



Wildfire-resistant biological soil crusts and fire-induced loss of soil stability in Palouse prairies, USA

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Abstract

Frequent low-intensity fires are a natural component of the ecology of the Palouse prairies of northwestern North America. To study the effects of fire upon biological soil crusts (BSCs) occurring in these grasslands, we sampled three burned (in 2000) sites and three unburned sites in the Hell's Canyon area (OR, USA) ~1 year post-fire. We measured vascular plant and BSC cover, soil microbe pigmentation, texture and chemistry, and soil surface physical properties (stability and rugosity). *Festuca idahoensis* was two times more abundant in unburned plots ($P = 0.0006$), and vascular plant and litter cover were generally higher in unburned plots. At the community scale, there was no difference in the lichen and moss species composition, suggesting much less drastic effects of fire on BSCs than reported in other systems. Soil surface stability (measured using slake value) was significantly lower in burned sites than unburned sites (median value = 5 versus 6, $P = 0.008$), a result which is likely due to the greater density of lichens and mosses encountered in the unburned plots. Soil microbe pigmentation was lower in burned plots ($P = 0.03$), suggesting that the biomass of photosynthetic microbes had decreased; however, the presence of intra- and extracellular pigments in burned soils indicates that microorganisms were not eradicated. Pigments most strongly associated with cyanobacteria were more abundant in unburned sites, suggesting that cyanobacteria may have been more strongly impacted by the fire than other BSC components. Composition of nutrients and surface rugosity did not differ significantly between treatments. We hypothesize that Palouse prairie soil crusts are relatively resistant to wildfire because of low fire intensity and their occupation of space away from the vascular plant fuel load.

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Keywords: Biological soil crusts; Soil stability; Fire ecology; Grasslands; Pigments

1. Introduction

Biological soil crusts (BSCs) are both successional and permanent soil surface features found in habitat types where open canopies permit light to reach the soil surface (reviewed by Belnap et al., 2001a).

BSCs are usually dominated by photoautotrophs and may have some or all of the following common constituents: cyanobacteria, chlorophytes, heterotrophic bacteria, microfungi, lichens, and mosses. All BSCs have the effect of binding soil surface particles into a cohesive crust with polysaccharide exudates (Mazor et al., 1996) and a matrix of fibers (Warren, 2001). Numerous important ecosystem services have been ascribed to BSCs, including reduction of soil erosion, entrapment of eolian silts and clays, nitrogen

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(N) fixation, Carbon fixation, hydrological effects, and others (Belnap et al., 2001b). Relatively little is known about BSCs in fire-adapted grasslands.

We hypothesized that fire would result in measurable differences in the cover, composition or function of BSCs in a fire-adapted grassland. (Fire-adapted can be defined as a system which historically experienced frequent fires and recovered quickly.) Literature on the effects of fire disturbance on BSCs is sparse (reviewed by Johansen, 2001). The resistance of the various BSC components to fire may be described as follows: diatoms > chlorophytes > large filamentous cyanobacteria > smaller heterocystic cyanobacteria > mosses > lichens (Johansen, 2001). The most commonly described effect of fire on BSCs is a loss of BSC biomass, cover, and diversity in shrub steppe and scrub communities (Johansen et al., 1982, 1984, 1993). Studies of the effects of rangeland fire on BSC functions are even fewer, but ecosystem services can be diminished (Johansen et al., 1998). Johansen (2001) asserts that, in contrast to wood-fueled fires, grassland wildfires do not attain sufficient heat to eliminate BSCs, and post-burn recovery can happen quickly. Recovery time varies with the type, severity and frequency of disturbance, and climatic factors, but in North American arid and semi-aridlands it is usually measured in decades to centuries (Belnap and Eldridge, 2001).

The Palouse prairies (Snake River grasslands), afford an opportunity to study the effects of fire on BSCs in a fire-adapted grassland. These prairies are dominated by bunchgrasses with interspaces colonized by BSCs. Frequent low intensity fires were an important part of the history of maintaining perennial grasses at a low fuel load (Ricketts et al., 1999). Prior to modern fire suppression, the fire return cycle was estimated to be ~10 years (Hall, 1976). The Hell's Canyon area of the Northwest USA constitute the largest remaining block of relatively intact Palouse grasslands (Ricketts et al., 1999). In August and September of 2000, 10 fires burned a total of ~38,000 ha in the Hell's Canyon area. The majority of the area burned experienced quick-moving low intensity fires according to aerial surveys conducted by the US Forest Service. Due to the lack of woody fuels and the wide interspaces between bunchgrasses, fuels are thought to be insufficient for high intensity wildfires (Robert Both, US Forest Service fire specialist, personal communication).

