The influence of biological soil crusts on mineral uptake by associated vascular plants

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Soil surfaces dominated by cyanobacteria and cyanolichens (such as *Collema* sp.) are widespread in deserts of the world. The influence of these biological soil crusts on the uptake of bioessential elements is reported for the first time for six seed plants of the deserts of Utah. This sample almost doubles the number of species for which the influence of biological soil crusts on mineral uptake of associated vascular plants is known. These new case studies, and others previously published, demonstrate that cyanobacterial or cyanobacteria-*Collema* crusts significantly alter uptake by plants of many bioessential elements. In studies now available, these crusts always increase the N content of associated seed plants. Uptake of Cu, K, Mg, and Zn is usually (>70% of reported cases) increased in the presence of the biological soil crusts. Soil crusts are generally negatively associated with Fe and P levels in associated seed plant tissue, while plant tissue levels of Ca, Mn, and Na are positively as often as negatively associated with the presence of soil crusts. Increases in bioessential elements in vascular plant tissue from biologically-crusted areas are greatest for short-lived herbs that are rooted primarily within the surface soil, the horizon most influenced by crustal organisms. The mineral content of a deeply rooted shrub (*Coleogyne ramosissima*) was less influenced by co-occurrence of biological soil crusts.

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Introduction

Many studies document the regular occurrence of cyanobacteria and cyanolichens in the deserts of the earth. These organisms, along with mosses, microfungi, green algae and bacteria, often form a dense biological crust on soil surfaces where mechanical disturbances are infrequent or light (Friedmann & Galun, 1974; Anderson & Rushforth, 1976; Harper & Marble, 1988; West, 1990). Available data demonstrate that the presence of such biological soil crusts (also called cryptobiotic, microbiotic, or cryptogamic soil crusts) are correlated with major alterations in the inorganic chemistry of surface soils (Shields & Durrell, 1964; MacGregor & Johnson, 1971; Harper & Pendleton, 1993; Belnap, 1995; Pendleton & Warren, 1995). Recent studies show that such alterations in

surface soil chemistry are correlated with significant changes in the content of bioessential elements in the tissue of associated seed plants (Belnap & Harper, 1995; Harper & Pendleton, 1993; Pendleton & Warren, 1995). In many of the reported cases, elements of critical importance to herbivorous animals are enhanced in plants growing in desert soils that support well-developed biological soil crusts (Harper & Pendleton, 1993; Pendleton & Warren, 1995).

In this paper, we present data on the correlation between the presence of cyanobacteria-*Collema* crusts and the bioessential mineral content of six desert plants not previously reported. We also summarize data from other published studies to present a generalized view of how the presence of biological soil crusts is correlated with the mineral contents of desert plants.

Methods

Our data are primarily from native plants of the deserts of south-eastern Utah (Colorado Plateau region), U.S.A. Sites were within Arches and Canyonlands National Parks at an elevation of 1700–1750 m. Annual rainfall is 215 mm, with 35% falling during the summer. Soils are relatively deep (>1 m) Rizzo sandy loams (Ustollic Calciorthids). Control plants grew beyond fences erected to prevent trampling by park visitors. Biological soil crusts in this study area were heavily dominated by the cyanobacterium *Microcoleus vaginatus*. The nitrogen-fixing lichen *Collema* contributed from 0 to 20% cover in the area. Treatment plants grew only a few meters away in an area where human trampling had destroyed the biological surface crusts. Soil chemistry at the site has been reported by Belnap & Harper (1995). Plants were collected in mid-flowering stage. Plant tissue collected at Arches included the current year's growth of mature *Coleogyne ramosissima* shrubs, *Coleogyne* seedlings emerging from rodent seed caches scattered around the mature plants, and the perennial bunchgrass *Stipa hymenoides*. Tissue of the herbs *Streptanthella longirostris* and *Lepidium montanum* var. *jonesii* tissue was collected from nearby Canyonlands National Park, Grand County, Utah. Soils and environment at the Canyonlands site are closely similar to those at the Arches National Park study site.

