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Biological Soil Crust Response to Late Season Prescribed Fire in a Great Basin Juniper Woodland ^{☆, ☆, ☆, ★}



Steven D. Warren ^{a,*}, Larry L. St.Clair ^b, Jeffrey R. Johansen ^c, Paul Kugrens ^{d,1},
L. Scott Baggett ^e, Benjamin J. Bird ^e

^a Research Ecologist, Rocky Mountain Research Station, U.S. Forest Service, Shrub Sciences Laboratory, Provo, UT 84606, USA

^b Professor, Department of Biology, Brigham Young University, Provo, UT 84602, USA

^c Professor, Department of Biology, John Carroll University, University Heights, OH 44118, USA

^d Professor, Department of Biology, Colorado State University, Fort Collins, CO 80523, USA

^e Statistician, Rocky Mountain Research Station, U.S. Forest Service, Fort Collins, CO 80526, USA

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ABSTRACT

Expansion of juniper on U.S. rangelands is a significant environmental concern. Prescribed fire is often recommended to control juniper. To that end, a prescribed burn was conducted in a Great Basin juniper woodland. Conditions were suboptimal; fire did not encroach into mid- or late-seral stages and was patchy in the early-seral stage. This study evaluated the effects of the burn on biological soil crusts of early-seral juniper. Fire reduced moss cover under sagebrush and in shrub interspaces. Mosses were rare under juniper; their cover was unaffected there. Lichens were uncommon under juniper and sagebrush and therefore not significantly impacted there. Their cover was greater in shrub interspaces, but because the fire was spotty and of low intensity, the effects of burning were minimal. Compared with unburned plots, the biomass of cyanobacteria was diminished under juniper and sagebrush; it was reduced in the interspaces in both burned and unburned plots, presumably in response to generally harsher conditions in the postburn environment. Nitrogen fixation rates declined over time in juniper plots and interspaces but not in sagebrush plots. Although fire negatively affected some biological soil crust organisms in some parts of the early-seral juniper woodland, the overall impact on the crusts was minimal. If the intent of burning is to reduce juniper, burning of early-seral juniper woodland is appropriate, as most affected trees were killed. Control of sagebrush can likewise be accomplished by low-intensity, cool season fires without eliminating the crust component. Intense fire should be avoided due to the potential for greater encroachment into the shrub interspaces, which contain the majority of biological soil crust organisms. Burning early-seral juniper may be preferred for controlling juniper encroachment on rangeland.

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Introduction

Since the mid-1800s, woodlands dominated or codominated by juniper have expanded dramatically in the western United States (Miller et al., 2008) and now occupy some 19 million ha (Buckman and Wolters, 1987). The expansion has often been attributed to the suppression of natural wildfires and the introduction of domestic

livestock (Miller and Rose, 1999). The reintroduction of frequent, low-severity fire is a commonly recommended management tool for controlling juniper encroachment and expansion (Baker and Shinneman, 2004; Board et al., 2011).

Biological soil crusts are a key component of many arid and semiarid ecosystems (Rosentreter and Belnap, 2001), including pinyon-juniper woodlands (Ladyman and Muldavin, 1996). Composed primarily of cyanobacteria, algae, lichens, and bryophytes (mosses) living on or near the soil surface (Belnap et al., 2001a), the crusts influence soil stability (Belnap, 2001; Warren, 2001a), hydrology (Warren, 2001b), and cycling of macronutrients and micronutrients (Belnap et al., 2001b; Evans and Lange, 2001). They also affect the dispersal and germination of vascular plant seeds and the survival and growth of plant seedlings (Belnap et al., 2001b).

Literature related to the response of biological soil crusts to fire, the secondary impacts to ecosystem functions they perform, and the dynamics of postfire recovery is limited. Scant published

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[★] At the time of research, Warren was Director, Center for Environmental Management of Military Lands, Colorado State University, Fort Collins, CO 80526-1490, USA.

* Correspondence: Dr. Steven D. Warren, U.S. Forest Service, Shrub Sciences Laboratory, 735 N 500 E, Provo, UT 84606-1856, USA.

E-mail address: swarren02@fs.fed.us (S.D. Warren).

¹ Deceased.

information from western shrubland and grassland communities suggests that biological soil crusts are highly susceptible to wildfire and slow to recover (Johansen, 2001). Recovery of their ability to perform ecological functions can also be expected to be slow, although this assumption remains largely untested. Information regarding the effects of fire on biological soil crust communities in pinyon-juniper woodlands is absent.