We investigated the potential decrease of BSC cover and function (focusing on the dominant photoautotrophic components) in response to fire by asking four primary questions: (1) Is cover/abundance of BSC organisms decreased in burned areas compared to similar unburned grasslands? (2) Are different types of BSC organisms differentially affected by fire in this system? Differential mortality of BSC organisms is a frequently reported pattern, but has scarcely been studied in fire-adapted systems (Johansen, 2001). (3) Can decreases in abundance and/or compositional shifts in the microscopic component of the BSCs be detected using photopigments? Quantification of multiple pigments may offer a time saving method for detecting changes in community structure that has scarcely been applied to BSCs. (4) Are BSC functions (stability of the soil surface and maintenance of surface rugosity) negatively impacted by fire, and if so, can this be linked to impacts to particular crust organisms? Fire effects on BSC function are the most understudied aspect of fire-BSC interactions (Johansen, 2001). In order to properly manage wildfire in this and other fire-adapted systems we must take BSCs into account because they may be significant contributors to the stability and function of the system.

2. Methods

2.1. Site selection

Six sites were selected in Hell's Canyon National Recreation Area (HCNRA) in eastern Oregon, USA. All sites were in the Cherry Creek watershed, which lies within the area of the Eastside Fire Complex of 2000. The sites were sampled in early August 2001, 11 months after the fires. Sites were selected representing burned and unburned grassland patches ($n = 3$ sites per treatment) based upon the presence or absence of burned detritus. The burned sites corresponded to low burn intensity according to US Forest Service aerial surveys and moderate burn severity according to the finer criteria of Johnson (1998). Because the area is typified by deep canyons with steep colluvial slopes, only sloping sites were sampled, keeping slope and aspect relatively constant (22–33° and 210–270°N, respectively) to reduce variability in BSC cover caused by these extraneous variables. Difficulty was

encountered in selection of sites of similar elevation, due to the steepness of the canyon so elevation was limited as much as possible (839–1370 m). All sites were dominated by *Agropyron spicatum* and *Festuca idahoensis*. Although impossible to avoid completely, dense patches of the exotic invasive *Bromus tectorum* were avoided during sampling because they likely represent altered fire and nutrient cycles. All soils were non-calcareous loams derived from Columbia River basalt (no published soil survey exists for the study area). Soil depth was generally <20 cm and soils were gravelly, unlike many parts of the Palouse region which were converted to agriculture. Cattle have been excluded from the study area since the early 1980s.

2.2. Survey methods

A walking point intercept method was used to quantify percent cover of vascular plants, ground cover, and BSCs in the six rectangular sites of about 30 m × 100 m. Ten ~30 m transects per site were sampled parallel to the short axis of the site (the upper and lower transects comprising the upper and lower boundaries of the site), and spaced ~10 m apart (estimated by pacing) along the long axis of the site. The transects were intended to represent the whole area. The starting point for the transects was determined haphazardly. About every meter (estimated by pacing) a pin flag was used to haphazardly intercept a point directly in front of the surveyor's leading foot, which was examined for the following characteristics (using a handlens where needed).

Ground cover was recorded at each of these points ($n = 30$ per transect, 300 per site) as one or more of the following: surface rock, exposed bedrock, burned detritus, thick litter (empirically determined as a continuous layer of litter >0.5 cm thick, sometimes attached to soil, and likely reducing light), light litter (not as above), vascular plant stem, vascular plant canopy, bare ground (including algal crusts which were not reliably distinguishable from bare ground), and moss or lichen (identified to species). At every fifth point a visual estimate was made of the maximal surface relief (to the nearest cm) of the 100 cm² area around the point. Due to the patchy occurrence of most BSC species and to increase replication for statistical analysis, species were later combined into morphological/functional groups: total mosses, total N-fixing

lichens, and total non-N-fixing lichens (Eldridge and Rosentreter, 2000). Percent cover values were calculated for each individual transect, giving each site 10 cover values. Lichen and moss cover was converted to percent of available habitat because preliminary analysis demonstrated that unavailable habitat (surface rock, exposed bedrock, thick litter, vascular plant stem) was more prevalent on the burned sites by chance alone. By definition (Belnap et al., 2001a), BSCs only occur on soil and variance caused by these extraneous variables could obscure fire effects.

The slake test measures the cohesiveness of soil aggregates against timed water immersion treatments, thus it provides a measure of soil stability against water erosion (Herrick et al., 2001). Stability is ranked according to a semi-quantitative scale of 0–6. Because performing this test on each cover transect would have been unnecessarily time consuming, the slake test was performed at each site along an additional 100 m transect running from the top of the site to the bottom (representing area covered by all transects and between them) At every 5 m along the transect a ped (small intact soil aggregate ~1 cm³) was collected randomly from the nearest soil surface (whether crusted or not) and tested. Eighteen such peds were tested per site. Peds were coded as containing mosses/lichens (which always scored the highest value for the slake test) or as bare soil, so that post-hoc investigations could determine if number of moss and lichen occurrences determined treatment differences in soil stability.

