Journal of Environmental Management (2002) 65, 135-152
doi:10.1006/jema.2002.0540, available online at http://www.idealibrary.com on IDEAL

Restoring fire as an ecological process in shortgrass prairie ecosystems: initial effects of prescribed burning during the dormant and growing seasons

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Received 23 April 2007; accepted 19 November 2007

Prior to Anglo-European settlement, fire was a major ecological process influencing the structure, composition and productivity of shortgrass prairie ecosystems on the Great Plains. However during the past 125 years, the frequency and extent of grassland fire has dramatically declined as a result of the systematic heavy grazing by large herds of domestic cattle and sheep which reduced the available levels of fine fuel and organized fire suppression efforts that succeeded in altering the natural fire regime. The greatly diminished role of recurrent fire in these ecosystems is thought to be responsible for ecologically adverse shifts in the composition, structure and diversity of these grasslands, leading specifically to the rise of ruderal species and invasion by less fire-tolerant species. The purpose of this study was to evaluate the ecological effects of fire season and frequency on the shortgrass prairie and to determine the means by which prescribed fire can best be restored in this ecosystem to provide the greatest benefit for numerous resource values. Plant cover, diversity, biomass and nutrient status, litter cover and soil chemistry were measured prior to and following fire treatments on a buffalograss-blue grama shortgrass prairie in northeastern New Mexico. Dormant-season fire was followed by increases in grass cover, forb cover, species richness and concentrations of foliar P, K, Ca, Mg and Mn. Growing-season fire produced declines in the cover of buffalograss, graminoids and forbs and increases in litter cover and levels of foliar P, K, Ca and Mn. Although no changes in soil chemistry were observed, both fire treatments caused decreases in herbaceous production, with standing biomass resulting from growing-season fire -600 kg/ha and dormant-season fire -1200 kg/ha, compared with controls -1800 kg/ha. The initial findings of this long-term experiment suggest that dormant-season burning may be the preferable method for restoring fire in shortgrass prairie ecosystems where fire has been excluded for a prolonged time period.

Keywords: Boutelouagracilis (Willd. ex Kunth) Lag. ex Griffiths, *Buchloe dactyloides* (Nutt.) Engelm., plant cover, species diversity, herbaceous biomass, litter, nutrients.

Introduction

Fire was a principal ecological process influencing the evolution of numerous plant species in Great Plains grasslands and a primary disturbance mechanism for sustaining the structure, diversity and productivity of these prairie ecosystems (Wright and Bailey, 1982; Anderson, 1990; DeBano *et al.*, 1998). Although grazing by large herds of free-roaming bison and occurrence of periodic drought also played a role, the historical development and persistance of grassland ecosystems have been closely linked to recurrent natural fires and fires ignited by humans (Axelrod, 1985; McPherson, 1995; Hart and Hart, 1997). The season of burning

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and the time interval between natural fires in these fire-dependent ecosystems have been largely determined by prevailing climatic, physiographic, edaphic and vegetation conditions (Daubenmire, 19681, while those for human-caused fires typically reflected the management goals of aboriginal people or European immigrants that later settled in the region (Pyne, 1982). Wildfires resulting from natural ignition sources such as lightning influenced grasslands long before the arrival of humans. Native Americans later discovered that burning existing vegetation was one of the easiest methods for effectively modifying their environment and ignited fires for a variety of reasons, including hunting, habitat improvement, crop harvesting, pest reduction, warfare and clearing areas for home sites, crops and travel (Pyne, 1982; Bahre, 1985; Arno, 1996; Williams, 1997). The use of fire was so widespread in aboriginal cultures that treeless grasslands are thought to be a product of repeated burning by these people (Sauer, 1944; Stewart, 1951). Indeed, early accounts document the prevalence and ferocity of prairie fires (Bradbury, 1819; Stansbury, 1852; Perrine, 1927; Schubert, 1979; Madson, 1982; Wood and Thiessen, 1985; Berg-on, 1989).