The objectives of the present study included 1) determine the nature and extent of the effects of fire on the biological soil crust community of a juniper woodland by documenting changes in the cover, biomass, species composition, and ecosystem functioning of the crust immediately after a prescribed burn and 2) document recovery dynamics over 2 subsequent years. On the basis of our understanding of the ecology of biological soil crusts, we hypothesized that prescribed burning would significantly diminish all organisms comprising the crusts in the juniper-dominated ecosystem and that recovery would be slow.

Methods

Study Area

The study area was located at approximately 1700-m elevation on the eastern foothills of the Onaqui Mountains, approximately 40 km south of Tooele, Utah (lat 40°13'48"N, long 112° 27'55"W). Long-term average annual precipitation near Tooele is 45 cm (Table 1). Vegetation at the study site ranged from early- to late-successional juniper woodland. The early-successional stage was dominated by Wyoming big sagebrush (*Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle & Young) with scattered Utah juniper (*Juniperus osteosperma* [Torr.] Little) of various ages. Bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve) and Indian ricegrass (*Achnatherum hymenoides* [Roem. & Schult.] Barkworth) were common grasses; various forbs, including bur buttercup (*Ceratocephala testiculata* [Crantz] Roth), were also common. Moving across the successional continuum to the late-successional juniper woodland, juniper increasingly dominated to the exclusion of most other plants in both the understory and overstory. The soil was Borvant gravelly loam derived from limestone alluvium; slopes were generally < 15% (USDA and NRCS, 2011).

A prescribed burn was scheduled to be implemented at the study area during the summer of 2006. However, the summer was characterized by multiple wildfires in the western United States and fire-fighting crews required to manage the prescribed burn were fully occupied until later than expected. The prescribed burn eventually occurred on 5 October 2006. Due to the lateness of the season, characterized by cool temperatures, elevated humidity, and low winds, in addition to above-normal precipitation during September and October 2006, the burn was only minimally effective. Less than 30% of the targeted area burned, and even those areas were spotty. The fire did not carry into mid- or late-successional juniper woodland. Hence, only the early-successional stage of juniper encroachment was included in the postburn evaluation.

Experimental Design

Before the burn, we established 10 sets of three adjacent plots in each of three vegetation patch types present in the early-successional juniper woodland (10 reps \times 3 adjacent plots \times 3 vegetation types = 90 plots in the area to be burned). These included juniper understory, sagebrush understory, and the interspaces between the scattered shrubs and trees. Plots measured 0.5 \times 0.5 m. In the case of juniper, 10 sets of three abutting plots were established under 10 different trees. For sagebrush, the three plots per set were established under three closely associated shrubs. In the interspaces, the three plots per set were established immediately adjacent to each other, but the sets were dispersed throughout the study site.

In order to measure the intensity of the fire, we placed an aluminum tag in the center of each plot. The tags measured 2 \times 8 cm and were painted with successive lines of Tempilaq temperature-sensitive paints. The lines of paint were subject to melting at 79°C, 121°C, 177°C, 232°C, 288°C, 343°C, 399°C, 454°C, and 510°C. The intensity of the fire at each plot was estimated by calculating the midpoint between the temperature rating of the last melted paint line and the subsequent unmelted line. Where none of the lines were melted, the temperature was estimated as 56°C (the midpoint between the average maximum ambient air temperature of 32°C and the lowest rated paint or 79°C). Where all of the lines were melted, the temperature was estimated as 540°C.

Because we could not predict the behavior of the fire in advance, subsequent to the prescribed burn, for purposes of comparing burned versus unburned conditions, a duplicate set of 90 plots was established in areas that escaped burning. Because the fire was spotty and discontinuous, unburned patches were plentiful and often located within a few meters from where the patchy fuel load carried the fire.

All plots were permanently delineated by driving 0.3-m lengths of 1-cm diameter metal rebar into the ground at each corner, with approximately 5 cm extending above the soil surface. Metal tags with the plot identification were attached to one of the rods at each plot. The locations of the plots were recorded with a global positioning system in order to assist in relocating them on subsequent visits.

One plot from each set of three was used for ocular estimation of the cover of biological soil crust organisms and vascular plants ("cover" plots). One plot was used for biotic analyses, including algal biomass and species identification ("biotic" plots). The remaining plot was used for destructive sampling to determine nitrogen fixation rates ("soil" plots).

Field Methodology

Data were collected in burned and unburned plots soon after the burn (mid-October 2006) and again in September 2007 and June 2008. For ocular estimates and sample collection, a 0.5 m \times 0.5 m plot frame was constructed of 1.9-cm diameter PVC pipe. The numbers 1–9 were inscribed at 5-cm intervals on one side of the plot frame, and the letters A–I were inscribed in a similar fashion on a perpendicular side. This design created a grid of 100 squares with 81 grid

Table 1
Mean monthly and annual precipitation (cm) at nearby Tooele, Utah during the course of the study. Also included are long-term (1896–2007) precipitation measures (Desert Research Institute, 2011).