Two composite soil samples were collected for each of the six sites using a flat bottomed mini trowel ($n = 12$ soil samples). Samples consisted of enough individual surface subsamples of the uppermost 0.5 cm of soil (~10–20 g of soil per scrape) sampled at 5 m intervals along the slake test transect to compile a ~300 g composite sample (never <20 scrapes). The first of the composite sample pairs was randomly sampled representing the entire soil surface of the site (whether BSC-available or not) and was sent to the Brigham Young University Soils and Plant Analysis Laboratory (Provo, UT, USA) for analysis of soil chemistry: total N using an automated Dumas method (McGeegan and Naylor, 1988), NaHCO₃-extractable P and K (Schoenau and Karanomos, 1993), NH₄OAc-extractable K, Ca, Mg and Na (Normandin et al., 1998), DTPA-extractable Fe, Mn, Cu and Zn

(Lindsay and Norwell, 1978), gypsum by water of hydration (Nelson, 1982), CaCO_3 measured as acid neutralizing potential (Allison and Moode, 1965), organic matter by dichromate oxidation (Walkley and Black, 1934), texture by hydrometer (Day, 1965), saturated paste extract pH and electrical conductivity (a.k.a. soluble salts; Rhodes, 1982). The second sample was collected from BSC-available surfaces not occupied by macroscopic mosses or lichens, and was analyzed for pigment content (detailed below) as an indicator of photosynthetic microbial abundance and composition.

2.3. Pigment extraction and quantification

Quantitative and qualitative HPLC analysis was performed according to a slightly modified version of the method of Karsten and Garcia-Pichel (1996), detailed in Bowker et al. (2002). Additional modifications are as follows: (1) Soils were initially ground in liquid nitrogen to shatter diatom frustules; (2) To improve chlorophyll *c* detection, the fluorometer settings were altered (excitation wavelength = 445, emission wavelength = 640, gain = 100). Pigments were identified by comparative retention times and characteristic absorption spectra, and were quantified as $\text{mg pigment g}_{\text{soil}}^{-1}$ using external standards.

2.4. Direct measurement of crust microbes

To verify pigment trends, frequency of soil crust microbes was estimated by viewing randomly selected microscope fields ($n = 20$, determined adequate by plotting frequency versus n) as in Bowker et al. (2002) with the following modifications: (1) soil used represented the surface 0.5 cm; (2) 1 g soil: 2 ml water dilution was used; (3) cyanobacteria, chlorophytes, fungal hyphae, pigmented (presumed live) diatoms, and non-pigmented (presumed dead) diatoms were quantified and not identified beyond this level.

2.5. Statistical analysis

To increase replication, data were pooled into burned and unburned treatments. For univariate hypotheses, data meeting the assumptions of normality and homoscedascity of variance (Bartlett's test

$P \geq 0.05$) were analyzed using independent *t*-tests; otherwise the Mann–Whitney *U* test was used. Multivariate hypotheses were tested using multiple logistic regression after independence of predictor variables had been confirmed using the Spearman rank correlation with $\alpha = 0.05$. Ordinal data from the slake test were analyzed using the likelihood ratio χ^2 -test (*G*-test). Statistics were done using JMP IN 4.0 (1997 SAS Institute). Multi-response permutation (MRPP) procedure (Zimmerman and Goetz, 1985) was used to detect significant grouping in pigment, soil nutrient, and moss and lichen community data. MRPP tests the hypothesis of no difference in multiple variables between groups (or treatments) of sampling units using a randomization test for significance. Data were rescaled from 0 to 1 by species, to equalize the influence of all "species" upon the analysis. The Bray-Curtis distance measure was used for analyses of community data, while Euclidean distance was used for the test upon soil nutrients. The former distance measure has been shown to be effective in evaluating similarity for community data, where abundant zeros and non-linear correlations confound metric distance measures (Faith et al., 1987). Because physical environmental data do not usually suffer from these distribution problems, Euclidean distance (an extension of the Pythagorean theorem) is appropriate. When significant grouping occurred, a post-hoc indicator species analysis was performed (Dufrene and Legendre, 1997). This test provides an index of perfect indication (presence of a species indicates a group or treatment without error) for a treatment and a test statistic (McCune and Grace, 2002). MRPP and indicator species analysis was performed in PC-ORD version 4 (1999 MJM Software Design). Due to the inherently patchy occurrence of BSCs (resulting in variable data and frequent occurrence of zeros), statistical significance was determined at $P < 0.10$.

