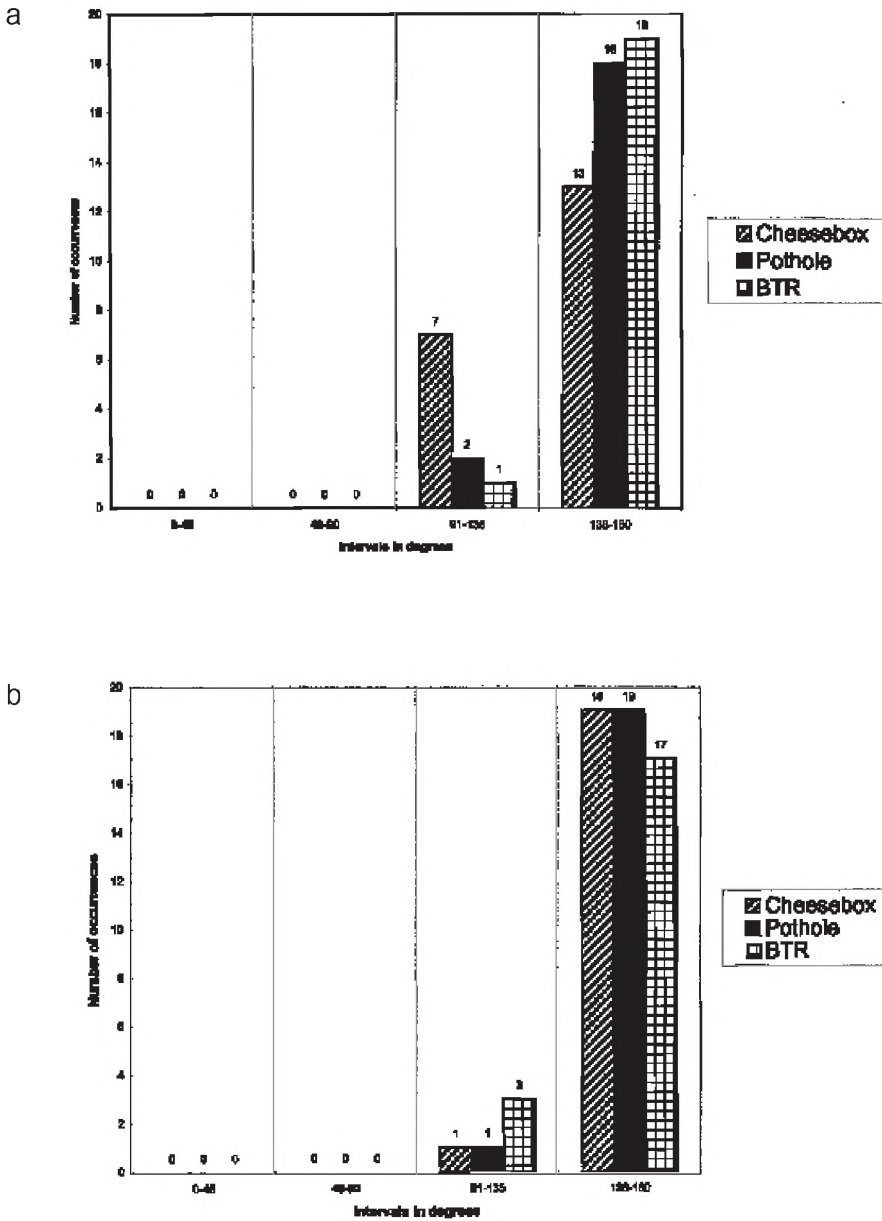


Fig. 4. Orientations of elliptical soil mounds dominated by cyanobacteria (a) and *Collema* spp. lichen (b) in microbiotic crusts at 3 sites on the Colorado Plateau in southeastern Utah. Histograms depict numbers of observations falling into each of 4 equal compass intervals between 0 and 180 degrees.

only that stronger performances of cyanobacteria and lichens on ENE mound exposures could produce greater substrate binding and perhaps nutrient binding on those exposures. Ultimately, this combination of physical and biological processes could produce elongation along the NNW–SSE axis.

Responses of Microorganisms to Mound Microhabitats

Some constituent species of the crust appear to respond to microtopography typical of crusts on the Colorado Plateau. As evidenced by measures of cyanobacterial material and lichen cover, respectively, early successional

