

Effects of dormant- vs. growing-season fire in shortgrass steppe: Biological soil crust and perennial grass responses

P.L. Ford^{a,*}, G.V. Johnson^b

^a*USDA Forest Service Rocky Mountain Research Station, 333 Broadway SE, Suite 115,
Albuquerque, NM 87102, USA*

^b*Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA*

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Abstract

This research experimentally examined seasonal effects of fire on biological soil crusts and perennial grasses in shortgrass steppe. We predicted dormant-season fire would have greater negative effects on biological soil crusts than fire during the growing season, but less of an impact on perennial grasses than fire during the growing season. Treatments were dormant- and growing-season fires and unburned reference condition plots. Response variables included biological soil crust and grass percent ground cover, and crust nitrogen fixation and chlorophyll *a* content. Results indicated shortgrass steppe can recover from fire in three to 30 months, dependent on fire season. Burning during the dormant-season had little effect on grass cover, but decreased nitrogen fixation and reduced chlorophyll *a* content in crusts. Growing-season fire negatively impacted grass cover, but reduced the impact of fire on soil crusts. Most of the fire effects in this study were of relatively short duration and strongly tied to weather patterns.

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Keywords: *Bouteloua gracilis*; *Buchloë dactyloides*; Biological soil crust; Fire; Shortgrass steppe

1. Introduction

The reestablishment of periodic fire is fundamental to the ecological restoration of grasslands in the Southwestern United States (Ford et al., 2004). However, prior to

*Corresponding author. Tel.: +1 505 724 3670; fax: +1 505 724 3688.

E-mail address: plford@fs.fed.us (P.L. Ford).

reintroducing large-scale fire as a management tool, the appropriate fire season and fire effects on ecosystem components need to be determined. This paper examines the effects of fire season on two different plant life forms in shortgrass steppe, non-vascular biological soil crusts and vascular perennial grasses.

Fire helps to maintain the stability of grasslands by reducing the establishment of trees and shrubs, releasing nutrients bound up in organic matter, and accelerating the rate of decomposition in the soil (Ford et al., 2004). When dry, fuels of semi-arid grasslands may support high rates of fire spread (Rothermel, 1983), whereas green or actively growing fuels promote a discontinuous or patchy fire regime (Andrews, 1986; Steuter and McPherson, 1995).

We predicted that burning during the dormant-season would have greater negative effects on the biological soil crusts than burning during the growing-season due to seasonal differences in fine fuels. The high moisture content of green, living plant tissue makes it more difficult to ignite, than dry plant litter which ordinarily promotes fire spread (White and Hanselka, 2000). Therefore, fire intensity and severity during the dormant season should be higher, resulting in more widespread damage and mortality to exposed surface crusts than growing-season fire.

Conversely, fire during the growing season has been shown to reduce regrowth in vascular plants because large portions of photosynthetically active tissue are killed (Briske, 1991; Briske and Richards, 1995). Therefore, it was predicted that dormant-season fire would have less of an impact on perennial grasses because most of the above-ground biomass during the dormant season is already dead.

1.1. Biological soil crusts

Biological soil crusts, also known as soil algal crusts, microbiotic crusts, or cryptogamic crusts, cover extensive portions of the arid and semi-arid regions of the world. They consist of water-stable surface soil particles and aggregates held together by algae, fungi, cyanobacteria, lichens, and mosses (Johansen, 1993). Many of the same components (i.e., cyanobacteria, green algae, lichens, and mosses) are the dominant biological crust components in the Great Plains (Rosentreter and Belnap, 2001).

Several researchers have suggested that biological soil crusts are critically important components of the arid and semi-arid lands in which they occur (Harper and Marble, 1988; Metting, 1991; Johansen et al., 1993). Input, loss, and cycling of nutrients are fundamental processes in any ecosystem (Evans and Johansen, 1999). Biological soil crusts are important contributors to nutrient cycling for many reasons, including the ability of cyanobacteria and lichens to fix atmospheric nitrogen (Evans and Johansen, 1999). Biological soil crusts also contribute to soil fertility through organic carbon contributions and accumulation of fine soil particles which provide the greatest amount of available plant nutrients (Johansen et al., 1993).

One of the most important effects that biological soil crusts can have on ecosystem dynamics is stabilization of soil surfaces (St. Clair and Johansen, 1993). They have the potential to affect soil stability through reduction of water runoff and reduced sediment production by both wind and water moving across the soil surface (Belnap, 2001; Warren, 2001). In addition they affect seed germination and seedling establishment by providing microsites for plant establishment (St. Clair et al., 1984; Harper and Marble, 1988; Belnap et al., 2001).