3. Results

3.1. Vascular plant cover and ground cover

Treatment differences were evident in vascular plant composition (Fig. 1). *Festuca idahoensis* cover was significantly lower by 47% ($P = 0.005$), while *Bromus tectorum* was less abundant in burned plots

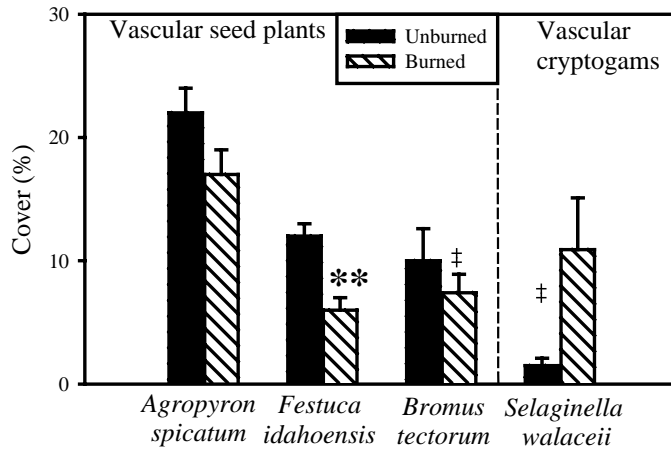


Fig. 1. Vascular plant cover was generally reduced by wildfire. *Festuca idahoensis* and *Bromus tectorum* were more abundant in unburned transects ($n = 30$) while *Selaginella walaceii* was significantly more abundant in burned transects ($n = 30$). Vascular seed plants are quantified as absolute percent cover, while *Selaginella* is quantified as percent cover of available habitat (‡ $P < 0.10$, ** $P < 0.01$).

by about 26% ($P = 0.09$). In contrast, *Selaginella walaceii* (the only vascular cryptogam encountered) cover was $\sim 7\times$ greater in burned plots than unburned (10.9% versus 1.5%, $P = 0.05$), although it was completely absent from one burned plot. Total litter (analyzed in a separate model) was 369% (Fig. 2, $P = 0.001$) as abundant on unburned transects as burned transects. Burning litter likely resulted in more exposed rock and more burned detritus. Cover of bare ground was not a significant effect in this model (Fig. 2, $P = 0.67$).

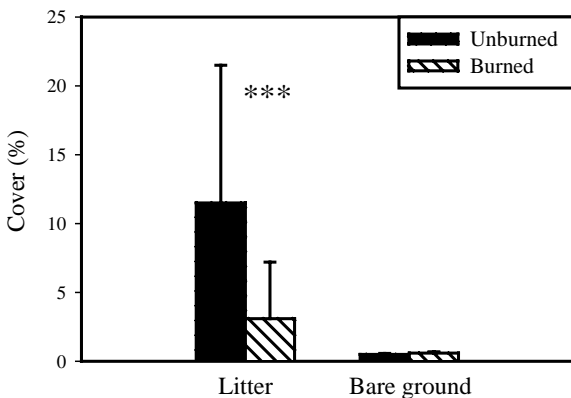


Fig. 2. Unburned sites had significantly more litter than burned sites. There was no difference in cover of bare ground between treatments (*** $P < 0.001$).

3.2. Soil chemistry and texture

All sites were remarkably similar in that they were composed of slightly acidic–neutral, non-saline, non-calcareous loams, with approximately 4–6% gypsum and 3–5% organic matter. No significant grouping ($A = 0.00$, $P = 0.47$) was detected in the composition of macro and micronutrients and exchangeable cations between treatments (Table 1). Chance-corrected, within-group agreement, represented by A , ranges from 1 (identical within-group data) to 0 (agreement expected by chance) to <0 (less than chance agreement).

3.3. Differences in moss and lichen cover and diversity

A community of 14 macrophytic BSC species was encountered in the Palouse prairie soils, including six mosses, and eight lichens (Table 2). At the community scale, no significant grouping ($A = 0.01$, $P = 0.33$) was observed in the moss and lichen species composition between treatments.

No relationship was detected between burn status and the effects total moss, total N-fixing lichen, total non-N-fixing lichen, and surface rugosity (Fig. 3, $P = 0.37$). Number of moss and lichen species per transect was approximately 30% higher in unburned plots (Fig. 4, $P = 0.08$).

Table 1

No significant differences were detected in nutrient composition between burned and unburned sites, and other soil properties were similar

Soil property	Unburned			Burned		
	1	2	3	1	2	3
N	1266.0	1516.0	1540.0	1536.0	1796.0	1247.0
P	30.1	29.6	28.9	34.3	45.1	37.1
K _{av}	272.0	227.2	361.6	304.0	435.2	390.4
Zn	1.6	1.7	1.7	1.5	3.0	1.8
Fe	67.9	65.0	40.8	59.0	46.2	50.0
Mn	18.7	21.1	30.4	25.4	35.1	25.1
Cu	2.2	3.4	1.6	1.3	4.5	2.2
Ca	2974.0	3132.0	3272.0	3854.0	3526.0	3198.0
K _{ex}	487.6	509.8	575.4	494.2	741.2	626.0
Mg	1046.2	1099.6	688.2	1311.0	122.4	924.4
Na	78.1	82.1	82.5	81.5	72.9	90.5
Electrical conductivity	0.2	0.3	0.3	0.3	0.4	0.3
pH	6.4	6.4	6.7	6.5	6.7	6.7
% Sand	50.0	46.4	46.0	40.0	48.0	50.0
% Silt	34.2	37.8	41.2	38.2	36.2	35.2
% Clay	15.8	15.8	12.8	21.8	15.8	14.8
% Organic matter	3.3	4.0	3.9	4.0	4.7	3.4
% CaCO ₃	0.2	0.5	0.3	0.8	0.0	0.9
% Gypsum	4.5	5.0	4.3	6.2	5.4	4.6

Some nutrients tend to be higher in burned plots such as P and K-exchangeable, and should be investigated in more detail. Macro- and micro-nutrients, and exchangeable cations are reported as ppm, and EC is reported as dS/M.