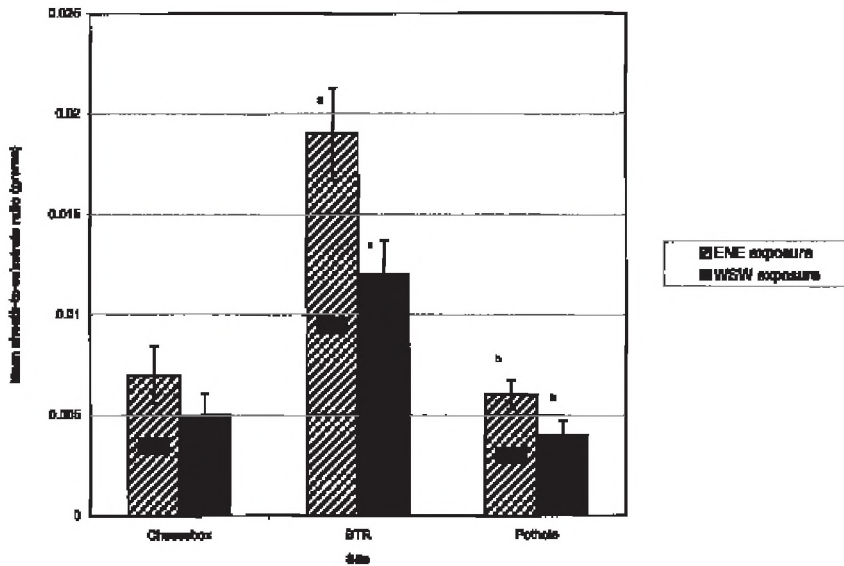


Fig. 5. Mean sheath-to-substrate ratios for ENE and WSW exposures of soil crust mounds at 3 sites on the Colorado Plateau. Vertical bars represent standard errors of the mean sheath-to-substrate ratios. The same letter above 2 columns indicates a statistically significant difference.

cyanobacteria and *Collema* spp. lichens exhibited greater growth and/or higher survivorship on ENE mound aspects than on WSW exposures. (Although dormancy during unfavorable conditions might limit mortality due to some factors, e.g., drought, differential erosion on the 2 sides [see below] could affect survivorship.) In addition, both *Collema* spp. lichens and later successional lichens and mosses colonized with greater frequencies on the former than on the latter mound aspect.

In contrast, cover by non-*Collema* lichens was not disproportionately high on ENE mound faces, and we can only speculate as to why. First, it is possible that differences are artifacts of disparities in sample size ($N = 60$ for *Collema* spp. and just 20 for each of the other lichen species), which influences the statistical power of the test. If differences are real, one possible explanation is that these later successional species colonize after the environment has been substantially altered in ways that diminish distinctiveness of microhabitat on ENE and WSW mound exposures. For example, although *Collema* spp. might grow more rapidly on ENE faces due to greater representation of soil-stabilizing and/or moisture-enhancing cyanobacteria there, soil stability and moisture may not vary significantly as a function of

mound exposure once *Collema* spp. have colonized all mound faces. That is, erosion of mounds by predominantly southwest winds may be less important later in succession.

An alternative explanation may involve differences in physical conditions favoring photosynthesis by gelatinous cyanolichens (i.e., *Collema* spp.) and green-algal lichens included in our study. These 2 types of lichen appear to specialize in using different moisture sources, the distribution of which varies seasonally in different ways (Lange et al. 1998, Lange in press). The very high compensation points of the gelatinous cyanolichens in the genus *Collema* leave them poorly adapted to use water vapor or dew (even if available) as a source of moisture for photosynthesis. In addition, their relatively high optimal temperatures for photosynthesis make it unlikely that they benefit significantly from moisture made available from snowmelt. Lange et al. (1998) consider these lichens to be "extreme-sun" species, limited in their geographic distributions to areas where sufficient moisture is available from summer rain showers. Although *Collema* lichens respond more slowly to summer storms than do green-algal species, due in large part to a depression in photosynthesis at high degrees of hydration, they are able to

TABLE 2. Comparison of sheath-to-substrate ratios for ENE and WSW exposures of cyanobacterial mounds at 3 sites in southeastern Utah.^a

Site	<i>t</i>	df	<i>P</i> -value (1-tailed)	Mean difference (ENE–WSW)	95% confidence interval of the difference	
					Lower	Upper
Cheesebox	1.346	19	.0971	1.73E-03	–9.60E-04	4.42E-03
BTR	3.166	19	.0025	6.95E-03	2.36E-03	1.16E-02
Pothole Point	2.958	19	.0040	2.29E-03	6.69E-04	3.90E-03

^aOne-sample *t* tests were used on paired data (ENE vs. WSW).

store more water. Larger storage capacity makes moisture available over longer time periods. Monsoonal summer showers on the Colorado Plateau tend to occur during afternoons, and ENE mound exposures would be somewhat shielded from direct sunlight at this time. Given these 2 facts, our data are consistent with the hypothesis that *Collema* spp. are able to store and use water over longer time periods on ENE faces of the mounds. Some stored moisture may even allow photosynthesis the following morning, when direct irradiation on ENE mound exposures would provide sufficient photosynthetic photon flux density (PPFD—a measure of light intensity in photosynthetic wavelengths) to fund the unusually high rates of photosynthesis of which *Collema* species are capable (Lange et al. 1998). Both temperature optima and light requirements of *Collema tenax* are much higher than those of green-algal species with which it coexists.