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
2006	7.1	2.8	8.3	7.5	1.8	2.2	4.1	1.0	5.3	5.8	1.6	3.4	50.8
2007	4.3	4.5	6.5	1.0	2.3	1.8	5.6	1.4	4.2	2.8	1.2	8.3	43.7
2008	4.3	6.4	3.4	1.9	8.9	6.5	0.2	3.5	1.0	1.9	1.0	-	38.0
1896–2007	3.4	3.9	5.4	5.4	5.0	2.6	2.1	2.2	2.7	4.0	4.1	3.5	45.4

intersections. On each sampling date, the plot frame was lowered over each “cover” plot, using the corner markers as guides for correct placement. We made ocular estimates of the percent cover of lichens and mosses. Lichens were recorded by species and as a total.

The plot frame was also placed over each of the “biotic” plots. Small cylindrical core samples (1-cm diameter and 1-cm deep) were taken at 10 predetermined random grid intersections on each sample date. The 10 samples per plot were combined into a single composite sample for use in determining algal biomass and algal species identification. Randomization was done without replacement such that no point was resampled over the course of the study.

Finally, the plot frame was placed over each of the “soil” plots. We collected two larger cores (10-cm diameter × 6-cm deep) per plot from randomly determined grid intersections on each sample date. These cores were collected intact and transported to the soil laboratory at Brigham Young University for determination of nitrogen fixation rates. As in the case of the “biotic” plots, the sample locations were determined randomly and without replacement for each plot.

Biotic Analyses

Algal Biomass

Chlorophyll *a* is often used as an index for measuring the productivity or biomass of cyanobacteria in the soil. To measure chlorophyll *a* content, we used the methods of Bell and Sommerfield (1987) as modified by Kasper (1994). Soil samples were passed through a 2-mm sieve to remove rocks and large organic particles. We took three 1.5-g subsamples from the composite sample from each “biotic” plot and placed them in centrifuge tubes. Five mL of dimethyl sulfoxide (DMSO) were added to each tube, and the tubes were shaken thoroughly. The samples were heated to 65°C in dim light conditions to prevent degradation of the chlorophyll. After 30 minutes, the samples were again shaken vigorously and returned to the oven for an additional 30 minutes. The samples were then removed from the oven and allowed to cool. After cooling, the samples were centrifuged, and the supernatant was decanted into test tubes. The supernatant was filtered through a glass fiber filter to remove residual clays and particles that could interfere with quantification. We deviated from the method of Kasper (1994) by determining chlorophyll fluorometrically. The fluorometer (Turner model 450) was restandardized for each sample date with known chlorophyll standards from Sigma Scientific Supply to ensure comparable results between sampling periods.

Algal Identification

In order to isolate and identify algal taxa present in the plots, dilution plate methods were employed (Johansen et al., 1993) utilizing Z-8 medium (Carmichael, 1986). We determined that 10³ dilution plates represented an ideal dilution rate for our sites, and all samples were plated in triplicate. The cultures were maintained at 200 μE

illumination on a 12:12-hour light-to-dark cycle. More than 200 strains were isolated, but far fewer species were recovered, as many species had numerous representative strains. Taxa were identified on the basis of morphology and life history as observed under a light microscope. Two photomicroscopes were utilized (Olympus B-Max, Zeiss Axioskop), both equipped with high-resolution Nomarski DIC and epifluorescence optics.

Nitrogen Fixation

Nitrogen fixation rates were estimated using acetylene reduction techniques (Terry and Jolley, 1994). Soil samples were collected from the field using a PVC coring device to remove undisturbed soil profiles 10-cm diameter and 6-cm deep from the “soil” plots. Core containers were sealed with plexiglass covers with predrilled holes designed to accommodate rubber stoppers equipped with glass tubes containing rubber septa. The cores were moistened with water, and a volume of acetylene gas was added to provide a 10% acetylene concentration in the air. Samples were incubated for 24 hours in a growth chamber. A 0.25-mL air sample was then taken from the incubation container and analyzed for ethylene using an HP 5890 series II gas chromatograph equipped with a flame ionization detector. The rate of nitrogen fixation from the samples was computed with the following equation:

$$\text{mmol N}_2 \cdot \text{m}^{-2} \cdot \text{hr}^{-1} = \left(\frac{\{(\text{ethylene peak})(\text{nL headspace})(1/27.8 \text{ nL})\}}{\{(24 \text{ h})(\text{surface area})\}} \right) / 3(10,000)$$