Table 2

Moss and lichen composition was similar in unburned and burned sites

Moss or lichen	Mean ± S.E.	
	Unburned	Burned
<i>Anomobryum argenteum</i>	1.2 ± 0.9	tr
<i>Brachythecium collinum</i>	tr	0.8 ± 0.5
<i>Ceratodon purpureus</i>	tr	tr
<i>Homalothecium nevadense</i>	1.1 ± 1.1	0.8 ± 0.8
<i>Polytrichum juniperum</i>	0.0 ± 0.0	0.3 ± 0.3
<i>Syntrichia ruralis</i>	25.6 ± 5.7	18.7 ± 4.7
<i>Cladonia chlorophaea</i>	6.3 ± 2.1	4.0 ± 2.0
<i>Cladonia fimbriata</i>	6.5 ± 2.6	6.7 ± 2.5
<i>Diploschistes muscorum</i>	0.6 ± 0.6	tr
<i>Endocarpon pusillum</i>	tr	0.0 ± 0.0
<i>Lepraria</i> sp.	tr	0.0 ± 0.0
<i>Leptogium lichenoides</i>	0.4 ± 0.4	0.0 ± 0.0
<i>Ochrolechia upsaliensis</i>	1.1 ± 1.1	0.7 ± 0.7
<i>Peltigera rufescence</i>	1.7 ± 1.7	2.5 ± 1.4

Fourteen taxa were encountered in surveys of the six sites. Values are reported as percentage of available habitat. Trace (tr) indicates that a species was present within site boundaries but was not intercepted on a transect.

3.4. Pigment and microbial composition

Eight pigments were extracted from the composite soil samples including chlorophyll *a*, chlorophyll *b*, chlorophyll *c*, leutein, β-carotene, canthaxanthin, and

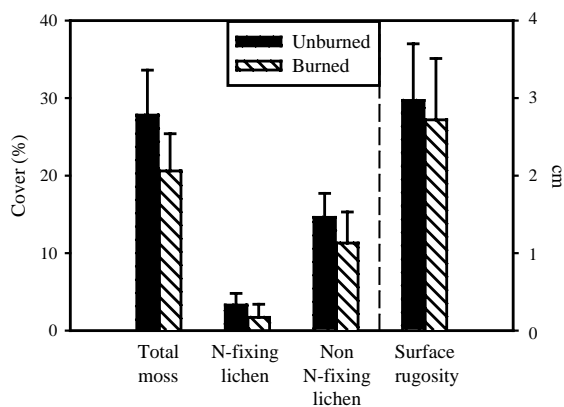


Fig. 3. Moss and lichen cover and surface rugosity of soils did not differ significantly between treatments ($P = 0.33$, $n = 30$). All measures tended to be lower in burned plots and were highly variable.

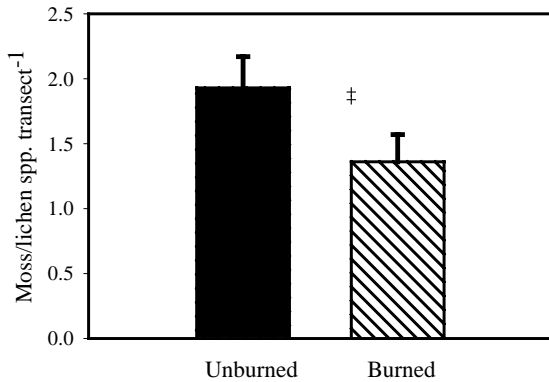


Fig. 4. Species richness was significantly higher in unburned plots ($P = 0.08$). Overall, richness was very low with averages of less than two species per transect in both treatments ($\ddagger P < 0.10$).

echinenone (Table 3). Significant grouping ($A = 0.15$, $P = 0.04$) was detected in pigment data for the treatments “burned” and “unburned” (Fig. 5). This result indicates only that pigment composition differed between treatments. Indicator species analysis revealed that all pigments were better indicators of unburned plots, meaning that they were more abundant in or more consistently occurred in unburned than burned transects. Two of the pigments, chlorophyll *a* and echinenone had significantly higher percent of perfect indication for the unburned treatment (Table 3).

Visible cyanobacterial crusts were not a common feature of the BSCs of Hell’s Canyon area, although cyanobacterial presence was confirmed microscopi-

cally and by the presence of echinenone and canthaxanthin. Chlorophytes were virtually absent from the soils and diatoms were the most frequently occurring organisms, ranging in frequency from ~15–30% (Fig. 6). Cyanobacteria (*Oscillatoria*-like species) were 6.6% (~2×) more frequent in unburned soils, while live diatoms were nearly 11.7% more frequent in burned soils. Fungal hyphae and dead diatoms occurred at similar frequencies between treatments (Fig. 6).