Biological soil crusts are considered fragile and easily damaged by disturbance. Estimates of time for natural recovery of biological soil crusts from disturbance have varied widely, ranging from a few years to over 1000 years for full recovery of all components (Anderson et al., 1982; Johansen et al., 1982; Johansen et al., 1984; Callison et al., 1985; Jeffries and Klopatek, 1987; Cole, 1990; Belnap, 1993; Belnap and Warren, 2002). The large range of recovery estimates can be attributed to variation in crust type, soil, climate, disturbance type and severity, and the variables used to assess recovery.

Several studies have suggested disturbance by fire damages biological soil crusts (Johansen et al., 1984; Callison et al., 1985; West and Hassan, 1985; Kasper, 1994). Johansen (1993) suggests that season of fire may influence the severity of damage caused to biological soil crusts. However, empirical evidence for this hypothesis is lacking (Johansen, 1993).

1.2. Perennial grass cover

Steppe is a mid-latitude, semi-arid, generally treeless grassland, dominated by short grasses and bunch grasses, and characterized by large grazing mammals and burrowing animals (Lincoln et al., 1998). It has a wide distribution ranging from Eurasia to the Great Plains of central North America, including the American Southwest.

Characteristic North American steppe vegetation includes the perennial grasses *Buchloë dactyloides* (buffalograss), a sod-forming shortgrass, and *Bouteloua gracilis* (blue grama), a bunchgrass (Bailey, 1995). In the past, the effect of fire on shortgrass steppe has been considered negative largely based on conclusions from studies primarily directed at the use of fire as a tool to increase the forage value of grassland vegetation. Perceptions about the value of fire in shortgrass steppe may have been influenced by a desire for rapid increases in grassland productivity to benefit domestic livestock (Ford, 1999). However, based on an analysis of early fire-effects literature spanning 42 years (Ford, 1999), buffalograss and blue grama responses to fire appear to be predominantly neutral or positive and depend mainly on levels of precipitation.

Clipping and grazing studies have indicated that perennial forage species (e.g., buffalograss and blue grama) can withstand much more defoliation during seasons of dormancy than during periods of active vegetative growth (Cook, 1971; Vallentine, 1990). The season during which fire occurs may also affect plant response. Both buffalograss and blue grama are perennial, warm-season plants that use the C₄ photosynthetic pathway. They are generally adapted to warmer climates and distributed toward lower latitudes where average temperatures during the growing season are higher (Raven and Johnson, 1996). Cool-season plants with C₃ photosynthesis tend to have early spring, winter, or fall growing seasons when temperatures are cooler. Seasonality of fire is thought to be differentially detrimental to plants based on their season of active growth.

Early studies on the effects of fire season on buffalograss and blue grama response to fire indicated mixed results. Four studies, including Anderson et al. (1970), Heirman and Wright (1973), Schacht and Stubbendieck (1985), and White and Currie (1983), reported results from spring fires ranging from negative or neutral, to positive responses, over a time frame of 3 months to 16 years (Ford, 1999). Separation of spring burns into early- and late-spring categories revealed that early spring (March) burns produced neutral or positive responses, and late-spring burning (May) produced negative results (Anderson et al., 1970; Heirman and Wright, 1973; Ford, 1999). Over time, fall burns produced more herbage

than did spring burns (White and Currie, 1983). However, a late-spring (April) burn by Schacht and Stubbendieck (1985) showed a positive response by blue grama and a neutral response by buffalograss (Ford, 1999).

Only one study, Heirman and Wright (1973), took place in the southern Great Plains. Their research, located on the High Plains of Texas, analyzed buffalograss response after a spring (March) fire. They reported that spring burning had no effect on yields of buffalograss 3–6 months after fire. Brockway et al. (2002), reported that dormant-season fire may be the preferable method for restoring fire in shortgrass steppe ecosystems in the southern Great Plains where fire has been excluded for a prolonged period of time. However, post-treatment measurements by Brockway et al. (2002), again were only analyzed 5–6 months after fire treatment. More research is needed to clarify long-term buffalograss and blue grama response to seasonal fire in the southern Great Plains.

2. Methods

2.1. Site description

The study site was located in southern Great Plains shortgrass steppe on the Kiowa National Grassland (36°31'20"N, 103°3'30"W) of the Cibola National Forest in Union County, New Mexico. The southern Great Plains includes the eastern third of New Mexico, the northern two-thirds of Texas, and most of Oklahoma (Wright and Bailey, 1982). Almost all of the grassland in this region is composed of mixed or shortgrass communities (Brown, 1994). While these communities have been altered by grazing, and the indirect effects of fire suppression followed by shrub invasion, much of the grassland remains a perennial grass dominated landscape (Brown, 1994). Shortgrass steppe (plains grassland) is the most extensive grassland type in New Mexico, making up approximately 50% of the state's grassland vegetation (Dick-Peddie, 1993).