Table 1. *Sample site, sample size, and analytical laboratory for different plant taxa*

Plant taxon	Collection site	Sample size		Analytical lab
		Control	Treatment	
Brassica rapa	Greenhouse, BYU	10	10	BYU†
Coleogyne ramosissima				
Seedlings	Arches NP‡	8	8	BYU
Adults	Arches NP	10	10	BYU
Lepidium montanum				
var. *jonesii*	Canyonlands NP¶	11	11	BYU
var. *montanum*§	CFC, Utah Co.**	11	11	UCLA, MS††
Stipa hymenoides	Arches NP	5	5	BYU

*Brigham Young University, Provo, Utah, under conditions identical to those reported for *Sorghum halepense* in Harper and Pendleton (1993).
†Soil and Plant Analysis Laboratory, Department of Agronomy and Horticulture, BYU.
‡Arches National Park, Grand County, Utah.
§Basic data from Marble (1990).
¶Canyonlands National Park, San Juan County, Utah.
**Camp Floyd Cemetery, Utah County, Utah.
††University of California Los Angeles, Medical School, Laboratories of Dr Arthur Wallace.

Another taxon (*Lepidium montanum* var. *montanum*) was collected from fine-textured, ancient lake sediments (Woodrow silt loam, a Xeric Torrifluvent) in Utah County, north-central Utah. Control plants were from unmodified soils, while soil crusts were removed (top 2 cm soil) within a 2·0-dm radius around treatment plants that were interspersed among the control plants. Crusts were removed 3 months prior to the time of rapid elongation of flowering stems from winter rosettes of this biennial plant. The chemical data for this taxon were initially reported by Marble (1990).

In addition, two non-native species (*Brassica rapa* and *Sorghum halepense*) were greenhouse-grown in Rizzo sandy loam soil taken from Sand Flats, Grand County, Utah, U.S.A. One source area supported a dense cover of the cyanobacterium *Microcoleus vaginatus* intermixed with about 30% cover of the cyanolichen *Collema tenax*. Another soil collection was taken from a site only a few dm away, where wind-borne sediment deposition precluded the growth of crustal organisms. *Brassica* and *Sorghum* were grown in pots on soils enriched by the cyanobacteria-cyanolichen crust growth or on the same soil uninfluenced by crust organisms. Experimental details are reported in Harper & Pendleton (1993), who also reported plant tissue chemistry for *Sorghum*.

Tissue and soil analyses were performed by the Soil-Plant Analysis Laboratory, Department of Agronomy and Horticulture, Brigham Young University. Soil and plant tissue samples were prepared and analysed as described in Harper & Pendleton (1993). Plant nomenclature follows Welsh *et al.* (1993).

Sample size and other descriptive information for the various plant taxa reported in this paper are given in Table 1. Differences between treatment and control means for any bioessential element in tissue of each plant taxon were determined using an unpaired *t*-test, since the strict criteria for paired *t*-tests could not be fully satisfied by our sample design (Snedecor & Cochran, 1967). Differences were declared significantly different when probability values were $p < 0.05$. Principal components analyses (PCA), based on content of the 10 bioessential elements in control and treatment tissue samples, were performed for several of the plant taxa using procedures described by Pielou (1984). The PCA provided a multivariate test that simultaneously evaluated the effect of biological soil crusts on the uptake of all bioessential elements by associated vascular plants.

Results

Elemental composition of six plant taxa (with two age classes for *Coleogyne*) is presented in Table 2. A total of 67 significance tests were possible for plants growing in crusted soils *vs.* uncrusted soils. If soil crusts have no significant influence (either positive or negative) on uptake of the 10 bioessential elements considered, chance alone would result in 3–4 differences exceeding the 0·05 probability level in a sample of 67 tests. However, results show 30 significant differences among the 67 individual tests performed. Such a large departure from random expectations demonstrates that the presence of cyanobacteria-*Collema* soil crusts is significantly correlated with the uptake of bioessential elements by associated vascular plants ($p < 0.001$, summation Chi-square = 242·3).

The strong influence of biological soil crusts on mineral uptake of associated seed plants can also be demonstrated using centered, standardized principal component analyses (PCA) based on the relative amounts of the 10 elements in control and treatment tissue samples for each plant taxon. Principal component analyses showed all taxa studied to have samples well separated in statistical space. A typical separation is shown in Fig. 1 for seedling tissue of the shrub *C. ramosissima*. The PCA results demonstrate further that the soil crusts significantly alter uptake of the 10 bioessential elements by the associated seed plants considered in these studies.