During the late 19th century, major ecological change occurred in grasslands throughout the West with the arrival of Anglo-Europeans and their large herds of cattle and sheep (Gottfried *et al.*, 1995; Hartnett *et al.*, 1997; Engle and Bidwell, 2000). Great Plains prairie ecosystems were thereafter subjected to widespread cultivation and systematic grazing by domestic livestock (McGinnies *et al.*, 1991; Hart and Hart, 1997; Frank *et al.*, 1998). Heavy grazing of native prairies by livestock substantially reduced the standing biomass of grass that normally serves as the fine fuel which carries fire (Ford and McPherson, 1996; DeBano *et al.*, 1998). Lower fuel levels resulted in a decreased probability of ignition and decline in the frequency of grassland fires (Johnsen, 1962; Young and Evans, 1981; Anderson, 1990). Soil cultivation and construction of transportation corridors fragmented the prairie landscape to a degree that limited the spread of fire for any single ignition event (Hart and Hart, 1997). Fire suppression programs implemented since the 1950s have further diminished the frequency and extent of grassland fires, virtually eliminating fire as an ecological process in most modern prairie ecosystems. The net effect of these changes has been a significant negative impact on many of the native species and natural communities of the Great Plains (Ostlie *et al.*, 1997; Engle and Bidwell, 2000). In the absence of periodic fire, ecological shifts in grassland community composition, structure and diversity have been observed, with non-native grasses and less fire-tolerant shrubs becoming more prevalent (Burkhardt and Tisdale, 1976; Axelrod, 1985; Ford and McPherson, 1998). Loss of species and erosion of biological diversity appear to result from fragmentation that interrupts landscape-scale processes, such as recurrent fire (Leach and Givnish, 1996).

As an ecological process, fire provides numerous benefits important to the persistence of grassland ecosystems. On a microscale, in semiarid environments where water availability is low and decomposition rates are too slow to sustain vigorous plant productivity, fire quickly reduces aboveground biomass and rapidly releases nutrients that were previously immobilized in accumulated organic matter (DeBano *et al.*, 1998). The resulting faster rates of nutrient turnover are essential for sustaining the high primary productivity typical of native tallgrass and mixed grass prairies (Woodmansee and Wallach, 1981a). On a macroscale, fire recycles not only nutrients, but entire plant communities, thus regulating successional trends (Pyne, 1982). Periodic burning favors grasses by reducing woody species (Wright and Bailey, 1982; Grover and Musick, 1990; McPherson, 1995) and suppressing less fire-tolerant plants like broom snakeweed (*Gutierrezia sarothrae)* that can become problem weeds in the absence of fire (Gatewood, 1992). Recurrent fire also acts as a stabilizing force in grassland ecosystems through discouraging invasion by non-native plant species, such as leafy spurge (*Euphorbia esula*) which has rapidly spread in the northern Great Plains since fire exclusion. Fire is known to enhance species richness and diversity, when re-introduced into fire-adapted ecosystems (Brown, 1995).

The frequent interaction of fire with ecosystems has through time caused its periodic occurrence to become an essential disturbance process vital to sustaining long-term ecosystem health (Franklin, 1988; Risser, 1988; Kilgore and Heinselman, 1990; Mutch, 1994). Ironically, the danger of excluding periodic fire from forests was recognized more than 50 years ago, but advocates for its restoration in these ecosystems (Weaver, 1943, 1967) were largely unheeded until the increasing frequency of catastrophic stand-replacement fires precipitated a change in national policy. While the close association between fire and shortgrass prairies is also widely recognized, substantial uncertainty exists concerning the seasons, frequencies and methods for safely restoring fire in grasslands that have been long unburned. Very little research has been conducted on the ecological effects of fire in shortgrass prairies (Ford and McPherson, 1996). Studies of fire in this ecosystem have typically been of limited scope and short duration (Hopkins *et al.*, 1948; Launchbaugh, 1964; Dwyer and Pieper, 1967; Trlica and Schuster, 1969; Heirman and Wright, 1973; Wright, 1974; Wright and Bailey, 1980). The effects of recurrent fire on primary productivity, species diversity and nutrient turnover rates in shortgrass prairies are not well understood. Since the process of fire interacts with numerous physical and biological components of the ecosystem, its effects can be expected to depend on past and present patterns of land use as well as prevailing environmental conditions (Ford and McPherson, 1996).

