Arid Land Research and Management 17: 271–281, 2003

ISSN: 1532-4982 print/1532-4990 online
DOI: 10.1080/15324980390191627

Growth and Nutrient Content of Herbaceous Seedlings Associated with Biological Soil Crusts

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Biological soil crusts of arid and semiarid lands contribute significantly to ecosystem stability by means of soil stabilization, nitrogen fixation, and improved growth and establishment of vascular plant species. In this study, we examined growth and nutrient content of Bromus tectorum, Elymus elymoides, Gaillardia pulchella, *and* Sphaeralcea munroana *grown in soil amended with one of three levels of biological soil crust material: (1) a low-fertility sand collected near Moab, Utah; (2) sand amended with a 1-cm top layer of excised soil crust; and (3) crushed crust material. In addition, all plants were inoculated with spores of the arbuscular mycorrhizal fungus,* Glomus intraradices. *Plants were harvested after 10 weeks growth, dried, weighed, and leaves were ground for nutrient analysis. Three aspects of root architecture were also quantified. Soil crust additions significantly affected nearly all variables examined. Both above- and below-ground vegetative biomass were significantly increased in the presence of crust material. Similarly, reproductive tissue of the three species that flowered was greatest in the crushed-crust medium. The effect of soil crust additions is likely due to the increased nitrogen content of the crusts. Nitrogen tissue content of all four species was greatly enhanced in crusted soils. All species showed a decline in root/shoot ratio and specific root length with crust additions, indicating a shift in plant allocation pattern in response to improved soil fertility. These data support other studies suggesting that soil crusts have a positive effect on the establishment and growth of associated vascular plant species.*

Received 15 October 2002; accepted 9 November 2002.

This work was supported by grants MIPR 94N107 and MIPR W2V5AA51113582 from the U.S. Army Corps of Engineers, Construction Engineering Research Laboratory, Champaign, Illinois. Technical assistance was provided by Susan Garvin, Jeff Ott, David Tarkalson, and Cari York. Dr. Larry St. Clair, BYU, provided identification of the soil crust organisms.

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Keywords AMF, arbuscular mycorrhizal fungi, arid lands, *Bromus tectorum*, cryptogamic crusts, *Elymus elymoides, Gaillardia pulchella*, microphytic crusts, nutrient cycling, semiarid lands, *Sphaeralcea munroana*

Biological soil crusts, complex communities composed of cyanobacteria, lichens, green or brown algae, mosses, microfungi and their byproducts, are a common surface feature of arid and semiarid lands throughout the world (West, 1990). While the importance and ecological role of these crusts varies according to their composition (Belnap et al., 2001; Evans & Johansen, 1999), available information indicates that biological soil crusts contribute to a variety of ecological functions, including soil stabilization, nitrogen fixation, nutrient availability, and vascular plant establishment (e.g., Belnap & Gardner, 1993; Belnap & Harper, 1995; Belnap et al., 2001; Harper & Belnap, 2001; Harper & Marble, 1988; Rychert & Skujiņš, 1974; Schulten, 1985; West, 1990; Williams et al., 1995a, 1995b). Harper & Pendleton (1993) present possible mechanisms for enhanced seedling establishment and growth, including increased nutrient content of soil surface layers, higher soil temperatures during early-season growth, and improved availability of essential elements due to chelating compounds present in cyanobacterial sheaths. They also found that plants growing on crusted soils had significantly higher levels of colonization by arbuscular mycorrhizal fungi (AMF).

In this study, we examined the effects of biological crust additions on the growth, mineral content, and root architecture of seedlings of four herbaceous plant species colonized by arbuscular mycorrhizal fungi. Three of the species, *Elymus elymoides* (Raf.) Swezey, *Gaillardia pulchella* Foug., and *Sphaeralcea munroana* (Dougl. ex Lindl.) Spach. ex Gray, are native to semiarid regions of the western United States. The fourth, *Bromus tectorum* L., is an invasive annual weed that is rapidly displacing native vegetation over vast portions of the U.S. west.