Table 2. *Elemental content of vascular plant tissue*

Element	Substrate	Shrub		Forb				Grass
		CORA seedlings	CORA adults	BRRA adults	LEMOJO adults	LEMOMO adults	STLO adults	STHY adults
Ca %	No Crust	0·88	3·13	2·98	0·62	1·17	1·16	1·42
	Crust	0·86	3·19	2·44★	0·64	1·41	1·80★★	1·00★★
K %	No Crust	1·19	0·80	1·72	2·19	3·03	1·49	1·50
	Crust	0·86★★	0·78	1·43★★	2·26★	4·15★	2·06★★	2·01★
Mg %	No Crust	0·49	0·41	0·45	0·29	0·34	0·20	0·14
	Crust	0·46	0·43	0·34★★	0·26★	0·43	0·25★★	0·14
N %	No Crust	5·60	0·98	NM	1·29	1·42	1·44	1·99
	Crust	5·83	1·07	1·24	1·41★	1·58	2·09★★	2·30★★
P %	No Crust	0·55	0·11	0·35	0·07	0·25	0·28	0·24
	Crust	0·69★	0·11	0·23★★	0·08★	0·28	0·27	0·13★★
Cu ppm	No Crust	13·80	4·00	4·80	8·60	3·08	5·80	8·60
	Crust	15·00★	4·00	3·80	8·80	6·33★	7·20★	9·10
Fe ppm	No Crust	765·40	138·60	66·60	29·70	474·10	419·20	130·40
	Crust	646·90	84·60★★	60·50	27·60	772·70	222·40★	117·90
Mn ppm	No Crust	0·49	0·41	119·10	49·50	52·50	28·80	24·20
	Crust	0·46	0·43	163·90★★	47·10★	102·50	25·00	71·90★★
Na ppm	No Crust	61·50	8·40	28·50	51·30	161·00	NM	NM
	Crust	69·80	9·20	22·50	50·70	281·00★	NM	NM
Zn ppm	No Crust	51·10	13·00	829·70	24·80	12·20	20·20	7·70
	Crust	74·10★★	11·20	917·10	23·90	15·20	19·80	12·60★

CORA = *Coleogyne ramosissima*, BRRA = *Brassica rapa*, LEMOJO = *Lepidum montanum* var. *jonesii*, LEMOMO = *L. montanum* var. *montanum*, STLO = *Streptanthella longirostris*, STHY = *Stipa hymenoides*. For adult CORA, leaves and current year twigs were analysed. For LEMOJO and STHY leaves were analysed. For BRRA, LEMOMA, and STLO, roots, stems and leaves were analysed. Crusted and uncrusted soils were separated by more than a 4·0 m linear distance. Sites were similar in soil type, aspect and vascular plant cover. ★ = $p < 0.05$, ★★ = $p < 0.01$. NM = not measured.
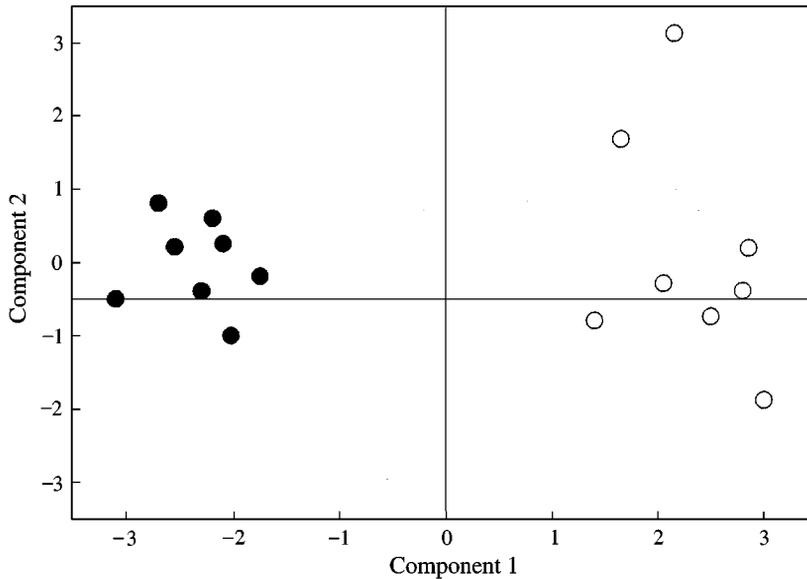
Figure 1. Principal component analysis of the influence of cyanobacteria and cyanolichens on tissue elemental composition of *Coleogyne ramosissima* seedlings. Without biological soil crust (●); with biological soil crusts (○).