A long-term experiment applying prescribed fire treatments during two contrasting seasons and at three different frequencies was established in a long-unburned shortgrass prairie ecosystem on the southern Great Plains. In measuring the post-treatment changes in plant cover, diversity, biomass, foliar nutrition, litter cover and soil chemistry, the objectives of this study were to (1) quantify the response of ecosystem properties to the season and frequency of burning, (2) identify fire regimes that are beneficial or harmful to numerous resource values and (3) assess the feasibility of safely restoring fire as an ecological process that will sustain the long-term ecological health of the shortgrass prairie ecosystem. Findings resulting from application of the initial dormant-season and growing-season fires are herein reported.

Methods

Study site

This experiment was conducted on the Kiowa National Grassland in Union County, northeastern New Mexico (36°31′20″N, 103°3′30″W). The study site is representative of the Buffalograss-Blue Grama *(Buchloe dactyloides-Bouteloua gracilis)* ecological landtype, characteristic of the Southwest Plateau and Plains Dry Steppe and Shrub Province (Bailey, 1995). The climate is semiarid continental and characterized by cool, dry winters and warm to hot summers (Trauger, 1987). Average monthly temperatures range from ll-24°C for the April to September period and from l-13°C during October to March. Most precipitation in this area originates as either air masses moving upslope from the Gulf of Mexico or monsoonal flow from the Pacific Ocean. This circulation feeds the development of convective afternoon thunderstorms from April through October, which contribute over 75% of the total annual precipitation of 400mm. The highest wind velocities occur in spring and originate from the west and southwest, with April being the windiest month. Strong winds from the north associated with fast moving cold fronts occur during the winter months. The average annual windspeed is about 25 kph, with winds exceeding 40 kph about 10% of the time.

The study area is -1465m above sea level on nearly level to gently rolling topography with surface slopes <5%. Surface geology is underlain by sands and gravels of the Ogallala Formation which dates to the Miocene. Soils developed as mollisols and aridisols in parent materials that were derived from basalt, sandstone, shale, eolian sand, alluvium and upland calcareous deposits (Maxwell *et al.*, 1981). The Gruver series (fine, mixed, mesic Aridic Paleustolls) occupies 25% of the site in the east-central portion of the area and was derived from the mixed alluvium of High Plains sedimentary deposits. The Sherm series (fine, mixed, mesic Torrertic Paleustolls) occupies 35% of the site in the northern and southeastern parts of the area and developed from eolian and alluvial deposits. The Spurlock series (coarse-loamy, carbonatic, mesic Ustollic Calciorthids) occupies 35% of the site in the western portion of the area and originated from calcareous sediments. The Dioxice series (fine-loamy, mixed, mesic Aridic Calciustolls) occupies 5% of the site in the east-central part of the area and was derived from mixed alluvium and eolian material over old caliche beds. All soils are deep and well drained, with little or no evidence of erosion.

Vegetation on this shortgrass prairie is dominated by blue grama and buffalograss, with galleta *(Hilaria jamesii)*, sideoats grama *(Bouteloua curtipendula)*, sand dropseed *(Sporobolus cryptandrus)* and purple threeawn *(Aristida purpurea)* being prominent on some portions of the site. Broom snakeweed is the only common shrub, while small soapweed yucca *(Yucca glauca)* and various cacti *(Opuntia* spp.) are less frequently observed. Forbs are very inconspicuous, with scarlet globemallow *(Sphaeralcea coccinea)*, scarlet gaura *(Gaura coccinea)*, upright prairie coneflower *(Ratibida columnifera)* and woolly milkvetch *(Astragalus mollissimus)* the most frequently noted species. While no trees grow on the study site, several Siberian elms *(Ulmus pumila)* are present along the southern margin of the area.

Site history and experimental treatments

Although originally settled in accordance with homestead laws, this land was never plowed. The area was used for cattle grazing under private ownership until the 1930s and thereafter grazed under stewardship of the federal government until 1990 when all consumptive resource utilization was terminated. Fire has been excluded from this site for many decades. The relatively uniform soil and plant community conditions at this location represented an excellent opportunity to evaluate the effects of restoring fire in the shortgrass prairie ecosystem.