Statistical Analyses

Dependent variables analyzed included the covers of bryophytes and lichens, chlorophyll *a*, and nitrogen fixation by cyanobacteria in the soil. These were modeled as generalized linear mixed models (GLMM) with random intercepts by plot and included factors for burn status (two levels), date (three levels), vegetation type (three levels), and all two-way and three-way interactions. Covers of bryophytes and lichens were modeled using a beta distribution with a logit link function and a zero-one adjustment (Smithson and Verkuilen, 2006), nitrogen fixation was modeled using a log-normal distribution with an adjustment for zeros (Stahel, 2002), and chlorophyll *a* was modeled with a normal distribution. Significance of treatments was assessed using Tukey pairwise comparisons of the groups defined by the three-way interaction within each vegetation type at a family-wise type I error rate (FWER) of 0.05. Results of these tests are included in the plots of group least squares means and 95% confidence intervals as compact letter displays where groups that share a letter were not significantly different at the 0.05 FWER. These analyses were conducted using SAS PROC GLIMMIX in Version 9.4 of the SAS System for Windows. Copyright © 2014 SAS Institute Inc. SAS and all other SAS Institute Inc.

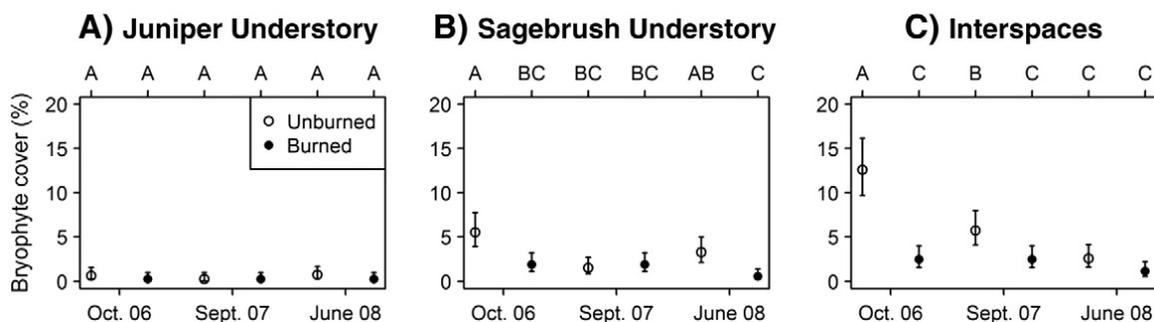


Fig. 1. Percent cover of bryophytes (mosses) in unburned and burned juniper, sagebrush and interspace plots following a prescribed burn south of Tooele, Utah on 5 October 2006. Groups with the same letter within the same vegetation patch type are not significantly different at $\alpha = 0.05$.

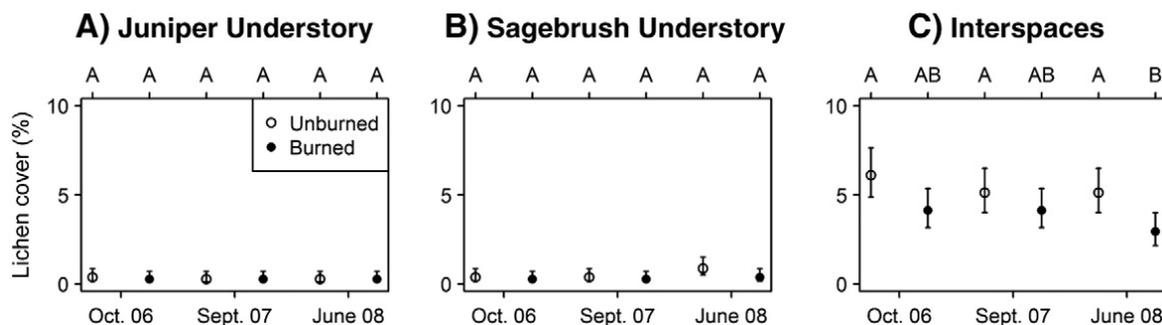


Fig. 2. Percent cover of lichens in unburned and burned juniper, sagebrush, and interspace plots following a prescribed burn south of Tooele, Utah on 5 October 2006. Groups with the same letter within the same vegetation patch type are not significantly different at $\alpha = 0.05$.

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Results

Burn Characteristics

Surface temperatures in the shrub interspaces during the burn were consistently below the minimum threshold for measurement (79°C). The mean temperature of the fire at ground level under sagebrush was 377°C. The mean temperature under juniper was significantly higher at 441°C. The temperature of the fire was not significantly correlated with any of the measured variables in the immediate postfire condition.