The study site consists of approximately 160 ha of shortgrass steppe that was never plowed, though it was grazed by livestock until 1990. The site is relatively homogenous and nearly flat, with an elevation of 1455 m at the southwest corner to 1472 m at the northwest corner. Average monthly temperatures range from 11 to 26 °C April through September, and from 3 to 12 °C October through March. Mean annual precipitation (MAP) between the years of 1931–1960 was 356 mm (Maxwell et al., 1981). In general, the majority of precipitation occurs from May through September, with peak rainfall in July (Fig. 1). Total precipitation was slightly below average in 1996 (346 mm), the year prior to fire treatments, as well as for 1997 (331 mm) and 1999 (272 mm). Total precipitation in 1998 (183 mm) was 50% below MAP (Fig. 2). Weather data were collected by the New Mexico State University State Climate Network at a climate station on the Clayton Livestock Research Center, located approximately 1 km from the study site.

2.2. Soil and vegetation

The soils consist of approximately 5% Dioxice loam (Aridic Calcistolls), 25% Gruver loam (Aridic Paleustolls), 25% Sherm clay loam (Torrtic Paleustolls), and 35% Spurlock loam (Ustollic Calciorthids) (Maxwell et al., 1981). Most of the soils mapping units contain pockets of other soil types resulting in a mosaic.

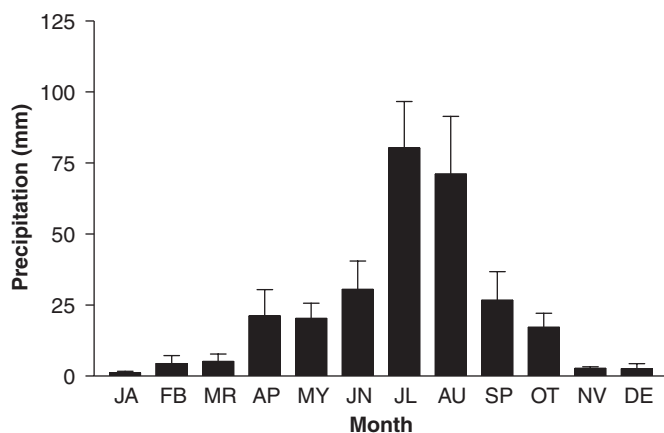


Fig. 1. Mean monthly precipitation 1996–1999 (New Mexico State University State Climate Network).

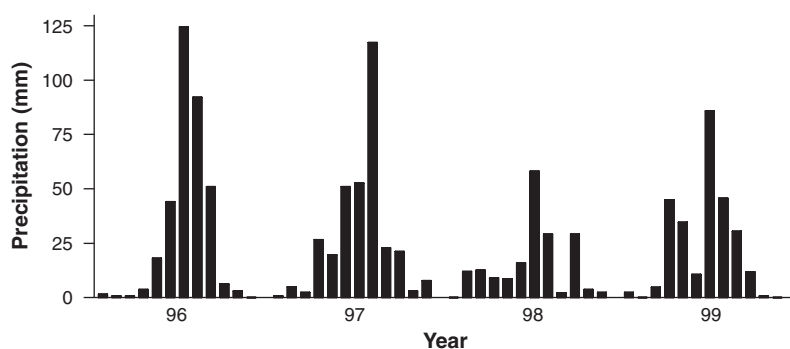


Fig. 2. Monthly precipitation 1996–1999 (New Mexico State University State Climate Network).

The loam soils are deep, well-drained and support almost shrubless native grassland dominated by *Buchloë dactyloides* (Nutt.) Engelm and *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths. These two species account for 85% of the plant cover (Maxwell et al., 1981). Of 99 total plant species, only five introduced species are found on the study site (Table 1). Grass fine fuel was estimated to be 1125 kg ha^{-1} (Paulette Ford, unpublished data).