3.5. Differences in soil stability

Soil stability of BSC-available habitat, measured as slake value, was significantly greater in unburned plots (median = 6) than burned plots (median = 5, Fig. 7, $P = 0.008$). Because moss and lichen peds always scored the highest possible value (6) we hypothesized that the difference between burned and unburned sites was due solely to greater frequency of moss or lichen peds in the unburned sites. With slake values associated with lichens and mosses excluded from analysis, there was no significant difference between treatments (Fig. 7).

4. Discussion

4.1. Fire reduced vascular plant biomass and litter

A reduction in aboveground living and dead biomass was expected to occur in the prairies in

Table 3

All pigments except chlorophyll *c* were more strongly associated with unburned plots than burned plots, and two significant indicator pigments, echinenone and chlorophyll *a*, were identified for unburned sites

Pigment	Unburned			Burned			Indicator values		
	1	2	3	1	2	3	Unburned	Burned	<i>P</i>
Chlorophyll <i>a</i>	31.0	27.9	37.1	16.1	22.1	17.0	64	36	0.10
Chlorophyll <i>b</i>	3.4	4.2	6.7	3.0	4.3	0.0	66	23	0.30
Chlorophyll <i>c</i>	0.6	0.6	0.7	0.6	0.9	0.6	48	52	0.80
Lutein	1.7	2.1	4.4	1.3	1.9	1.1	53	47	0.20
Canthaxanthin	1.6	1.1	0.9	0.0	0.9	0.8	65	35	0.22
Unknown	2.9	3.3	2.2	1.7	3.9	1.8	67	22	0.81
Echinenone	2.1	2.1	1.8	0.6	1.3	1.1	67	33	0.10
β-Carotene	0.0	0.0	6.1	0.0	0.0	0.0	–	–	–

These results indicate that microbial biomass was likely lower in burned plots, and that cyanobacteria in particular experienced mortality. Pigments are reported as $\text{mg}_{\text{pigment}} \text{g}_{\text{soil}}^{-1} \times 10^{-4}$, except the unknown pigment which is reported in chromatogram area units $\times 10^6$. Significant indicator pigments are in bold, and (–) indicates that a pigment was too rare to perform this test.

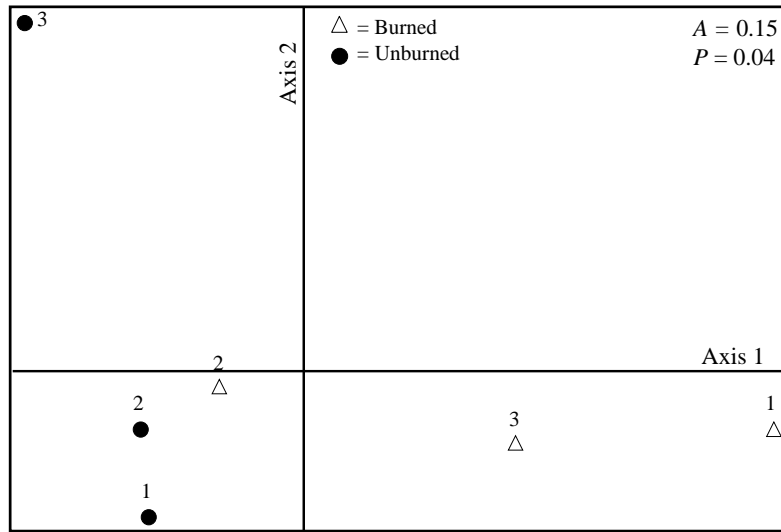


Fig. 5. Pigment composition differed significantly between treatments. The Bray-Curtis ordination (using the Bray-Curtis distance measure) is presented to illustrate the grouping.

response to the fire, as had been documented previously (Johnson, 1998). Our findings suggest a fire-induced shift toward greater relative importance of *Selaginella*, and lesser relative importance of *Bromus* and *Festuca*. The observed lack of expansion of *Bromus tectorum* cover (even 1 year after fire) is unusual and may be due to lack of soil disturbances since the area is rested from domestic livestock. Alternatively,

soil chemistry may not favor *Bromus* colonization (Belnap et al., 2001b). The much greater *Selaginella walaceii* cover in two of the three burned plots, suggests that this species may increase in cover post-fire, perhaps due to more light reaching the soil surface due to removal of live and dead grass and litter.