In August 1995, a completely randomized experimental design was established on the study site. Five replications of seven experimental treatments were distributed across the 160 ha study area. Each 2 ha (140 m x 140 m) plot was separated from all adjacent plots by a 60 m buffer zone. Aside from the unburned control plots, all treatments consisted of using backing-fire and flanking-fire along the downwind plot margins to create black-line firebreaks that would contain the headfire which subsequently consumed most of the aboveground biomass on each plot. Nearly all of the plant materials in the standing biomass were characterized as non-volatile fine fuel, with no significant medium or coarse fuels present. Earlier literature indicated that at least 3 years were required for the biomass production in shortgrass prairies to recover following fire (Launchbaugh, 1964). Therefore, we selected prescribed burning treatments that consist of (1) one dormant-season fire every 3 years, (2) one growing-season fire every 3 years, (3) one dormant-season fire every 6 years, (4) one growing-season fire every 6 years, (5) one dormant-season fire every 9 years and (6) one growing-season fire every 9 years. Established as a long-term study, these treatments will be applied for a period of at least 2 decades, for a minimum of 2 complete fire cycles. The initial dormant-season and growing-season fires were applied to 15 plots each during April 1997 and July 1997, respectively.

Measurements

In September and October 1995, measurements of plant cover, species diversity, litter cover, litter mass, herbaceous biomass, foliar nutrient concentrations and soil chemical properties were conducted on all plots to assess the pretreatment status of this ecosystem. Repeated post-treatment measurements were then completed during August and September 1997 on plots burned during the dormant season and October and November 1997 on plots burned during the growing season to ascertain the ecological changes resulting from alternative fire treatments. Total foliar cover (vertical projection of canopy) of all plant species was measured using the line-intercept method along two 50m transects (oriented north and south) within each plot. Identification and nomenclature for plant species were consistent with taxonomic authorities (Kartesz et al., 1994; Weber, 1976; Nickerson *et al.*, 1976; Hermann, 1966; Humphrey, 1956; Hitchcock, 1950). Litter mass and aboveground herbaceous biomass were quantified on three randomly selected 1 m^2 sampling subplots within each larger treatment plot. Standing biomass was destructively sampled by clipping all herbaceous vegetation at the groundline and placing samples into paper bags. All litter was then collected and placed in separate paper bags. Soils were sampled to a depth of 15 cm, using a 5cm diameter coring device, at 10 m intervals along two 50m transects (oriented parallel to the plant transects) within each plot.

All herbaceous plant and litter samples were dried to a constant mass in a force draft oven at 75°C for 48h and weighed. Herbaceous plant biomass data were then used to construct productivity estimates for vegetation relative to experimental treatment. These samples were subsequently ground in a Wiley mill using a 20 mesh screen and chemically analyzed to determine the concentrations of N, P, K, Ca, Mg, Na, Fe, Mn, Zn, B and Al present in the plant and litter tissue. Data on the foliar cover of each species were summarized as estimates for each plot and analyzed by treatment and change through time. Foliar cover data were then used as importance values to compute several indices of alpha diversity, including species richness, species evenness and species diversity (Ludwig and Reynolds, 1988). Species richness is the total number of species present (N_0), evenness describes how abundance is distributed among species (modified Hill ratio, E_5), approaching one when all species are of equal abundance and declining toward zero when few species dominate, and species diversity mathematically combines richness and evenness components into a single numeric value (Shannon index, H'). Soil samples were air dried, passed through a 2mm sieve to remove coarse fragments and chemically analyzed to measure NO,-N, NH_4-N, total N, P and K, exchangeable Ca, Mg and Na, sodium adsorption ratio (SAR), electrical conductivity, pH and organic matter content.

All data for dependent variables were summarized as estimates of the mean for each plot and these means were then used to estimate the mean and variance for each of the seven treatments. For each dependent variable, a comparison of differences among experimental treatments and over the time sequence of repeated measurements was then undertaken. A repeated measures ANOVA, using initial conditions as covariates, was used to evaluate time and treatment effects and interactions. Treated responses were compared to the untreated response using orthogonal polynomials. Because post-treatment litter levels were insufficient to allow repeated sampling, pretreatment litter mass and nutrient concentrations were evaluated using an analysis of variance rather than the analysis of covariance. Statistical analysis of the time and treatment interaction for computed diversity indices was completed using the bootstrap technique PROC MULTTEST in SAS (Efron and Tibshirani, 1993; Westfall and Young, 1993; SAS Institute, 1996). Adjusted p-values, which maintain a constant Type I error across the full range of comparisons, were used to determine significant differences among means (10 000 bootstrap iterations were used). A probability level of 0·05 was used to discern significant differences.