2.3. Experimental design

The experimental design was completely randomized, with three treatments replicated five times. Five replicates/treatment were sampled twice, four replicates/treatment were sampled three times. The treatments were: (1) dormant-season fire April 1997, (2) growing-season fire July 1997, and (3) unburned. Treatments were randomly assigned to 15 $140 \text{ m} \times 140 \text{ m}$ plots. At least 60 m of unburned area separated the plots. Drip torches were used to burn “black lines” around the inside perimeter of each burn plot. The interior

Table 1

Plant list (family, species and common name), experimental fire research site, Kiowa National Grassland, Union County, New Mexico, USA

Agavaceae, Century-plant family	Euphorbiaceae, Spurge family
<i>Yucca glauca</i> , soapweed yucca	<i>Argythamnia mercurialina</i> , silverbush
Asclepiadaceae, Milkweed family	<i>Chamaesyce fendleri</i> , Fendler's sandmat
<i>Asclepias engelmanniana</i> , Engelmann's milkweed	<i>Chamaesyce lata</i> , hoary sandmat
<i>Asclepias latifolia</i> , broadleaf milkweed	<i>Euphorbia marginata</i> , snow on the mountain
<i>Asclepias pumila</i> , Plains milkweed	Fabaceae, Pea family
Asteraceae, Aster family	<i>Astragalus missouriensis</i> , Missouri milkvetch
<i>Ambrosia psilostachya</i> , western ragweed	<i>Astragalus mollissimus</i> , woolly locoweed
<i>Artemisia ludoviciana</i> , white sagebrush	<i>Caesalpinia jamesii</i> , James' holdback
<i>Berlandiera lyrata</i> , chocolate flower	^a <i>Melilotus officinalis</i> , yellow sweetclover
<i>Brickellia eupatorioides</i> , false boneset	<i>Psoraleidium tenuiflorum</i> , scurfpea
<i>Chaetopappa ericoides</i> , rose heath	<i>Sophora nuttalliana</i> , silky sophora
<i>Ericameria parryi</i> , Parry's rabbitbrush	Loasaceae, Loasa family
<i>Cirsium ochrocentrum</i> , yellowspine thistle	<i>Mentzelia nuda</i> , bractless blazingstar
<i>Conyza canadensis</i> , Canadian horseweed	<i>Mentzelia reverchonii</i> , Reverchon's blazingstar
<i>Dyssodia papposa</i> , fetid marigold	Malvaceae, Mallow family
<i>Engelmannia peristenia</i> , Engelmann's daisy	<i>Sphaeralcea coccinea</i> , scarlet globemallow
<i>Erigeron flagellaris</i> , trailing fleabane	Nyctaginaceae, Four-o'clock family
<i>Grindelia nuda</i> , curlytop gumweed	<i>Mirabilis linearis</i> , narrowleaf four o'clock
<i>Gutierrezia sarothrae</i> , broom snakeweed	Onagraceae, Evening Primrose family
<i>Helianthus annuus</i> , common sunflower	<i>Gaura coccinea</i> , scarlet gaura
<i>Heterotheca villosa</i> , hairy false goldenaster	Plantaginaceae, Plantain family
<i>Hymenopappus filifolius</i> , white ragweed	<i>Plantago patagonica</i> , woolly plantain
<i>Lactuca</i> sp., lettuce	Poaceae, Grass family
<i>Liatis punctata</i> , dotted gayfeather	<i>Andropogon gerardii</i> , big bluestem
<i>Lygodesmia juncea</i> , rush skeletonweed	<i>Aristida adscensionis</i> , sixweeks three-awn
<i>Machaeranthera pinnatifida</i> , lacy tansyaster	<i>Aristida purpurea</i> , Fendler three-awn
<i>Machaeranthera tanacetifolia</i> , tansyaster	<i>Aristida havardii</i> , Harvard's three-awn
<i>Ratibida columnifera</i> , upright prairie coneflower	<i>Bothriochloa laguroides</i> , silver beardgrass or bluestem
<i>Ratibida tagetes</i> , short-rayed prairie coneflower	<i>Bouteloua curtipendula</i> , sideoats grama
<i>Senecio riddellii</i> , Riddell's ragwort	<i>Bouteloua gracilis</i> , blue grama
<i>Packeranemexicanus</i> , New Mexico groundsel	<i>Bouteloua hirsuta</i> , hairy grama
<i>Stephanomeria pauciflora</i> , brownplume wirelettuce	^a <i>Bromus japonicus</i> , Japanese brome
<i>Tetraeneuris scaposa</i> , yellow daisy	<i>Buchloë dactyloides</i> , buffalograss
<i>Thelesperma megapotaicum</i> , greenthread	<i>Chloris verticillata</i> , tumble windmillgrass
^a <i>Tragopogon</i> sp., salsify	<i>Elymus elymoides</i> , squirreltail
<i>Vernonia marginata</i> , Plains ironweed	<i>Erioneuron pilosum</i> , hairy wooly grass, hairy tridens
<i>Zinnia grandiflora</i> , Rocky Mountain zinnia	<i>Hordeum pusillum</i> , little barley
Boraginaceae, Borage family	<i>Muhlenbergia arenicola</i> , sand muhly
<i>Cryptantha</i> sp., catseye	<i>Muhlenbergia torreyi</i> , ring muhly
Brassicaceae, Mustard family	<i>Monroa squarrosa</i> , false buffalograss
<i>Descurainia</i> sp., tansymustard	<i>Panicum capillare</i> , witchgrass
<i>Erysimum capitatum</i> , Pursh's wallflower	<i>Panicum hallii</i> , Hall's panicgrass
Cactaceae, Cactus family	<i>Panicum obtusum</i> , vine mesquite
<i>Echinocereus viridiflorus</i> , hedgehog cactus	<i>Pasocopyrum smithii</i> , western wheatgrass
<i>Opuntia imbricata</i> , tree cholla	<i>Pleuraphis jamesii</i> , James' galleta
<i>Opuntia phaeacantha</i> , prickly pear	<i>Schedonnardus paniculatus</i> , tumblegrass
<i>Opuntia polyacantha</i> , plains prickly pear	<i>Schizachyrium scoparium</i> , little bluestem
Chenopodiaceae, Goosefoot family	<i>Sporobolus cryptandrus</i> , sand dropseed
<i>Chenopodium berlandieri</i> , pitseed goosefoot	<i>Achnatherum</i> sp., needlegras
<i>Chenopodium incanum</i> , mealy goosefoot	<i>Vulpia octoflora</i> , sixweeks fescue
<i>Chenopodium pratericola</i> , desert goosefoot	Polygonaceae, Buckwheat family