In contrast to gelatinous, cyanobacterial *Collema* lichens, green-algal species, such as the 3 examined in our study, tend to lose moisture more quickly after rainfall. However, they are better able to use dew and water vapor as a moisture source, and their lower temperature optima for photosynthesis may enable them to benefit more than do *Collema* spp. from snowmelt during winter (Lange et al. 1998). Also, unlike gelatinous species, green-algal species do not suffer a depression of photosynthesis at high levels of hydration. This fact, coupled with rapid dry down after wetting, might mean that they benefit only briefly from summer monsoonal storms. Also, with photosynthesis saturating at lower levels of PPFD than in *Collema* spp., gross photosynthesis, and perhaps also net photosynthesis, might be more or less equivalent on ENE and WSW mound faces. Winter frontal rains are less well correlated than are convective sum-

mer thunderstorms with time of day, and the same may be true of snowmelt. Thus, it is difficult to predict whether these moisture sources might affect growth differentially on the 2 mound exposures. Finally, dew and water vapor are not likely to be important water sources for lichens on the arid Colorado Plateau (Lange et al. 1998). In summary, physiological constraints of moisture acquisition for gelatinous cyanolichens may subject them more strongly to abiotic selective regimes imposed by different mound exposures. In addition, the greater diversity of seasonal water sources used by green-algal species may make it less likely that these lichens will exhibit the same patterns as do *Collema* species in their relative abundances across mound faces.

Site-specific Differences

Data from the Cheesebox site stood out in a number of ways from those for the other 2 sites. First, although orientation of cyanobacterial mounds was nonrandom at all sites, mean mound orientation differed significantly between Cheesebox and BTR and marginally between Cheesebox and Pothole Point (Table 1, Fig. 3), but not between BTR and Pothole Point. This was so despite no differences among sites in orientations of lichen mounds. Second, only at Cheesebox did compass orientations of cyanobacterial mounds differ from those of lichen mounds. Because lichens colonize later in succession than do cyanobacteria (Johansen et al. 1984, Belnap 1993), cyanobacterial mounds should be younger than lichen mounds on average. If one assumes that directionality of mounds develops gradually over time since disturbance, the most parsimonious and plausible explanation for the discrepancies between cyanobacterial mounds and lichen mounds at Cheesebox would be more recent and/or locally intense disturbance there than at the

TABLE 3. Comparison of relative cover of the *Collema* spp. lichens on ENE and WSW exposures of mounds at 3 sites in southeastern Utah.^a

Exposure	N	Observed prop.	Test prop.	P < (2-tailed)
WSW	11	.22	.50	.000
ENE	39	.78		
Total	50	1.00		

^aAs determined by a binomial test

other 2 sites. We noticed that the Cheesebox area was visually more disturbed than were the other sites. Situated 100–200 m from a major highway, our study area lies near a vehicle pull-off area that is frequented by campers and hikers. In contrast, study sites at Pothole Point and BTR were potentially more protected from disturbance, as consequences of national park status and remoteness, respectively.

If mounds are indeed younger on average at Cheesebox, this, coupled with the slightly different compass orientation of mounds, might help explain 2 other distinctions in data from this site. Although both lichen colonization events and cyanobacterial sheath material were better represented on ENE than WSW exposures at all sites, patterns were not significant at Cheesebox. Early in mound formation, differential representation of cyanobacterial fiber on ENE and WSW exposures may not yet have had an opportunity to develop. Moreover, in comparing both cyanobacterial sheath material and lichen colonization events, we sampled mounds oriented in the “typical” direction at each site. Since the “typical” direction differed slightly between Cheesebox and the other sites, so did exposures on which we sampled. If organisms responded to these subtle differences in exposure, this could have affected the results of our comparisons.

If interpretations given here are correct (and they do need to be verified by explicit tests), several of our results may be useful in evaluating disturbance histories of soil crusts. Across areas with similar climates and exposures, more recent and more frequent disturbances should be associated with greater disparities in orientations of cyanobacterial and *Collema* mounds, and less pronounced discrepancies in both lichen colonization events and cyanobacterial sheath-to-substrate ratios on opposing long sides of mounds.

SUMMARY

In summary, specific microhabitats created by topography of soil mounds appear to be particularly conducive to prolific growth of *M. vaginatus* and to subsequent lichen recruitment. Relatively slow rates at which mounds form may thus help explain why disturbed and experimentally scalped crusts take so long to recover. Increased understanding of determinants of mound building and mound orientation, as well as effects of microhabitat variation on growth and recruitment of cyanobacteria and lichens, may suggest ways to assist natural regeneration of crusts. Microtopographic patterns in recruitment and growth of microorganisms across mound microhabitats may also prove useful in interpreting biogeographical distributions of component species in soil crusts across landscapes and biogeographic regions.

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