Organic Cover

Mean cover of live juniper on juniper plots was 98% before the burn. Although dead juniper remained standing, cover of live juniper was eliminated by burning, indicating complete kill of all trees sampled. No seed germination was detected during the first 20 months following the fire.

Mean cover of live sagebrush was 97% on sagebrush plots before the prescribed burn. Where the fire burned through the sagebrush plots, it typically consumed all organic matter above the soil surface. Live sagebrush cover on those plots was eliminated by the fire, suggesting complete kill of sagebrush that was burned. No germination of seeds was noted in the 20 months following the burn.

Mosses were rare beneath juniper and, as such, their cover was not immediately changed by burning or over time (Fig. 1). Moss cover was more prevalent under sagebrush and in the interspaces. It declined immediately as a result of the fire in both vegetation

types. Cover of mosses remained significantly depressed on burned and unburned sagebrush plots over the course of the study but recovered to preburn levels on unburned plots by the second year. Fire, likewise, significantly reduced moss cover on interspace plots that burned, and it did not recover over the 2 years of the study. Moss cover declined on unburned plots after 1 year, although less than burned plots. Moss cover continued to decline on unburned plots until it did not differ significantly from burned plots by the second year post burn.

Lichens were scarce beneath juniper and sagebrush before the burn. Hence, the fire had little impact on their abundance there (Fig. 2). Although there were more lichens in the interspaces, the effect of the burn there was minimal. By the second year post burn, the cover of lichens was less in the burned condition; no other differences were significant. A number of lichen species were present. These included *Aspicilia fruticulosa* (Eversm.) Flagey, *A. hispida* Mereschk., *Buellia elegans* Poelt, *Caloplaca tominii* Savicz, *Collema tenax* (Sw.) Ach., *Fulgensia bracteata* (Hoffm.) Räsänen, *Psora cerebriformis* W.A. Weber, *P. decipiens* (Hedwig) Hoffman., *P. tuckermanii* R. Anderson ex Timdal, *Placidium squamulosum* (Ach. Bruess), and *Toninia sedifolia* (Scop.) Timdal. The species that occurred most frequently were *A. hispida*, *C. tominii*, and *C. tenax*.

Biotic Analyses

Algal Biomass

As a measure of algal biomass, the chlorophyll *a* content in the soil of all plots was measured and is presented in Figure 3. Chlorophyll *a* content of the soil beneath juniper declined as a result of the burn and remained at a reduced level over the next 2 years, although the content after 1 year did not differ significantly from the unburned plots. Chlorophyll *a* content in the soil beneath sagebrush tended to decline in burned plots but increase in unburned plots. Chlorophyll *a* content in the interspaces was not reduced immediately by the

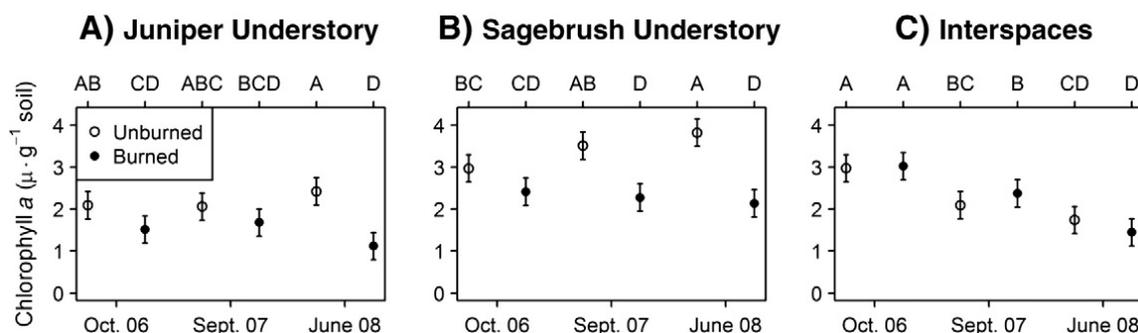


Fig. 3. Chlorophyll *a* content of the soil of unburned and burned juniper, sagebrush, and interspace plots following a prescribed burn south of Tooele, Utah on 5 October 2006. Groups with the same letter within a vegetation patch type are not significantly different at $\alpha = 0.05$.

Table 2
Algal species present in vascular plant communities before and after the fire.