Table 1 (continued)

^a <i>Kochia scoparia</i> , fireweed	<i>Eriogonum annuum</i> , annual buckwheat
^a <i>Salsola kali</i> , Russian thistle, tumbleweed	Portulacaceae, Purslane family
Convolvulaceae, Morning-glory family	<i>Portulaca</i> sp., purslane
<i>Evolvulus nuttallianus</i> , shaggy dwarf morning-glory	Scrophulariaceae, Figwort family
<i>Ipomoea leptophylla</i> , bush morning-glory	<i>Penstemon</i> sp., beardtongue
Cucurbitaceae, Cucumber family	Solanaceae, Potato family
<i>Cucurbita foetidissima</i> , buffalo gourd	<i>Physalis hederifolia</i> ., ivyleaf groundcherry
	<i>Solanum elaeagnifolium</i> , silverleaf nightshade
	<i>Solanum rostratum</i> , buffalobur nightshade
	Verbenaceae, Verbena family
	<i>Glandularia bipinnatifida</i> , mock vervain

^aIndicates introduced species.

of each plot was then burned using a strip headfire. Winds were gusting at approximately $9\text{--}18\text{ km h}^{-1}$ when treatments were applied for both fire seasons. Dormant-season fire maximum flame height was estimated to be 18–24 m in the center of the plots, and each plot took approximately 15 min to completely burn. Growing-season fire maximum flame height was estimated to be around 6 m, and plots took 30–40 min to burn.

2.4. Ground cover

Response variables were percent ground cover of perennial grasses, herbaceous dicots (live/dead), shrubs, cactus, litter, bare ground, and biological soil crust, in addition to biological soil crust nitrogen fixation (acetylene reduction), and chlorophyll *a* content. Biological soil crust was differentiated from non-biotic soil crust by the dark colored, rough, and cohesive surface of the former. However, biological soil crust was not differentiated from bare ground until after the dormant-season fire treatment. The ground cover variables were measured once a month during five time periods: (1) pre-treatment, March 1997, (2) post dormant-season fire, April–June 1997, (3) post growing-season fire, July–October 1997, (4) July–October 1998, and (5) October 1999. Crust samples were collected three times, in July 1997 and 1998, and October 1999. Due to time and funding constraints crust samples collected after 1997 were only analyzed for nitrogen fixation activity. Crust and soil samples collected in 1997 were analyzed for both nitrogen fixation activity and chlorophyll *a* content.

One, 100-m, 500-point, basal area line-point transect per plot (a point was dropped every 20 cm) was used to measure the ground cover response variables. Transects were randomly located within the inner 100 m × 100 m area of the plots. Four to five biological soil crust samples, and one soil sample were collected along the transects. The soil sample was collected from bare ground, at a depth of 0–1 cm, along the transects to measure background levels of nitrogen fixation and chlorophyll *a* content. Each sample was collected in a 9 cm petri dish.