The influence of cyanobacterial-*Collema* soil crusts on chemical composition of tissue of seed plants is summarized for all known studies and for 10 essential elements in Table 3. For tissue content of N and P, a total of 14 or 15 different trials were available for analysis. The results show that soil crusts enhanced N content of associated seed plants in every one of the 14 trials available: 11 of those differences were statistically significant. In contrast, results for P show that seed plants associated with biological surface crusts had reduced tissue P as often as they have enhanced levels (15 trials available).

Eight to ten trials are available for analysis of the influence of biological soil crusts on tissue content of the other eight bioessential elements (i.e., Ca, Mg, K, Cu, Fe, Mn, Na, and Zn; Table 3). The presence of soil crusts was usually associated with enhanced plant tissue levels of K, Cu, and Zn. Elemental tissue content was greater in plants growing in crusted soils at least 70% of the reported trials, but only about half of those differences were statistically significant.

Tissue content of Fe was reduced 70% of the time (10 trials available for comparison) in seed plants grown in soils that supported soil crusts, but half of those decreases fell short of statistical significance (Table 3). Sodium uptake by plants grown in soil with soil crusts was often increased (63% of the time) relative to soils without soil crusts but, again, most of the differences were not statistically significant and the sample size is small ($n = 8$). Content of Ca, Mg, and Mn in tissue of seed plants grown in crusted soils show no consistent differences from control plants (Table 3).

The results summarized in Table 3 strengthen patterns observed for our data presented in Table 2. A total of 107 trials are summarized in Table 3. Assuming that the presence of biological soil surfaces is not correlated with elemental uptake of associated seed plants, one would expect only 5–6 of the control *vs.* treatment differences to differ significantly by chance (at the probability level of 0·05). However, Table 3 shows 53 statistically significant differences (37 positive and 16 negative) and 54 differences that do not differ significantly (at the $p = 0·05$ level). This result is

Table 3. *Summary of the influence of cyanobacterial-dominated soil-surface crusts on uptake of essential elements by associated seed plants from all known publications. Responses are grouped into four categories: 1) positive effects that are statistically significant at the < 0·05 level of probability, 2) positive effects not significant at that level, 3) negative effects not significant at that level, and 4) negative effects significant at that level*

Response	Significance	Source of data	No. taxa studied	Bioessential element									
				Ca	Mg	N	P	K	Cu	Fe	Mn	Na	Zn
Positive	yes	This study	7	1	1	3★	2	4	3	0	2	1	2
Positive	no			3	3	3	2	0	3	1	2	2	2
Negative	yes			2	2	0	2	2	0	2	1	0	0
Negative	no			1	1	0	1	1	1	4	2	2	3
Positive	yes	Belnap & Harper (1995)	2	1	2	2	1	1	0	2	0	1	0
Positive	no			1	0	0	0	1	1	0	1	1	2
Negative	yes			0	0	0	1	0	0	0	0	0	0
Negative	no			0	0	0	0	0	1	0	1	0	0
Positive	yes	Harper & Pendleton (1995)	1	0	0	1	0	0	1	0	0	0	1
Positive	no			0	0	0	0	1	0	0	0	0	0
Negative	no			0	1	0	0	0	0	1	0	0	0
Negative	yes			1	0	0	1	0	0	0	1	1	0
Positive	yes	Pendleton & Warren (1995)	5			5	0						
Positive	no			N/A†	N/A	0	2	N/A	N/A	N/A	N/A	N/A	N/A
Negative	no					0	2						
Negative	yes					0	1						
Summary		Sample size		10	10	14	15	10	10	10	10	8	10

★Tissue limitations precluded analysis for N for 1 sample.
†No analyses made for elements marked N/A.

a highly significant departure from random expectations ($p < 0.001$, summation Chi-square $= 529.2$, df. $= 2$).

It is also of biological interest to ask whether the statistically significant differences in plant tissue observed in Table 3 are randomly distributed between positive and negative responses between plants from biologically-crusted soils versus non-crusted control soils. A Chi-square evaluation of that question (e.g. are 37 significant positive responses significantly more frequent than 16 significant negative responses?) yields a Chi-square value of 8.32 (df. $= 1$). That result has a probability of < 0.01 of occurring by chance alone. Thus, we conclude that the presence of biological soil crusts is positively associated with uptake of different essential elements by seed plants at a rate greater than expected by chance.