	UI	US	UJ	BI	BS	BJ
CYANOBACTERIA						
Synechococcineae						
<i>Leptolyngbya crispata</i>	I	I		I		
<i>Leptolyngbya foveolarum</i>	C	I		C	P	
<i>Leptolyngbya tenuis</i>	I				P	
<i>Leptolyngbya</i> sp.	C	C			C	
<i>Protolyngbya</i> sp.				I		
<i>Trichocoleus</i> sp.	I					
Oscillatorineae						
<i>Aphanothece</i> sp.					P	
<i>Borzia perikleii</i>					I	
<i>Cyanosarcina</i> sp.					I	
<i>Microcoleus steenstrupii</i>					P	
<i>Microcoleus vaginatus</i>	A	I	P	I		
Nostocineae						
<i>Hassallia bouteillei</i>	P					
<i>Hassallia</i> sp.	P					
<i>Nostoc desertorum</i>				I	P	
<i>Nostoc indistinguendum</i>	I	I		C		
<i>Nostoc sphaericum</i>	P					
<i>Nostoc</i> sp.	A	I		C		
<i>Tolypothrix distorta</i>	P					
<i>Tolypothrix tenuis f terrestris</i>					P	
<i>Tolypothrix</i> sp.	I				C	
<i>Trichormus</i> sp.	C				P	
CHLOROPHYTA (green algae)						
<i>Bracteacoccus</i> sp.	P	I	I	P	I	P
<i>Chlamydomonas</i> sp.						P
<i>Chlorella minutissima</i>	I	C	I	I	I	C
<i>Chlorella</i> sp.	P		P	I		
<i>Chlorococcum</i> sp.					I	
<i>Chlorosarcina</i> sp.						
<i>Coccomyxa</i> sp.	P	P	P		P	
<i>Cystomonas</i> sp.		P				
<i>Dictyochloris</i> sp.	P					
<i>Diplosphaera chodatii</i>		P	P			
<i>Diplosphaera</i> sp.		I				
<i>Elliptochloris</i> sp.			P			
<i>Fasciculochloris</i> sp.		P				
<i>Follicularia</i> sp.					P	
<i>Macrochloris</i> sp.		I			P	
<i>Myremecia</i> sp.	I	P	I		I	P
<i>Neochloris</i> sp.						
<i>Pseudotetracystis</i> sp.	I	I	P	P		P
<i>Radiosphaera</i> sp.		P		I		
<i>Scenedesmus</i> sp.	P	I	P	P		
<i>Spongiochloris</i> sp.	P					
<i>Stichococcus bacillaris</i>		P				
<i>Tetracystis</i> sp.	P	P				
<i>Trebouxia showmanii</i>	P					
<i>Trebouxia</i> sp.	P	I				
<i>Trochisciopsis tetraspora</i>		P			P	I
TRIBOPHYTA (yellow-green algae)						
<i>Botrydiopsis</i> sp.	P					
<i>Heterococcus capitatus</i>				P		
<i>Heterococcus</i> sp.		P		C	P	P
<i>Xanthonema montanum</i>	P					
<i>Xanthonema</i> sp.	C	C	I	C	I	
Cyanobacterial species richness	14	6	1	15	3	0
Eukaryotic species richness	15	18	10	12	8	7
Total algal species richness	29	24	11	27	11	7

UI = unburned interspace between shrubs, US = unburned sagebrush understory, UJ = unburned juniper understory, BI = postburn interspace between shrubs, BS = postburn sagebrush understory, BJ = postburn juniper understory. Abundance codes are based on the number of isolates obtained for each species and are: P = present (only 1 isolate), I = infrequent (2–4 isolates), C = common (5–10 isolates), A = abundant (11–25 isolates).

burn but declined in the months following the fire on both burned and unburned plots, which did not differ from each other.

Algal diversity

An effort was made to isolate all algal species present in burned and unburned plots soon after the burn to ascertain the effect of the fire on algal species diversity. A total of 52 distinct algal morphotypes were observed, including 21 cyanobacteria, 26 chlorophytes, and 5 tribophytes (Table 2). The shrub interspace areas had highest algal diversity, with little difference in preburn and postburn species richness (29 and 27 taxa, respectively). The preburn sagebrush understory area had comparable diversity, with 24 taxa. However, the fire appeared to damage the algal community in sagebrush understory, as diversity dropped to 11 taxa after the fire. Juniper understory supported notably fewer algal species, with only 11 taxa before the fire and 7 taxa after the fire. It is also notable that under juniper there were relatively few algae present, as most taxa collected in these communities were represented by a single isolate.

Nitrogen Fixation

Nitrogen fixation of soil-dwelling organisms did not appear to be reduced as an immediate consequence of burning in any of the vegetation types (Fig. 4). Nitrogen fixation declined with time in both burned and unburned plots of juniper understory and interspaces; the variation was minimal in sagebrush understory.