Materials and Methods

The experimental design consisted of three soil treatments: (1) sand, (2) crushed crust material, and (3) intact circles of crust material placed over sand. Ten plants of each of four species were grown in each soil treatment for a total of 120 plants. Four western herbaceous plant species, comprised of an introduced annual grass (*Bromus tectorum*; BRTE), a perennial grass (*Elymus elymoides*; ELEL), an annual forb (*Gaillardia pulchella*; GAPU), and a perennial forb (*Sphaeralcea munroana*; SPMU) were used in the experiment. Plant nomenclature follows Kartesz and Meacham (1999). *B. tectorum* seed was collected from the foothill area east of Provo, Utah. *E. elymoides* was collected at the Browse exit of Interstate highway 15 in Washington County, Utah. *S. munroana* seed was collected along Interstate highway 70, 66 km east of Green River, Utah. *G. pulchella* seed was purchased from Granite Seed Company, Lehi, Utah. Seeds were sown 3–4 per cell in 6-celled books ("Ferdinands", Hummert Int., Earth City, Missouri, USA) filled with a steam-sterilized sandy loam from Grand County, Utah. Cells were later thinned to one plant per cell.

Fourteen days following emergence, seedlings were transplanted into 15-cm pots containing one of the three soil treatments. A loose sand of a Rock Outcrop Ustic Torripsamment was collected from between plants at Sand Flats near Moab, Utah, and steam-sterilized at 65°C for one hour. Crust material for the crushed-crust treatment was collected near sandstone outcrops at the same location and thoroughly broken up using a small cement mixer. Intact soil crust 15-cm circles, collected in large petri dishes from Behind-the-Rocks, also near Moab, were placed over the top of the steamed sand to make up the third soil treatment. The crust material used in this experiment was dominated by the cyanobacterium, *Microcoleus vaginatus*, and by the dinitrogen-fixing soil lichen *Collema tenax*. Additional crust components included the soil lichens *Fulgensia fulgens*, *Catapyrenium lachneum*, *Psora decipiens*, *Squamarina lentigera*, and *Buellia elegans*, and moss of the genus *Tortula*. Soil properties of the treatment components are given in Table 1. Pot-cultured mycorrhizal inoculum of *Glomus intraradices* was obtained from Brokaw Nursery in Saticoy, California. Approximately 20 mL of the inoculum (300–700 spores) was added to the root zone of each plant at the time of transplanting.

Plants were maintained in a glasshouse during the summer months of 1993 and harvested at the end of 70 days growth in the treatment soils. Pots were bottom-watered as needed using a capillary matting system fitted with a drip irrigation system (Hummert, Int.). Plants were sprayed three times during the experiment with Cygon 2E systemic insecticide ($2.5\,mL\,L^{-1}$) to control aphid infestation. At harvest, shoots were excised at ground level, dried at 65°C, weighed, and ground for nutrient analysis. Reproductive tissue, when present, was weighed separately. Heights of the two forb species were also recorded at the time of harvest.

Leaf tissue analysis was done by the Soil-Plant Analysis Laboratory, Department of Agronomy and Horticulture, Brigham Young University. Nitrogen content was determined using micro-Kjeldahl procedures (Kane, 1995). Concentration of other bioessential elements was determined using atomic absorption procedures following digestion in concentrated perchloric and nitric acid (Johnson & Ulrich, 1959). Reproductive tissue samples from two or more plants were combined when necessary to make up sufficient material for analysis. Total uptake of minerals by plant shoots was calculated as follows: Total shoot uptake (μg) = [vegetative shoot

TABLE 1 Soil Characteristics for Components of the Three Soil Treatments (Mixed Bulk Samples were Used for Blow Sand and Crushed-Crust Treatments. For the Crust-Over-Sand Treatment, the Mean and Range Representing Five Crust Circles are Given.)