Results

Plant cover

Following dormant-season fire, a modest increase (<10%) in total graminoid cover was observed at the end of the first post-treatment growing season (Table 1). Of the many grasses present, only blue grama contributed substantially to this rise. However, these values were not significantly different from controls, therefore this increase was largely time driven ($P < 0.05$). A similar increasing trend (from 1–3·4%) was noted for all forbs, but this rise was also not significantly different from that observed on controls. Only the cover of scarlet globemallow was significantly greater than that on control plots. The cover of shrubs, mostly broom snakeweed, decreased slightly following dormant-season burning, but this decline was not significantly different from that on the controls. A slight decrease in the cover of litter was noted which contributed to an increase in soil exposure. However, these values were not significantly different from those found on control plots.

Table 1. Cover response to fire (% foliar and litter cover or soil exposure)

	Control	Dormant-season fire	Growing-season fire
Shrubs			
1995	0·6	0·9	0·4
1997	0·1	0·2	0·2
Adjusted Mean^a	0·1	0·2	0·2
Graminoids			
1995	90.9	95·6	95.3
1997	106·3	103·4	92.8
Adjusted Mean	106·4	103.3	92·8^b
Blue grama			
1995	57.4	62.3	70.3
1997	67.3	70·6	69.0
Adjusted Mean	73.3	70·5	67.3
Galleta			
1995	25.3	12·9	6.5
1997	24.5	13.7	7·3
Adjusted Mean	13.8	12.9	11·6
Buffalograss			
1995	2.8	7·1	6·6
1997	5·7	6.4	0·5
Adjusted Mean	6·7	6·1	0·5^b
Sideoats grama			
1995	3.9	4.5	7·0
1997	4.3	4.8	10·6
Adjusted Mean	6.5	6.2	8·5
Threeawn			
1995	1·3	6·4	4·1
1997	3·3	7.6	4.3
Adjusted Mean	5.6	6.5	4.7
Sand Dropseed			
1995	0·1	1·8	0·3
1997	0·7	1·4	0·7
Adjusted Mean	0·9	1·1	0·9
Tumblegrass			
1995	0·2	0·1	0·3
1997	0·2	0·2	0·2
Adjusted Mean	0·2	0·3	0·2
Ring Muhly			
1995	0·1	0·5	0·1
1997	0·2	0·4	0·1
Adjusted Mean	0·3	0·2	0·1
Forbs			
1995	1·0	1·0	2·1
1997	3·0	3·4	0·6
Adjusted Mean	3·0	3.4	0·5^b

(continued on next page)

Table 1. *(continued)*

	Control	Dormant-season fire	Growing-season fire
Scarlet Globemallow			
1995	0·5	0·3	0·3
1997	0·8	1.2	0·3
Adjusted Mean	0·8	1·2^{b}	0·3^{b}
Prairie Coneflower			
1995	0·1	0·1	0·1
1997	0·4	0·2	0·1
Adjusted Mean	0·3	0·2	0·1
Scarlet Gaura			
1995	0·0	0·0	0·0
1997	0·3	0·2	0·1
Adjusted Mean	0·3	0·2	0·1^{b}
Milkvetch			
1995	0·0	0·0	0·0
1997	0·1	0·1	0·0
Adjusted Mean	0·1	0·1	0·0^{b}
Litter			
1995	1·1	1·1	0·7
1997	0·9	0·3	8·4
Adjusted Mean	0·9	0·3	9·2^{b}
Soil			
1995	0·5	0·9	0·1
1997	3·7	7.5	7.9
Adjusted Mean	3·7	7.2	**7.9**

[a] Post-treatment mean adjusted by analysis of covariance.
‘Significantly different from control plots, $P \leq$ O-05.