Discussion

That the prescribed fire in this study was spotty and limited to the early-successional juniper woodland was not entirely unexpected given the suboptimal burn conditions. In addition, fine fuel loads typically decline as juniper stands mature (Barney and Frischknecht, 1974). Consequently, later-successional juniper stands are often difficult to burn (Martin, 1978; Bunting, 1987), as was noted at our study site.

Within the early-successional juniper, the fire carried more readily, affecting juniper, sagebrush, and, to a more limited extent, the interspaces. Utah juniper is susceptible to fire (Barney and Frischknecht, 1974). Mortality is highest among mature trees when 60% or more of the canopy is scorched (Springfield, 1976). Where the fine fuel load was adequate, many older trees growing in the early successional area of the present study were scorched and died. Except for individual trees that escape burning, recovery is by seed. It typically requires 10 years or more for juniper to reappear (Barney and Frischknecht, 1974). Predictably, no recruitment was noted in the 20 months following the burn in this study.

Wyoming big sagebrush typically ignites readily and produces a hot fire (Neuenschwander, 1980). As confirmed in this study, most individuals are killed if affected by fire (Wambolt and Payne, 1986). Reproduction is by seed, and seedlings may appear within 3 years (Barney and Frischknecht, 1974). Seedlings had not yet appeared at our study site after 20 months.

In this study, the prescribed burn caused a significant and long-term reduction in moss cover in the sagebrush and interspace vegetation types where it was most abundant. A significant decline in moss cover following fire has been noted in other published studies related to rangelands of the western United States (Antos et al., 1983; Johansen et al., 1984, 1998). Bowker et al. (2004) detected a large but statistically insignificant decline in moss cover following a fire in the Palouse region of the Pacific Northwest. Schulten (1985) also reported a reduction in moss cover following burning of sand prairie in southeastern Iowa, but the difference was not statistically significant. What seemed less intuitive was the decline of moss cover in unburned plots. However, as mosses tend to occur in protected environments, it should not be unexpected that they would decline when subjected to warmer, windier conditions

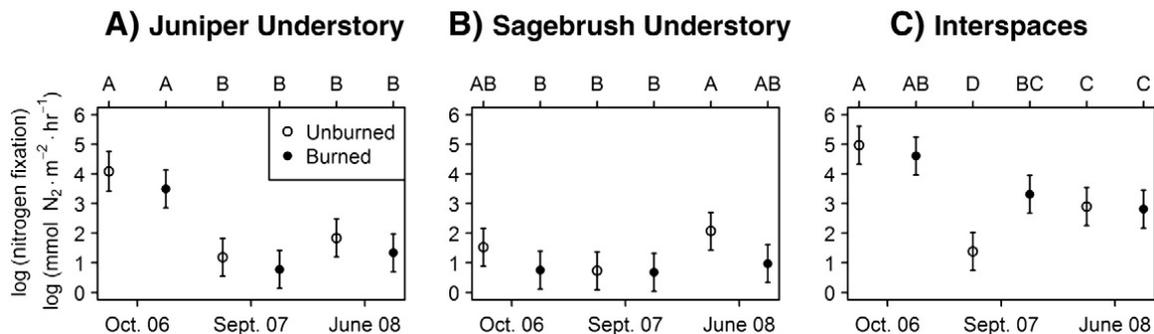


Fig. 4. Nitrogen fixation rates ($\text{mmol N}_2 \text{ m}^{-2} \text{ hr}^{-1}$) in mineral soil in unburned and burned juniper, sagebrush, and interspace plots following a prescribed burn south of Tooele, Utah on 5 October 2006. Bars with the same letter within a vegetation patch type are not significantly different at $\alpha = 0.05$.

associated with the general loss of surrounding vegetation that would otherwise protect them from warmer temperatures and desiccating wind.

Other studies have suggested that fire significantly diminishes lichen cover in rangeland communities (Antos et al., 1983; Johansen et al., 1984; Schulten, 1985; Hilty et al., 2004; Ponzetti et al., 2007). Of the studies suggesting a decline in lichens, only Antos et al. (1983) were able to provide sufficient information on the timing and aftermath of the burn to suggest that it was intense. Nevertheless, it stands to reason that intense fires are likely detrimental to lichen survival. Bowker et al. (2004) found that a low-intensity fire in the Palouse prairie had minimal impact on lichen cover. This corroborates the results of the present study where the low-intensity, spotty fire produced no significant difference in lichen cover between burned and unburned plots in any vegetation type.