Characteristic	Blow sand	Crushed crust	Crust circles
Reaction (pH)	7.4	7.2	7.2 (7.0–7.5)
Organic matter (mg g^{-1})	4.5	12.3	18.8 (13.7–21.7)
Sodium absorption ratio	0.03	0.08	0.67 (0.46–1.15)
Conductivity (EC, dS m^{-1})	0.72	1.48	1.81 (1.26–2.25)
	mg kg^{-1} "available"		
Ca	184.5	231.0	249.1 (156.5–403.0)
Cu	0.18	0.24	0.45 (0.34–0.58)
Fe	17.10	3.56	3.63 (3.08–4.64)
Mg	15.0	41.5	63.0 (40.5–94.5)
Mn	9.38	10.98	7.24 (6.28–8.46)
NO_3^--N	4.06	79.54	34.62 (8.16–104.23)
P	12.18	7.53	9.81 (6.12–12.45)
K	147.2	108.8	160.6 (102.4–201.6)
Na	1.60	5.12	43.62 (26.56–63.52)
Zn	2.16	0.22	0.47 (0.40–0.54)

biomass (g)] [vegetative tissue concentration ($\mu g\ g^{-1}$)] + [reproductive shoot biomass (g)] [reproductive tissue concentration ($\mu g\ g^{-1}$)].

Roots were washed and fixed in 70% denatured ethanol. Subsequently, roots were picked free of sticks and other debris, dried at 65°C, weighed, and rehydrated in fixative, pending analysis of root architecture and examination for mycorrhizal colonization. Quantification of root architecture proceeded as follows. Roots were cut into 1–2 cm segments and dispersed over a 3-cm grid in a shallow plexiglass tray. Total root length was calculated using a modified line intersect method developed by Tennant (1975). Root diameters of 50 random pieces were measured to the nearest 0.1 mm using an ocular micrometer. Specific root length was calculated as meters root length per gram dry root weight. Mycorrhizal colonization of each plant was confirmed by microscopic examination of root pieces following clearing and staining using the procedure of Koske & Gemma (1989).

Statistical analyses were performed using SAS version 8.1 for personal computers (SAS Institute Inc., 1999–2000). Variables were analyzed separately by species, first using a MANOVA procedure to determine the significance of treatment effect, followed by univariate analyses using a one-way ANOVA or GLM procedure. Mean separations were accomplished using the Student-Newman-Keuls multiple range test. Comparisons were considered significant at $P = 0.05$. Pearson correlation values were attained using the CORR procedure.

Results

Soil treatment had a significant effect on nearly all variables examined (Table 2). Attained significance values for Wilks' lambda from MANOVAs for biomass and root variables were highly significant ($P < 0.0001$) for *G. pulchella, S. munroana*, and *B. tectorum*, and significant ($P = 0.013$) for *E. elymoides*. The addition of microbiotic crust material to the growing medium significantly enhanced growth and biomass production of all four species used in the experiment. *S. munroana* plants grown in the crushed-crust treatment had 6–8 times the plant biomass of plants grown in the other soils. They also had significantly greater measures of shoot biomass, root biomass, and plant height. Flowering of *S. munroana* occurred only in the crushed-crust treatment.

G. pulchella plants grown in the crushed-crust medium had 5–6 times the biomass of plants grown in the other treatments. Measures of shoot biomass, root biomass, and total plant biomass were all significantly greater in crushed crust. Measures of plant height and reproductive biomass were also greatest in the crushed-crust treatment, however, these differences were not significant due to high variability among plants. Unlike *S. munroana*, *G. pulchella* plants bolt prior to flowering and plant height is correlated with the production of reproductive tissue ($r^2 = 0.4337$; $P < 0.0001$). Seven of ten plants had begun flowering in the crushed-crust treatment, as compared with six and five, respectively, for the crust-over-sand and sand treatments.