2.5. Nitrogen fixation and chlorophyll analysis

Nitrogen fixation activity was measured using acetylene as a substitute substrate for nitrogen gas. Nitrogen fixing organisms enzymatically reduce acetylene gas to ethylene gas

which then is measured by gas chromatography. The presence of nitrogen gas in the incubation does not significantly interfere with the reduction of acetylene. Soil crust samples were exposed to acetylene using methods similar to those of Rychert and Skujins (1974). Because of the uncertainty of the conversion factor for acetylene reduction (Liengen, 1999) to nitrogen fixed, data are reported as nanomoles of ethylene $\text{cm}^{-2} \text{h}^{-1}$ formed by the crust samples.

Assays were conducted in 25 ml serum vials which had been modified by removal of the bottom of the vial. The serum vial was pressed into the crust sample to extract a subsample with an area of 6.16 cm^2 . The bottom of the vial was sealed with a rubber stopper and the crust saturated with ca. 3 ml of distilled water. Approximately, 1.5 h after moistening the crust, the mouth of the vial was sealed with a serum stopper and acetylene gas was injected into the vial to obtain a 10% acetylene atmosphere in air. Crusts were incubated in a plant growth chamber at 25°C with illumination of approximately $280 \mu\text{mol s}^{-1} \text{m}^{-2}$. After an incubation period of 4–4.5 h, duplicate 0.25 ml gas samples were removed and ethylene measured by gas chromatography. Ethylene formed by crust samples was corrected for the presence of a small amount of ethylene as an impurity in the added acetylene gas.

After the acetylene reduction assay, crust samples were stored in a refrigerator at $0\text{--}4^\circ\text{C}$, and subsequently a chlorophyll analysis was performed on samples to estimate the abundance of photosynthetic cryptogamic organisms present. Chlorophyll was measured using the monochromatic method of Lorenzen (Wetzel and Likens, 1991). Crust samples were removed from the refrigerator and shaken in the dark in 90% acetone for 2 h. Samples were then stored in the dark in a refrigerator, at $0\text{--}4^\circ\text{C}$, for 20–24 h. The extract was then filtered and absorbance measured at 650 and 750 nm with a spectrophotometer. The samples were then acidified by addition of HCl and the measurements repeated. The absorbance at 750 nm was used to correct for the presence of turbidity in the samples.

2.6. Statistical analysis

Permutation methods in SAS PROC MULTTEST (SAS Institute Inc., 1988, 1989–1996) were used for sets of three pairwise comparisons of percent ground cover response variables among treatments (Tables 2 and 3). Across treatment comparisons of acetylene reduction rates and chlorophyll content were made with Kruskal–Wallis one-way analysis of variance by ranks (SAS Institute Inc., 1989–1996). The Dunn Procedure (Rosner, 1995) was used for comparisons of specific treatment groups. See Table 4 for maximum, minimum, and median values. All comparisons were considered significant at $p \leq 0.05$.

3. Results

3.1. Reference condition grassland

In general, grass was the dominant ground cover ($>60\%$) on the untreated “reference condition” plots, followed by litter (16%), bare ground (13%), and biological soil crust (7%). Herbaceous dicots, shrubs, and cactus combined usually made up less than 1% of ground cover. Cyanobacteria were identified as the dominate component of the biological crust based on the samples’ dark, rough surface appearance and infrequent occurrence of lichen structures. Cyanobacteria occurrence was verified by microscopic examination (personal communication David Hanson). Crust-free soil on untreated plots did not have

Table 2

Percent ground cover, mean and standard deviation (SD), by treatment over time

Sample period	Treatment (<i>N</i>)	Crust (%)	Bare ground (%)	Litter (%)	Grass (%)
		Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)
March 1997 (Pre-treatment)	Unburned (4)	No data	13 (5)	16 (7)	66 (9)
	Dormant (4)	No data	13 (3)	17 (4)	64 (94)
	Growing (4)	No data	20 (6)	18 (3)	60 (8)
April–June 1997 (Post dormant-season fire)	Unburned (5)	5 (4)	8 (3)	23 (6)	69 (5)
	Dormant (5)	5 (4)	18 (3)	33 (4)	44 (4)
July–October 1997 (Post growing-season fire)	Unburned (5)	10 (2)	6 (3)	31 (10)	57 (7)
	Dormant (5)	8 (4)	16 (4)	46 (2)	50 (4)
	Growing (5)	5 (3)	16 (4)	25 (4)	32 (5)
July–October 1998	Unburned (4)	7 (1)	5 (2)	22 (1)	64 (3)
	Dormant (4)	7 (4)	15 (3)	22 (5)	54 (3)
	Growing (4)	3 (1)	25 (8)	26 (3)	43 (6)
October 1999	Unburned (4)	6 (4)	7 (2)	16 (4)	66 (6)
	Dormant (4)	5 (4)	11 (8)	9 (3)	74 (7)
	Growing (4)	2 (1)	17 (4)	12 (6)	68 (11)