Over time, the four-fold reduction of litter cover may confer benefits to BSC communities and other

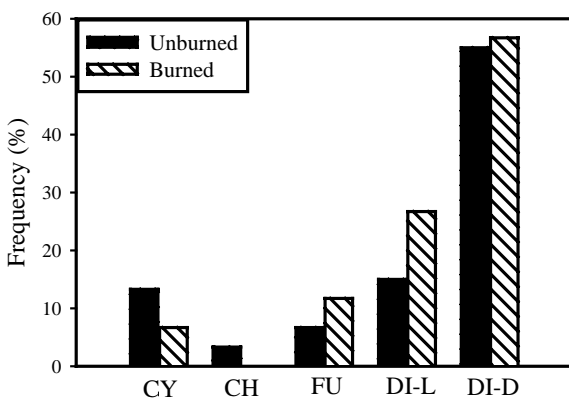


Fig. 6. Cyanobacteria were twice as abundant in unburned soils, consistent with decreases in the pigments chlorophyll *a* and echinenone. Diatoms were the most numerous organisms (CY, cyanobacteria; CH, chlorophytes; FU, fungal hyphae; DI-L, live diatoms; DI-D, dead diatoms).

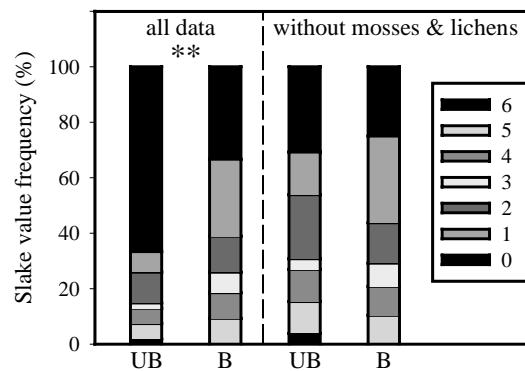


Fig. 7. The relative proportion of high slake test values (Herrick et al., 2001) of randomly selected peds, was greater in unburned than burned plots, suggesting that fire reduces soil stability. To test the hypothesis that more lichen and moss occurrences in unburned plots accounted for this difference, lichen and moss containing peds were excluded and the test was rerun with no significant result (UB, unburned; B, burned; ** $P < 0.01$).

low growing primary producers such as *Selaginella*. Because litter covered over 12% of the ground surface in unburned sites, it is probably a major factor affecting various biotic communities (autotrophic and heterotrophic) in the soil via mediation of light, temperature, moisture, and nutrients.

4.2. Biological soil crusts of Hell's Canyon contrasted with those of other areas

BSCs have not been studied extensively in prairie ecosystems. BSC communities of the Great Plains of the USA may consist of macroscopic thalloid colonies of the cyanobacterium *Nostoc commune*, vagrant lichens, and abundant bryophytes (Rosentreter and Belnap, 2001). *Nostoc* is reported to be the dominant N-fixer in tall grass prairies (Eisele et al., 1989).

To our knowledge, the BSCs of the Palouse prairies have not previously been described in detail in the literature. The BSCs of Hell's Canyon, unlike those of the Great Plains, lacked vagrant lichens and macroscopic *Nostoc* colonies and were dominated by the moss *Syntrichia ruralis*, as are BSCs in the Great Basin and Columbia Basin. No hepatics were encountered in the surveys, although spring ephemeral liverwort taxa (*Riccia* spp. and *Athalamia hyalina*) have been collected by R.R. in prairie habitats in the general area. The pigment scytonemin, which indicates the presence of the major heterocystic cyanobacterial taxa, was not detected in measurable quantities in the soil samples, despite the fact that the sampling time favored high concentrations due to high irradiance (Bowker et al., 2002). This may indicate that free-living cyanobacteria do not contribute significant biologically-fixed N and that lichens (particularly *Peltigera rufescens*) are the primary N-fixers of soil crusts in this ecosystem. However, the N-fixing cyanobacterium *Scytonema* has been collected in Hell's Canyon by one author (R.R.). The foliose lichen *Peltigera* is known to fill the N-fixing niche in BSCs in cool season (frigid) grasslands (Belnap et al., 2001c), and is common in mid to high elevation Great Basin habitats. Diatoms, followed by cyanobacteria, were the most frequent microbial component of the BSC. Thus it would appear that Palouse prairie soil BSCs have little affinity with those of Great Plains prairie systems (Booth, 1941; Schulten, 1985a; Eisele et al., 1989).

4.3. Differentially greater mortality of cyanobacteria compared to other BSC components

We detected scant significant low-intensity fire impacts upon BSCs. No difference was observed in moss and lichen community composition between the two treatments. The MRPP method is sensitive to community-level differences in cover and to shifts in species composition, thus the majority of species were retained and not drastically reduced. Species-level comparisons are generally difficult because of the patchy nature of distributions and the preponderance of zeros in the resultant data. We found that moss and lichen species richness per transect was higher in unburned plots, indicating that on a small scale, fire may cause rarer species to be distributed more patchily. Unlike on the Colorado Plateau (George et al., 2000), BSCs are not pedicelled and do not contribute considerably to surface rugosity in Hell's Canyon, therefore fire has little, if any, effect on this attribute and its hydrological effects.