The crushed-crust soil treatment also significantly increased biomass production of both grass species (Table 2). *E. elymoides* produced 4–8 times the total plant biomass in the crushed-crust treatment as compared with other soils. *B. tectorum* produced 3–7 times as much biomass in the crushed-crust treatment. Shoot and root biomass of both grasses were greatest in the crushed-crust treatment. Crushed-crust *E. elymoides* plants also began flowering much sooner than plants of the other two treatments and produced significantly more reproductive biomass. Very little reproductive tissue had been produced in either of the other two soil treatments by the time of harvest.

Although more modest, significant growth differences also occurred between crust-over-sand and blow-sand treatments (Table 2). Shoot biomass of all four species was significantly greater in the crust-over-sand treatment. Similarly, root

TABLE 2 Means and Attained Significance Values from ANOVAs for Nine Variables (Means Followed by Different Letters are Significantly Different at $P \leq 0.05$ Using the Student-Newman-Keuls Multiple Range Test)

	Plant height (cm)	Shoot biomass (g)	Reproductive biomass (g)	Root biomass (g)	Total plant biomass (g)	Root:shoot ratio	Root diameter (mm)	Root length (m)	Specific root length (m g^{-1})
Sphaeralcea munroana									
Crushed crust	33.45 a	3.91 a	0.30 a	0.86 a	4.77 a	0.21 a	0.23 a	6128 a	7848 a
Crust over sand	4.35 b	0.51 b	0 b	0.29 b	0.80 b	0.57 b	0.25 a	2698 b	9434 b
Sand	2.75 c	0.30 c	0 b	0.25 b	0.55 c	0.84 c	0.21 a	3257 b	13054 c
P value	< 0.0001	< 0.0001	0.0053	< 0.0001	< 0.0001	< 0.0001	0.0897	0.0021	< 0.0001
Gaillardia pulchella									
Crushed crust	30.95 a	4.66 a	0.08 a	1.14 a	5.80 a	0.26 a	0.20 a	10796 a	9622 a
Crust over sand	17.95 a	0.83 b	0.01 a	0.36 b	1.19 b	0.45 b	0.22 a	3989 b	10927 a
Sand	16.60 a	0.62 c	0.03 a	0.31 b	0.93 b	0.51 b	0.24 a	3301 b	10846 a
P value	0.0572	< 0.0001	0.1565	< 0.0001	< 0.0001	< 0.0001	0.0709	< 0.0001	0.3900
Elymus elymoides									
Crushed crust	ND*	1.48 a	0.43 a	0.26 a	1.74 a	0.18 a	0.27 a	2246 a	9731 a
Crust over sand	ND	0.30 b	0 b	0.14 a	0.45 b	0.44 b	0.23 b	1921 a	16442 b
Sand	ND	0.16 c	0 b	0.06 a	0.22 c	0.46 b	0.21 b	1175 a	20997 b
P value	ND	0.0073	0.0207	0.1621	0.0129	0.0051	0.0075	0.5606	0.0137
Bromus tectorum									
Crushed crust	ND	3.19 a	0	0.90 a	4.09 a	0.26 a	0.17 a	13662 a	14496 a
Crust over sand	ND	0.79 b	0	0.40 b	1.19 b	0.54 b	0.14 b	9182 a	24238 b
Sand	ND	0.40 c	0	0.22 c	0.62 c	0.58 b	0.14 b	5571 a	24422 b
P value	ND	0.0004	ND	0.0099	0.0008	< 0.0001	0.0079	0.1439	0.0051

*Not determined

biomass and total plant biomass were greater in the crust-over-sand treatment as compared with the sand treatment. These differences were significant for total biomass in three of the four plant species and for root biomass in *B. tectorum*.