Table 3

Comparison of ground cover categories by treatments; unburned (U), dormant-season fire (D), and growing-season fire (G)

Sample period	Crust (%)	Bare ground (%)	Litter (%)	Grass (%)
	Contrast, <i>P</i> value	Contrast, <i>P</i> value	Contrast, <i>P</i> value	Contrast, <i>P</i> value
March 1997 (Pre-treatment)	No data	U vs. D 0.99	U vs. D 1.00	U vs. D 1.00
	No data	U vs. G 0.46	U vs. G 1.00	U vs. G 0.95
	No data	D vs. G 0.73	D vs. G 1.00	D vs. G 0.99
April–June 1997 (Post dormant season fire)	U vs. D 1.00	U vs. D 0.02*	U vs. D 0.16	U vs. D 0.0004*
July–October 1997 (Post growing-season fire)	U vs. D 0.69	U vs. D 0.02*	U vs. D 0.91	U vs. D 0.54
	U vs. G 0.17	U vs. G 0.03*	U vs. G 0.02*	U vs. G 0.0001*
	D vs. G 0.91	D vs. G 1.00	D vs. G 0.001*	D vs. G 0.01*
July–October 1998	U vs. D 1.00	U vs. D 0.29	U vs. D 1.00	U vs. D 0.18
	U vs. G 0.27	U vs. G 0.005*	U vs. G 0.83	U vs. G 0.003*
	D vs. G 0.27	D vs. G 0.15	D vs. G 0.91	D vs. G 0.10
October 1999	U vs. D 0.99	U vs. D 0.96	U vs. D 0.47	U vs. D 0.92
	U vs. G 0.51	U vs. G 0.24	U vs. G 0.97	U vs. G 1.00
	D vs. G 0.92	D vs. G 0.76	D vs. G 0.98	D vs. G 0.99

*Indicates $p \leq 0.05$.

Table 4
Biological soil crust acetylene reduction and chlorophyll *a* content by treatment over time*

Sample period	Treatment (<i>N</i>)	Nanomoles ethylene (cm ⁻² h ⁻¹)	Chlorophyll content (µg cm ⁻²)
		Max–Min (Median)	Max–Min (Median)
July 1997	Unburned (4)	4.72–0.004 (2.09) ^b	4.06–2.39 (2.88) ^b
	Dormant-season (4)	0.006–0.003 (0.004) ^a	2.27–0.57 (1.42) ^a
	Growing-season (4)	3.28–0.007 (0.109) ^{a,b}	3.88–1.44 (2.18) ^{b,a}
July 1998	Unburned (4)	0.134–0.014 (0.09) ^b	
	Dormant-season (4)	0.543–0.038 (0.136) ^b	
	Growing-season (4)	0.945–0.047 (0.436) ^b	
October 1999	Unburned (3)	7.710–2.31 (6.22) ^b	
	Dormant-season (3)	5.28–5.19 (5.24) ^b	
	Growing-season (3)	4.96–3.66 (4.78) ^b	

*Median values with the same letter for each sample period are not significantly different ($p \leq 0.05$).

significant acetylene reduction activity (activity ranged from 0 to 0.005 nanomoles ethylene cm⁻² h⁻¹), and had low or non-detectible chlorophyll content (contents ranged from 0 to 1.0 µg cm⁻² of chlorophyll *a*).

3.2. Biological soil crust

Percent biological soil crust cover did not differ among treatments for all sampling periods (Tables 2 and 3). In late July/August 1997, acetylene reduction (reported as nanomoles ethylene cm⁻² h⁻¹) significantly differed among treatments ($p = 0.05$) (Table 4). The Dunn Procedure, with an adjusted alpha level of 0.008 and critical value $z = 2.41$, indicated that 3 months post fire, dormant-season (April 1997) fire treated crusts had significantly lower rates of acetylene reduction than unburned crusts ($z = 2.65$). Growing-season (July 1997) fire treated crusts did not significantly differ from unburned ($z = 0.97$) or dormant-season fire treated crusts ($z = 1.81$). One year later (July 1998) there were no significant differences among treatments ($p = 0.24$). There were no significant differences up to 2.5 years after the fire treatments ($p = 0.30$) (Table 4).