Following growing-season fire, a significant decline in total graminoid cover was measured during the initial fall season (Table 1). A significant decrease in buffalograss cover was largely responsible for this decline. The cover of buffalograss resulting from growing-season fire was significantly lower than that on unburned controls and plots burned during the dormant season. Total forb cover was similarly reduced, being significantly less than that on controls and plots burned in the dormant season. Scarlet globemallow, scarlet gaura and woolly milkvetch were the only forbs with foliar cover significantly lower than that on control plots. As with dormant-season fire, the cover of shrubs, primarily broom snakeweed, declined following growing-season fire. Shrub levels were not significantly different from those on controls, however. Litter cover was substantially increased and significantly greater than that measured on control plots. Soil exposure increased to a degree similar to that resulting from dormant-season fire, but these levels were not significantly different from those on controls.

Species diversity

A total of 43 vascular plant species were found growing on the Kiowa Prairie study plots (Table 2). The plant community is dominated by grasses, with blue grama being by far the most abundant species. Other prominent graminoids include buffalograss, galleta, sideoats grama, purple threeawn and sand dropseed. While forbs comprise over half of the observed taxa, none were abundant on this site. Forbs persisted at very low levels both prior to and following prescribed burning. Very few shrubs were present on the plots, with broom snakeweed being the only species having more than a trace occurrence.

At the end of the initial post-treatment growing season, species richness (N_0) was increased significantly on plots burned during the dormant season (Table 3). The number of species present rose from an average of 10 to over 15 on most of these plots. However, these richness values were not significantly different from those on controls, thus this increase was essentially time driven. Species richness was largely unaffected by burning in the growing season. Species diversity (H') increased on plots treated by dormant-season fire and generally declined on those burned by growing-season fire. But these fluctuations were quite modest and none of these values were significantly different from those on control plots- Plant species evenness was unaffected by either the dormant-season or growing-season prescribed fire treatment.

Herbaceous biomass

Both prescribed fire treatments resulted in profound declines in the standing biomass of herbaceous vegetation by the end of the initial post-treatment season (Table 4). The pretreatment biomass, averaging -2700 kg/ha, was reduced on plots burned during the dormant season and growing season by 56% and 78%, respectively. The post-treatment biomass of -1200 kg/ha on plots burned during the dormant season was significantly lower than the -1800 kg/ha standing biomass on controls. The -600 kg/ha biomass on plots burned during the

Table 2. Vascular plants present on the Kiowa study site

	Scientific name	Common name
Shrubs:	*Echinocereus viridiflorus*	Green-flowered hedgehog cactus
	Gutierrezia sarothrae	Broom snakeweed
	Opuntia phaeacantha	Tulip pricklypear
	Opuntia polycantha	Plains pricklypear
	Yucca glauca	Small soapweed yucca
Graminoids:	*Aristida purpurea*	Purple threeawn
	Bouteloua curtipendula	Sideoats grama
	Bouteloua gracilis	Blue grama
	Buchloe dactyloides	Buffalograss
	Chloris verticillata	Tumblewindmill grass
	Elymus elymoides	Longleaf squirreltail
	Erioneuron pilosum	Hairy tridens
	Hilaria jamesii	Galleta
	Monroa squarrosa	False buffalograss
	Muhlenbergia torreyi	Ring muhly
	Panicum obtusum	Vine mesquite
	Schedonnardus paniculatus	Tumblegrass
	Schizachyrium scoparium	Little bluestem
	Sporobulus cryptandrus	Sand dropseed
Forbs:	*Artemisia fiiifolia*	Sand sagebrush
	Artemisia ludoviciana	Louisiana wormwood
	Astragalus mollissimus	Woolly milkvetch
	Chaetopappa ericoides	Roseheath
	Cirsium ochrocentrum	Yellowspine thistle
	Conyza canadensis	Canadian horseweed
	Cryptantha spp.	Catseye
	Erigeron flagellaris	Trailing fleabane
	Euphorbia marginata	Snow on the mountain
	Gaura coccinea	Scarlet gaura
	Grindelia nuda	Curlytop gumweed
	Helianthus annuus	Common sunflower
	Hymenopappus spp.	White ragweed
	Linum spp.	Flax
	Liatris punctata	Dotted gayfeather
	Machaeranthera pinnatifida	Lacy tansyaster
	Plantago patagonica	Wooly plantain
	Psoralidium tenuiflorum	Wild alfalfa
	Ratibida columnifera	Upright prairie coneflower
	Salsola kali	Prickly Russian thistle
	Solanum elaeagnifolium	Silverleaf nightshade
	Sphaeralcea coccinea	Scarlet globemallow
	Stephanomeria pauciflora	Brownplume wirelettuce
	Thelesperma megapotamicum	Indian tea

Total species = 43.

growing season was significantly less than that on those treated with dormant-season fire and the control plots.