The observed differences in growth and biomass production represent a response to the increased N levels of crusted soils. Percent organic matter, Mg, and NO_3^--N were all substantially higher in the crusted soils (Table 1). The crushed-crust soil contained nearly 20 times the amount of available NO_3^--N as did the sand. The increased amount of N available for plant growth is reflected not only in increased biomass, but in higher tissue concentrations of N (Table 3). For the two forb species, the highest concentration of N occurred in plants grown in the crust-over-sand treatment, followed closely by the crushed-crust treatment. Nitrogen concentrations of grass plants were highest in crushed-crust followed by crust-over-sand. In contrast, tissue concentrations of most other nutrients were lower in crusted soils. Concentrations of Zn, Mn, K, Ca, Mg, and P were, for the most part, lowest in the crushed-crust treatment. *G. pulchella* was exceptional in that the crust-over-sand treatment had the highest tissue concentrations of K, Ca, Mg, and P. Lower concentrations in the crushed-crust treatment indicate that shoot uptake did not keep up with the rapid growth of these plants. Total shoot uptake of plant nutrients (concentration x biomass) was uniformly greatest in the crushed-crust treatment, followed by the crust-over-sand treatment (data not shown). Element concentrations of N, P, K, Ca, and Mg were significantly higher in reproductive tissue than in vegetative tissue, reflecting the importance of these elements in plant reproduction (data not shown).

The relative allocation between root and shoot biomass was also affected by the addition of crust material. Root:shoot ratios of all species decreased with increasing crust additions, indicating that plants invested proportionately fewer resources in root tissue as nutrient availability increased. Root:shoot ratios were significantly lower in the crushed-crust treatment for all four species (Table 2). Root:shoot ratios also tended to be lower in the crust-over-sand treatment as compared with the sand treatment, but was significantly so only for *S. munroana*.

Soil treatment had a significant effect on all three measures of root morphology (Table 2). *S. munroana* plants grown in the crushed-crust medium produced significantly greater root lengths and significantly lower specific root lengths than did plants grown in sand. A similar pattern was observed in the other three species, although these differences were not always significant. Total root length was largely a reflection of root biomass. Correlation coefficients between the two variables ranged from $r^2 = 0.59307$ in *B. tectorum* to $r^2 = 0.84576$ in *E. elymoides*. The slope of all four correlations was highly significant ($P < 0.0001$). In contrast, specific root length is a measure of the relative proportion of fine feeder roots to larger conducting roots. Higher values for specific root length mean a proportionately finer root system. The addition of crust material to the growing medium resulted in smaller values for specific root length, indicating that plants growing in higher nutrient soils invested proportionately less biomass in fine feeder roots. Specific root lengths were significantly lower in the crushed-crust medium for all species but *G. pulchella*. The same trend was observed between the crust-over-sand and sand treatments of both *S. munroana* and *E. elymoides*, although significant only in *S. munroana*. Similarly, root diameter values were significantly larger for the two grass species grown in the crushed-crust treatment.

Bromus tectorum was the only species to have significantly greater root biomass in the crust-over-sand treatment than in the sand treatment. Of particular interest in this regard was the mining of crust nutrients through the production of numerous fine feeder roots that grew up into the crust itself. Biomass of feeder roots within the crust comprised 10.5% of the total root biomass. Root diameters within the crust averaged 0.106 mm as compared with an average diameter of 0.145 mm for roots within the soil zone.

TABLE 3 Means and Attained Significance Values from ANOVAs for Leaf and Stem Element Concentrations (Means Followed by Different Letters are Significantly Different at $P \leq 0.05$ Using the Student-Newman-Keuls Multiple Range Test)