One of the most consistent effects of fire on BSCs cited in the literature is the drastic reduction or complete eradication of moss and lichen cover (Johansen et al., 1984; Hilty et al., in press). In contrast, one study conducted in an Iowa prairie reported no change in moss cover after a prescribed burn (Schulten, 1985b). In the present study there was no significant difference in moss or lichen cover between treatments, and they retained substantial cover in the burned sites. While surveying, we often observed living lichens or mosses with some fire damage and blackening in the burned sites, indicating that although damage was incurred, survival was common. One study incorporated the effect of fire intensity upon BSCs and concluded that there were no significant differences between unburned patches and low intensity fire sites (Johansen et al., 1998). Intensity comparisons are not possible in our study area under natural conditions because BSCs occur primarily in grassland patches (as opposed to forest patches) which inherently burn at a low intensity. Our findings are consistent with those of Schulten (1985b) and support the assertion of Johansen (2001) that fires in perennial bunch grass stands do not attain sufficient heat to completely destroy BSCs and impair their functions.

Aside from the low intensity of the bunch grass fires, the spatial position of BSCs may partially

explain the lack of significant impacts in the Palouse prairie system. The Palouse prairies experience limited sunny days during the winter and spring growing season, thus cloudy days are more common than in nearby *Artemisia*-dominated ecosystems (Daubenmire, 1942). This may explain why a large percentage of the moss cover was present in the interspaces (>70% in unburned sites) rather than under vascular plant canopies as in other systems like the Great Basin. Lichens presented an even more extreme case, as 96% of occurrences in unburned plots were in interspaces between bunch grasses. Because the interspaces experience much lower fire and heat intensity than plant canopies, the mosses and lichens are less likely to be damaged by the fire.

The finding that soil microbe pigmentation was greater in unburned plots may indicate that some mortality was induced by the fire in the microscopic component of the BSCs (primarily cyanobacteria). However, microscopic BSC components were not eradicated as most pigments were present post-fire. Chlorophyll *a* is frequently used as a surrogate measure for photosynthetic microbial biomass in BSC communities (Belnap, 1993). The response of the pigment chlorophyll *a* to fire is variable dependent on the system studied, but generally its concentration is higher in unburned than burned areas in systems not adapted to fire, or in frequently burned than infrequently burned areas in fire-adapted systems (Belnap et al., 1996; Johansen et al., 1998; Hawkes and Flechtner, 2002).

Apart from indicating a general slight decrease in pigmentation, the pigment data (reduction of chlorophyll *a* and echinenone) suggest that cyanobacteria, but not the other microbial BSC components, experienced mortality. These pigments are useful indicators of cyanobacterial presence and/or abundance (Goodwin, 1980). The direct observation of only half as many cyanobacterial occurrences in burned soils corroborates this conclusion. These results agree well with the literature (Johansen, 2001), suggesting that cyanobacteria tend to be less resistant to fire than other microbes. It is unknown what the source of the chlorophyll *b* was, since chlorophytes were very rare. The simplest explanation is that, although multiple steps were taken to prevent sampling bryophytes, some contamination with cryptic forms such as moss protonemata occurred. Although it is a useful method

to monitor shift in algal composition of BSCs, it is important to interpret pigment data cautiously, and may be advantageous to couple it with some form of direct observational method.

4.4. Fire impacts soil stability

We measured significantly lower mean slake test values in burned plots. No significant difference was observed in the stability of soil peds not associated with mosses or lichens (probably containing diatoms and cyanobacteria) between burned and unburned sites. This result may suggest that soil stability was higher in unburned plots only because mosses and lichens were encountered more frequently, and because mosses and lichens confer much more stability than a diatom-cyanobacterial BSC. Previously, decreased soil stability following fire was measured as increased sediment production in two different communities (Johansen et al., 1998), and increased soil erosion has also been attributed to fire (St. Clair et al., 1986). The present study provides a direct link between surface coverage of mosses and lichens and increased soil stability in plant interspaces. The results also indicate that diatom-cyanobacterial BSCs retain similar stability when burned in this system.

4.5. Conclusions

Despite community composition shifts in the vascular plant component of a Palouse prairie system, we detected scant evidence that BSCs are significantly damaged by low-intensity wildfires. Despite minor decreases, there were no significant reductions in moss and lichen cover. Cyanobacterial prevalence was decreased, but additional impacts to the microscopic BSC components were not detected. Pigment analysis proved to be a useful method for detecting changes in community structure among BSC photosynthetic microbes. Burning decreased soil stability, possibly due to the minor loss of mosses and lichens. More frequent natural fire cycles could potentially benefit BSCs by increasing available habitat and allowing more light to reach the soil surface via the removal of litter and plant biomass. This study may serve as a model for BSC response to fire in fire-adapted, widely spaced, clumped grassland ecosystems. Future studies should determine if fire suppression is actually detrimental

to BSCs and what ecosystem functions this might impair. These questions could be addressed experimentally in the field with controlled frequency, intensity (possibly involving fuel addition) and timing of fire.

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