Plant nutrients and soil chemistry

Prior to burning, litter mass averaged 860 kg/ha and litter nutrient concentrations were relatively consistent across the study plots, with no significant differences among treatments (Table 5). Values for total N, P, K, Ca, Mg, Na, Mn, Zn and B fell within the normal range, while levels of Fe and Al were somewhat high. Both dormant-season and growing-season prescribed fire influenced the concentrations of nutrients in the foliar tissues of herbaceous plants in a similar manner (Table 6). Burning during the dormant season resulted in significant increases in the foliar levels of P, K, Ca, Mg and Mn and fire during the growing season led to significantly increased foliar values for P, K, Ca and Mn. Foliar concentrations of N, Na, Fe, Zn, B and Al

Table 3. Plant species richness, diversity and evenness responses to fire

	Control	Dormant-season fire	Growing-season fire
Number of species:			
1995	8·4	10·0	10·1
1997	14·0^b	15·5^b	10·6
Shannon index:			
1995	0·87	0·95	0·82
1997	1·05	1·11	0.68
Modified hill ratio:			
1995	0·64	0·58	0·54
1997	0·62	0·54	0.50

[a] Significantly different from control plots, $P \leq 0·05$.
[b] Significant change through time following treatment, $P \leq 0·05$.

Table 4. Aboveground herbaceous plant biomass response to fire (kg/ha)

	Control	Dormant-season fire	Growing-season fire
1995	2358	2817	2605
1997	1790	1248	584
Adjusted Mean^a	1822	1231^b	589^c

[a] Post-treatment mean adjusted by analysis of covariance.
[b] Significantly different from controls and plots burned during the growing season, $P \leq 0·05$.
‘Significantly different from controls and plots burned during the dormant season, $P \leq 0·05$.

Table 5. Pretreatment litter mass (kg/ha) and nutrient content (mg/kg)

	Control	Dormant-season fire	Growing-season fire
Mass	739	**907**	**934**
N	9918	**9938**	10245
P	765	707	759
K	2143	2224	2293
Ca	4815	5163	4523
Mg	1211	1403	1260
Na	246	239	254
Fe	3500	4147	3652
Mn	139	150	139
Zn	35	38	36
B	50	61	55
Al	4711	5734	5032

[a] Significantly different from control plots, $P < 0·05$.

Table 6. Plant nutrition response to fire (mg/kg)

	Control	Dormant-season fire	Growing-season fire
N			
1995	6910	6836	6443
1997	7176	8749	8088
Adjusted Mean^a	7226	8783	8037
P			
1995	1059	962	1037
1997	1727	2187	2414
Adjusted Mean	1634	2267^b	2362^b
K			
1995	3034	3005	2999
1997	4829	9487	8334
Adjusted Mean	4827	9488^b	8335^b
Ca			
1995	3034	3230	3168
1997	3530	5705	5017
Adjusted Mean	3524	5707^b	5017^b
Mg			
1995	615	656	610
1997	988	1499	1108
Adjusted Mean	989	1497^b	1110
Na			
1995	114	100	105
1997	260	305	212
Adjusted Mean	258	306	211
Fe			
1995	421	458	418
1997	267	327	262
Adjusted Mean	276	315	272
Mn			
1995	45	45	44
1997	45	78	72
Adjusted Mean	45	78^b	72^b
Zn			
1995	0	0	0
1997	16	19	17
Adjusted Mean	16	19	17
B			
1995	14	13	12
1997	37	56	62
Adjusted Mean	38	56	61
Al			
1995	682	772	672
1997	265	386	256
Adjusted Mean	282	359	277

‘Post-treatment mean adjusted by analysis of covariance.
‘Significantly different from control plots, $P \leq 0·05$