	n	Zn mg kg^{-1}	Fe mg kg^{-1}	Mn mg kg^{-1}	Cu mg kg^{-1}	K mg kg^{-1}	Ca mg kg^{-1}	Mg mg kg^{-1}	N mg g^{-1}	P mg g^{-1}
Sphaeralcea munroana										
Crushed crust	5	32.2 a	58.2 a	412.7 a	5.32 a	1.39 a	2.81 a	0.66 a	23.9 a	2.5 a
Crust over sand	5	42.3 a	41.2 b	362.9 a	5.60 a	2.00 b	2.62 a	0.67 a	24.9 a	6.2 b
Sand	5	39.2 a	25.5 c	700.0 b	5.04 a	1.88 b	2.88 a	0.67 a	19.9 b	5.7 b
P value		0.4692	0.0002	0.0006	0.6789	0.0280	0.6485	0.9666	0.0254	0.0004
Gaillardia pulchella										
Crushed crust	10	41.6 a	91.0 a	434.0 a	6.58 a	1.53 a	3.79 a	0.53 a	13.0 ab	1.9 a
Crust over sand	10	98.6 b	91.3 a	221.6 c	8.40 a	2.24 b	5.14 b	0.60 a	14.5 a	2.4 b
Sand	10	103.3 b	152.6 b	301.8 b	12.60 b	1.82 a	4.77 b	0.53 a	11.1 b	2.3 b
P value		< 0.0001	0.0017	0.0004	< 0.0001	0.0008	0.0021	0.2136	0.0433	0.0098
Elymus elymoides										
Crushed crust	6	18.0 a	152.1 a	40.1 a	2.33 a	1.22 a	0.64 a	0.17 a	16.6 a	1.5 a
Crust over sand	6	19.1 a	152.1 a	67.2 b	4.90 b	1.43 b	0.40 c	0.19 a	16.5 a	2.1 b
Sand	3	37.3 b	125.1 a	68.6 b	7.00 b	1.41 b	0.51 b	0.24 b	14.4 a	2.4 b
P value		0.0012	0.7962	0.0198	0.0018	< 0.0001	< 0.0001	0.0030	0.3900	< 0.0001
Bromus tectorum										
Crushed crust	10	22.4 a	96.0 a	108.8 a	7.28 a	1.58 a	1.06 a	0.25 a	16.4 a	1.1 a
Crust over sand	6	30.3 a	143.0 b	182.0 a	6.48 a	1.74 a	0.96 a	0.30 ab	10.9 b	4.8 b
Sand	8	30.3 a	74.2 a	367.5 b	6.30 a	1.55 a	1.34 b	0.33 b	9.6 c	6.9 c
P value		0.0661	0.0180	< 0.0001	0.2153	0.5167	0.0185	0.0198	< 0.0001	< 0.0001

Discussion

Biological soil crusts contain a large reservoir of bioessential elements that are slowly released and become available for plant growth (Belnap & Harper, 1995; Hawkes, in review). The high concentration of nutrients relative to the underlying soil comes from the active fixation of N and C, as well as the accumulation of small aeolian dust particles that affect nutrient content and cation exchange capacity (Belnap et al., 2001; Blank et al., 2001; Harper & Pendleton, 1993). Soil crust material used in this study had higher levels of organic matter, electrolytic conductivity, N, Ca, Mg, Na, and Cu, and lower levels of Fe relative to the underlying sand substrate (Table 1). Other studies of Colorado Plateau crusts also found soil crusts to be high in organic matter, N, and Ca, as well as P and K (Belnap & Harper, 1995; Harper & Pendleton, 1993; Kleiner & Harper, 1977). Additional attributes of crusted soils that may affect plant growth include higher soil temperatures during early spring growth, reduced soil evaporation, and increased availability of essential elements due to chelating compounds present in cyanobacterial sheaths (Belnap et al., 2001; Harper & Pendleton, 1993).

In this study, we examined the effects of biological soil crusts on seedling growth and mineral content of four herbaceous species inoculated with arbuscular mycorrhizal fungi. Previous studies have reported increased growth or mineral content of vascular plant species grown in crusted soils (Belnap & Harper, 1995; Harper & Belnap, 2001; Harper & Pendleton, 1993; Pendleton et al., 1999), however, mycorrhizal colonization was controlled in only one of these experiments. Our data support the view that crusts provide important reservoirs of nutrients that slowly become available for plant growth. Plants grown in the crust-over-sand treatment produced significantly more plant biomass than did plants grown in the uncrusted sand. The crust-over-sand treatment is analogous to soil conditions commonly found in undisturbed aridland soils. Total shoot uptake for all nutrients was higher in the crust-over-sand treatment than in sand alone. Lower root:shoot ratios and/or specific root lengths of plants from crusted soils further corroborate this view. Numerous studies have found that plants undergoing nutrient stress produce proportionately more root biomass than plants growing in more fertile soils (Chapin, 1980; Kachi & Rorison, 1989; Redente et al., 1992).