In 1997, chlorophyll *a* content significantly differed between treatments ($p = 0.05$) (Table 4). The Dunn Procedure, again with an adjusted alpha level of 0.008 and critical value $z = 2.41$, indicated dormant-season (April 1997) fire treated crusts had significantly lower chlorophyll content than unburned crusts ($z = 2.45$). Plots burned during the growing-season (July 1997) did not significantly differ from unburned plots ($z = 1.07$) or plots burned during the dormant-season ($z = 1.37$).

3.3. Grass, bare ground, litter

Pre-treatment (March 1997) grass cover was not significantly different between experimental plots. Dormant-season fire (April 1997) initially reduced grass cover compared to unburned plots. Two to three months later plots burned in the dormant season did not significantly differ from unburned plots. Approximately, 2½ years later there

still were no statistically significant differences in grass cover between unburned plots and plots burned during the dormant season (Tables 2 and 3).

Growing-season fire (July 1997) initially reduced grass cover compared to unburned and dormant-season fire plots. One year post fire, growing-season fire plots continued to have lower grass cover than unburned plots, but did not differ significantly from dormant-season fire plots. Approximately, 2 years post fire there were no statistically significant differences in grass cover among treatments (Tables 2 and 3).

Pre-treatment percent bare ground cover was not significantly different between the experimental plots. Dormant-season fire significantly increased percent bare ground compared to unburned plots. Approximately, 3 months post fire, percent bare ground continued to be significantly higher on dormant-season burn plots. Approximately, $1\frac{1}{2}$ years post fire there were no significant differences in percent bare ground between unburned and dormant-season fire plots (Tables 2 and 3).

Growing-season fire significantly increased bare ground compared to unburned plots.

One year post fire, plots burned in the growing season continued to have significantly higher bare ground, but did not differ significantly from dormant-season fire plots. Approximately two years post fire there were no significant differences in bare ground among treatments (Tables 2 and 3).

Pre-treatment litter cover was not significantly different between experimental plots. The only significant differences in litter cover between treatments occurred when plots burned during the growing season initially had significantly lower litter cover than the unburned plots and the plots burned during the dormant season (Tables 2 and 3).

4. Discussion

In the short-term, burning during the growing-season appears to reduce fire severity and the impact of fire on biological soil crusts compared to burning during the dormant-season. One year post fire there were no longer significant differences among the treatments. This may be attributed to low rainfall in late 1997 and extreme drought in 1998 (Fig. 1). The large differences in acetylene reduction between July 1998 and October 1999 samples (Table 4) can be attributed to abundant precipitation in the months prior to the October sample collection.

Recovery rates of all aspects of crustal communities depend on several factors. The type and severity of disturbance, as well as environmental variables will greatly influence time to recovery (Belnap, 1993). Biological soil crusts are metabolically active with adequate soil surface moisture. As a result, abundant precipitation following fire will allow faster recovery than low precipitation (Belnap, 1993; Johansen et al., 1984, 1993).

Overall grass cover recovered quickly from fire, and the long-term effect of fire was neutral. Burning during the dormant-season had little effect on grass cover by the subsequent sampling in as little as 2 months, but burning during the growing-season appears to negatively impact grass cover for up to 2 years after fire. These results were consistent with a majority of studies on fire response of buffalograss and blue grama that suggest a predominantly neutral response to fire that is dependent on rainfall, time since fire, and season of fire (Ford, 1999). Results were also consistent with studies predicting fire is differentially detrimental to plants based on their season of active growth, with C₄ plants like buffalograss and blue grama predicted to be least vulnerable to dormant-season burning and most vulnerable to burning during the growing season.

5. Conclusions

Damage to soil crusts during dormant-season fire decreased acetylene reduction activity in the months following fire, compared to unburned crusts, or crust subjected to growing-season fire. Following several months of drought in 1998, acetylene reduction was very low on all sites. Two years post fire, followed by several months of high precipitation, crust activity in burned and unburned plots, regardless of season of burn, increased to similar levels. These results indicate that dormant-season fire in the shortgrass steppe is more damaging to soil crusts than growing-season fire. However, with adequate precipitation the nitrogen enriching function of the soil crusts recovered within 2 years. Weather patterns (increased precipitation) appear to have superseded any fire effects in our study. This result is congruent with research indicating plant response to fire in shortgrass steppe depends mainly on precipitation levels (Ford, 1999).

In summary, shortgrass steppe has the ability to recover from fire relatively quickly, i.e., 3–30 months. Even though perennial grasses and biological soil crusts responded differentially to season of fire, with growing-season fire negatively impacting grass, while at the same time reducing the impact of fire on soil crusts, most of the fire effects in this study were of relatively short duration.

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