The reduction in chlorophyll *a* content under both juniper and sagebrush following the fire suggests immediate mortality among chlorophyll-bearing organisms. Similar mortality following fire was detected in a sagebrush community in Idaho (Rychert, 2002), a greasewood community in Utah (Kasper, 1994), and the Palouse prairie of Oregon (Bowker et al., 2004). Ford and Johnson (2006) reported a decline in chlorophyll *a* following a dormant season burn in the shortgrass steppe of New Mexico, but not following a growing season burn. The continued decline in chlorophyll *a* content of the interspaces over the 20 months following the burn may be indicative of greater insolation and exposure to desiccating winds following the removal of nearby shrubs. The lack of a significant difference between burned and unburned plots in the interspace patches confirms the minimal direct impact of the burn there.

The higher diversity of cyanobacterial species compared with the green algal flora noted in this study is similar to that previously reported from this region (Johansen et al., 1984; Johansen and Rushforth, 1985; Johansen and St. Clair, 1986). Some notable shifts occurred in the cyanobacterial communities following the burn, even in the less affected shrub interspaces. In dilution plates before the burn, *Microcoleus vaginatus* was a clear dominant and more than 20 isolates were made from these plates. This easily identified species decreased in abundance after the fire. We suspect the increase in Oscillatorineae in interspace plots after the fire may be an artifact due to the absence of *M. vaginatus* from many of the plates. This taxon overgrows the plates when present and likely prevents the emergence of the slower growing taxa, *Aphanothece* sp., *Borzia perikleii*, and *Microcoleus steenstrupii*. We also noted a shift in the distribution of *Nostoc* species in these communities (Table 2). The heterocystous taxa, which have the potential to fix atmospheric nitrogen, were clearly more abundant in the shrub interspaces. Their presence was depressed in the sagebrush understory, and they were absent altogether from the juniper understory. The eukaryotic algae (chlorophytes and tribophytes) demonstrated more

even species richness across vegetation patch types than was seen in the cyanobacterial community. Depression in richness was evident in the juniper understory and occurred in response to fire. Species diversity for eukaryotic species was highest in the sagebrush understory, although after the fire diversity had dropped by over half. The dominant genera were *Chlorella* and *Xanthonema*.

Although few other studies have examined the effects of fire on nitrogen fixation by biological soil crusts in western ecosystems, they tend to confirm the absence or diminutive nature of short-term effects. Burns (1983) found no difference in nitrogen fixation between unburned and recently burned sagebrush grasslands about 50 km east of our study site. Ford and Johnson (2006) detected a significant reduction in nitrogen fixation soon after a dormant season burn in a desert grassland in New Mexico, but not after a growing season burn. Within a year, the differences had disappeared. Four years following a summer burn in a desert shrubland in Utah, Johansen et al. (1998) found reduced nitrogen fixation in burned plots compared with unburned plots, but the difference was not significant. There were, likewise, no differences in nitrogen fixation between burned and unburned plots 2 years following a burn in a creosote bush (*Larrea divaricata*) grassland north of El Paso, Texas (Johansen et al., 1998). The absence of significant and/or sustained reductions in nitrogen fixation in the present study, as well as in others, may be related to the presence of heterotrophic bacteria, which can also fix nitrogen (Klubek and Skujinš, 1980; Jeffries et al., 1992). Heterotrophic bacteria are not dependent on sunlight like the photoautotrophic cyanobacteria; they can live below the surface and are less likely to be damaged by intense surface heat. The longer-term depression of nitrogen fixation in juniper understory and interspaces may, like bryophyte and lichen cover, and chlorophyll *a*, be attributable to the general harsher environments within and adjacent to the burned areas.

Implications

Although this study was limited to a single burn at a single site, it suggests that, while prescribed burning can negatively affect some biological soil crust components in some parts of the early successional stage of a juniper woodland, the overall impact of low-intensity fire on biological soil crusts in juniper woodlands may be of minimal concern. If the intent of prescribed burning is a reduction in juniper, burning of early successional juniper woodland is appropriate because most affected trees were killed. Control of sagebrush can likewise be accomplished by low-intensity, cool-season fires without serious damage to the biological soil crust. Due to the spotty nature of the fire in the shrub interspaces, intact biological soil crusts may provide cyanobacterial inoculants to recolonize the soil in the juniper and sagebrush vegetation patch types, which were more affected by the fire. Intense fires should be avoided due to the potential

for greater encroachment into the shrub interspaces, which contain the best developed biological soil crusts. This information, plus the fact that late successional juniper woodlands are difficult to burn, suggests that burning of early succession juniper may be a preferred method to control juniper encroachment on western rangelands.

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