Nitrogen is thought to be a key element in determining community structure and succession (Tilman, 1986). Arid regions are generally low in N content compared to other regions, and have few dinitrogen-fixing plant species (Evans & Belnap, 1999; Farnsworth et al., 1976; Wullstein, 1989). Studies using stable isotopes have concluded that most of the N used by higher plants in arid and semiarid regions was originally fixed by soil crust organisms (Belnap, 1995; Evans & Belnap, 1999; Evans & Ehleringer, 1993). Estimates of the amount of dinitrogen fixed by soil crusts range from 2 to 365 kg ha^{-1} a^{-1} (Belnap et al., 2001; Kapustka & DuBois, 1987; Ladyman & Muldavin, 1996; Rychert et al., 1978), depending on temperature and precipitation patterns, as well as species composition of the soil crust.

The increased growth reported here for plants grown in crusted soils results from the increased N content of the crust material. Plants grown in the crust-over-sand treatment contained significantly higher tissue concentrations of N than did plants growing in sand. Total amount of N in above-ground tissue of crust-over-sand plants was twice that of plants grown in sand. In other case studies examining the influence of biological crusts on plant nutrient uptake, crusts were consistently found to increase the N content of associated seed plants (Harper & Belnap, 2001). Mycorrhizal plants in particular may benefit from the fixation of atmospheric N_2 by cyanobacteria present in soil crusts (Hawkes, in review). Mycorrhizal fungi are known to aid in host plant uptake of P, however considerable evidence also indicates an important role in N uptake (Faure et al., 1998; Hodge et al., 2001, and references therein). Further studies are needed to clarify the interaction of mycorrhizal fungi with soil crust forming organisms.

Anthropogenic activity resulting in disturbance of the crust surface can disrupt the natural dynamics of N cycling, profoundly affecting the structure and function of biological crust communities and, ultimately, the associated plant communities as well (Belnap et al., 2001; Evans & Belnap, 1999). Trampling or other compressional disturbance can destroy the integrity of the crust, resulting in a short-lived flush of nutrients similar to that experienced by plants growing in the crushed-crust treatment. Plants grown in the crushed-crust treatment showed tremendous increases in growth and nutrient uptake due to this nutrient flush. A rapid increase in nutrient availability would disrupt community dynamics, possibly resulting in differential establishment and reproductive success of exotic annual species such as *Bromus*. McLendon & Redente (1991) postulated that the establishment and persistence of exotic annuals on disturbed sites may be related to nutrient availability, particularly that of nitrogen. They found that *Bromus tectorum* remained dominant on disturbed sites where N was more readily available (McLendon & Redente, 1991). Allen (1995) also reported cover of weedy annual versus native perennial species on California roadsides to be correlated with soil nitrogen availability.

In the Colorado Plateau region, compressional disturbance when crusts are dry and brittle destabilizes the crust surface, significantly reducing nitrogen inputs from crust organisms and changing the composition of the crust biota (Evans & Belnap, 1999). The exposed underlying soil is more susceptible to wind erosion, leaving adjacent areas of crust open to burial by particle deposition (Belnap et al., 2001, and references therein; Evans & Johansen, 1999). Disturbance also leads to a reduction in the number of mycorrhizal propagules and other microorganisms associated with the crust layer (Harper & Pendleton, 1993). The resulting reduction in soil fertility and stability of such a degraded ecosystem would have profound and lasting consequences (Evans & Belnap, 1999). This study supports previous studies documenting the positive effects of crust on plant growth and nutrient content.

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