Discussion

This study demonstrates that the presence of biological soil crusts is associated with significantly different elemental levels in associated vascular plant tissue. A similar result has been reported by all authors previously testing this hypothesis (Harper & Pendleton, 1993; Belnap & Harper, 1995; Pendleton & Warren, 1995). These studies report on the relationship between soil crusts and vascular plant nutrition using comparisons of crusted and uncrusted soil surfaces under a variety of circumstances that span different years (and thus different soil nutrient and moisture conditions) and different treatments, including several different trampled sites (this study, Harper & Pendleton, 1993; Belnap & Harper, 1995), sites covered with blowing sand (thus precluding crust development) (Belnap & Harper, 1995), and in greenhouse studies (Harper & Pendleton, 1993; Pendleton & Warren, 1995). Thus, the observed effect of crusts on vascular plant nutrition appears independent of changes in soil conditions that could be associated with any given disturbance (e.g. compaction, moisture, temperature, nutrient levels) or plant growth stage.

One can postulate reasonable explanations for negative and positive influences of biological soil crusts on the uptake of essential elements by associated seed plants. Negative effects may be related to competition between the soil crust organisms and the roots of seed plants for bioessential elements. Significant negative influences of soil crusts on ion uptake by seed plants occur for Fe, Mn, Na, P, and Zn (Table 3). Since all of these elements are often in short supply in calcareous, sandy soils (Black, 1968) such as those reported here, it is reasonable to believe that micro-organisms of the surface crusts may compete with vascular plant roots for these elements under certain conditions. This competitive effect is expected to be most severe for small, short-lived (especially annual) plants that root heavily near the soil surface, the area most influenced by the biological soil crust organisms. We have observed that many desert plants produce hair-like feeder roots in the surface 2 cm of soil in seasons of abundant rainfall (Belnap & Harper, 1995). Such roots could scarcely escape competition for bioessential elements with organisms of the microbiotic surface crusts.

Biological growth on soil surfaces may also exert positive influence on uptake of essential elements in a variety of ways. Crusted soil. surfaces often have a greater silt/clay fraction than uncrusted soils (Danin, 1976; Anderson et al., 1982; Verrecchia et al., 1995); thus exchangeable bases and P could be expected to be higher in crusted areas (Black, 1968). Clay particles stick to the mucilaginous sheath material, especially when wet (Belnap & Gardner, 1993). Both materials are negatively-charged and bind positively-charged plant nutrients, thus increasing soil fertility (Black, 1968). Cyanolichens and many soil cyanobacteria are known to fix atmospheric nitrogen. Up to 70% of the nitrogen fixed is released immediately into the surrounding soil environment, and is available to associated organisms including vascular plants, mosses, fungi, and other microbes (Mayland & MacIntosh, 1966; Stewart, 1967). Multiple studies have reported

that the presence of soil crusts increase surrounding soil N by up to 200% (Shields & Durrell, 1964; Jeffries & Klopatek, 1987; Rogers & Burns, 1994; DeFalco, 1995). Data in Tables 2 and 3 show that nitrogen is consistently higher in shallow-rooted seed plants associated with biological crusts.

In addition, all crustal organisms secrete extracellular polymers. In cyanobacteria, these secretion can represent up to 50% of total fixed carbon (Lewin, 1956; Fogg, 1966). As a result, presence of soil crust organisms increase soil polysaccharides and total carbon by up to 300% (Rao & Burns, 1990; Rogers & Burns, 1994), thus benefitting soil heterotrophs that are often carbon-limited in desert soils. Additions of N can be expected to increase decomposition rates, thus enhancing the flow of essential nutrients to associated organisms (Ingham et al., 1985).

Microbial exopolymers not only add carbon to soils; they also modulate metal-ion concentrations at the microbial cell surface by providing both cationic and anionic metal binding sites that differ in affinity and specificity (Greene & Darnall, 1990). Under natural conditions, most of the polymers act as polyanions that can attract growth-promoting nutrients sometime present at low concentrations in the surrounding environment (such as Na, K, Mg, Ca, Mn, Fe, Ni, Cu, and Zn) (Lange, 1976; Geesey & Jang, 1990).

External soil factors also influence the binding properties of microbial exopolymers. In soils above pH 7 (true for most desert soils), cation exchange capacity is significantly increased by all microbial species (Gadd, 1990a; Pirszel et al., 1995). Polysaccharide production can be simulated by soil Mg, K, and Ca. In turn, more polysaccharides result in greater availability of these same nutrients. Also, inorganic compounds may bind to crustal organisms (e.g., sulphides of copper, Zn, Pb, zinc dust, magnesic oxide and ferric hydroxide) (Lange, 1974; Gadd, 1990b; McLean & Beveridge, 1990). Most adsorbed metals stay on or within the extracellular sheath and are not absorbed by the microbial cells, but they do remain available to vascular plants (Geesey & Jang, 1990).

Cyanobacteria (including the common soil genera *Anabaena*, *Anacystis*, *Lyngbya*, and *Nostoc* found in the soils considered in this study) green algae, fungi, and bacteria secrete powerful metal chelators such as siderochromes (Lange, 1974; McLean & Beveridge, 1990) that maintain metals in a biologically-available form. They effectively sequester essential trace metals (in available form) from environments in which the metals occur at exceedingly low ambient concentrations (Paerl, 1988). This is especially important in soils of high pH (as in many deserts). Cyanobacteria also secrete peptide nitrogen and riboflavin. Together with siderochromes, these substances form complexes with tricalcium phosphate, Cu, Zn, Ni, and ferric iron, keeping them plant-available. These chelators are water soluble and capable of being translocated in soil. Consequently, chelated compounds enhance nutrient availability to associated, non-chelating plants or microbes (Bose et al., 1971; Gadd, 1990a; Geesey & Jang, 1990; Lange, 1974).

Cyanobacteria also secrete other compounds that can influence vascular plant growth. Glycollate is a common extracellular product. Secretion of glycollate is increased at low cyanobacterial cell density (as in soils) and when cyanobacteria are alternately exposed to low and high light intensities, as on partly cloudy days. Glycollate stimulates uptake of phosphate (Fogg, 1966). In addition, cyanobacteria secrete various vitamins (e.g., B_{12}), auxin-like compounds, and other substances that promote growth and cell division in plant and animal tissue (Fogg, 1966, Venkataraman & Neelakantan, 1967).

Harper & Pendleton (1993) showed a strong positive correlation between mycorrhizal infections of roots of four seed plant species (in three different families) and greater plant size on soils that supported well-developed biological soil crusts. Others have demonstrated that mycorrhizal-root symbioses enhance uptake of P and several other essential minerals (Allen, 1991). In addition, consistent increases in non-chelating biogenic mineral elements in crusted soils and associated plants suggest that mycorrhizal fungi associated with crusts may be involved in observed increases in uptake of those elements by associated seed plants (Harper & Pendleton, 1993; Belnap & Harper, 1995).

All studies, including the present study, show that the content of bioessential elements in associated seed plants is enhanced more often than reduced when plants grow on biologically-crusted soils (Harper & Pendleton, 1993; Belnap & Harper, 1995; Pendleton & Warren, 1995). Such enhanced nutrient uptake is expected to have positive effects on establishment and growth of some plants, as well as on quality of forage provided to associated animals. Belnap (1995) and Harper & Pendleton (1993) refer to several cases in which plant size and survival were shown to be greater on soils that supported well-developed biological crusts. Robbins (1983) suggests that protein content is one of the most critical factors in determination of forage quality for animals. Since our results show that nitrogen content (usually measured as a surrogate for protein content of forage) was consistently greater in plants grown on crusted surfaces, such plants probably provide better quality forage than plants grown on soils without such surfaces. This consideration should be evaluated in light of the probability that anthropogenic disturbances have severely damaged soil crusts on literally millions of hectares of the world's arid and semi-arid wildlands (Harper & Marble, 1988). Such damage may have altered significantly the quality of the forage produced on those lands. If such has occurred, the change has likely had some impact on the nutrition of associated animals, especially small herbivores that are confined to small home-ranges (Harper & Pendleton, 1993).

A variety of research projects are needed before managers can gauge accurately the full role of biological soil crusts in rangeland ecosystems. Available studies show that biological crusts reduce both wind and water erosion (Williams *et al.*, 1995*a,b;* Belnap & Gillette, 1997, 1998). Certainly, these biological crusts increase local biodiversity, a concern that has attracted progressively more attention from managers and the public at large in recent years (Ladyman & Muldavin, 1996). This paper strongly supports the idea that intact, biologically crusted soil surfaces alter significantly the uptake of bioessential minerals by associated vascular plants. Thus the quality of forage available to animals endemic to ecosystems having depleted biological soil crusts may be adversely affected. More case studies of such relationships are needed from a wide cross-section of the world's arid and semi-arid rangelands.

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