Table 7. Soil chemistry response to fire

	Control	Dormant-season fire	Growing-season fire
NO_3-N (mg/kg)			
1995	6·4	4·7	5·9
1997	0·7	0·5	0·8
Adjusted Mean[a]	0·8	0·5	0·8
NH_4-N (mg/kg)			
1995	0·0	0·0	0·0
1997	2.4	2.3	2.2
Adjusted Mean	2.4	2·3	2.1
Total N (mg/kg)			
1995	1114	891	973
1997	1532	1313	1472
Adjusted Mean	1435	1355	1463
Total P (mg/kg)			
1995	631	595	631
1997	228	206	277
Adjusted Mean	216	222	265
Total K (mg/kg)			
1995	4018	3908	3959
1997	2752	2520	2570
Adjusted Mean	2698	2548	2560
Exch. Ca (meq/100 g)			
1995	18·5	20.3	19.3
1997	9·6	7·3	7·4
Adjusted Mean	9·9	7·1	7.5
Exch. Mg (meq/100 g)			
1995	3·3	4·9	4·0
1997	1·5	1·3	1·1
Adjusted Mean	1·5	1·3	1·1
Exch. Na (meq/100 g)			
1995	3.58	4.32	3·01
1997	0.04	0·04	0.03
Adjusted Mean	0.04	0.04	0·03
SAR			
1995	0.22	0·23	0·17
1997	0·18	0.29	0.24
Adjusted Mean	0.18	0·29	0.25
Elec. Cond. (ds/m)			
1995	0.13	0·15	0·13
1997	0·12	0·19	0·18
Adjusted Mean	0·14	0·17	0·19
pH			
1995	8·60	8.98	8.76
1997	7.33	7.43	7.32
Adjusted Mean	7.37	7·41	7.33
Organic Matter (%)			
1995	1·44	1·40	1·52
1997	1·23	1·01	1.25
Adjusted Mean	1.25	1.04	1.22

‘Post-treatment mean adjusted by analysis of covariance.
‘Significantly different from control plots, $P \leq 0{\cdot}05$.

were unaffected by fire treatment. Neither dormant-season nor growing-season prescribed burning resulted in significant changes in surface soil chemistry (Table 7). Values for NO_3-N, NH_4-N, Ca, Mg, Na, SAR and electrical conductivity were relatively low, while levels of total N, P, K, organic matter and pH were within the normal range for arid and semiarid soils.

Discussion

Cover changes

Prescribed fire during the dormant season and growing season resulted in a differential response among the plants of this shortgrass prairie ecosystem. While dormant-season burning caused only small increases in the cover of graminoids (mostly blue grama) and forbs and slight decreases in the cover of shrubs and litter, growing-season fire significantly reduced the cover of grasses (primarily buffalograss) and forbs and increased litter cover by end of the initial post-treatment season. Although burning generally favors grasses and forbs (Brockway and Lewis, 1997; DeBano *et al.*, 1998; Boyd, 1999), this variation in response among herbaceous plants was not completely unexpected. Following fire, some grassland perennials increase significantly, while others increase only slightly and still others are generally unaffected (Harnett, 1991; Pyne et *al.*, 1996). Despite these overall trends among the various groups of plants, it is noteworthy that the data do not indicate any major floristic shifts among plant species at this time. During the initial phase of this study, no vascular plant species were eliminated by fire and none were observed as newly occurring following fire. However, as prescribed fire is repeatedly applied to this site over the long-term, loss of fire-sensitive plants and emergence of pyrophytic species are likely outcomes.

The rather small increase in blue grama following dormant-season fire may in part be due to difficulty in recruitment from seedlings. Although blue grama seedheads were very abundant following fire, little evidence of newly established seedlings was apparent on any of the plots. Favorable moisture conditions and gap disturbances which diminish or eliminate belowground competition from adult plants may be necessary for seedling establishment (Lauenroth et al., 1994; Aguilera and Lauenroth, 1995). Also, the postfire seedcrop was likely not available for germination until the following spring. Although forbs are usually more abundant in burned than long-unburned grasslands (Bailey and Anderson, 1978), the small increase in forb cover on plots burned by dormant-season fire was likely related to the fact that forbs are seldom a major component of shortgrass prairies (Wright and Bailey, 1980). Regardless of season, prescribed fire slightly reduced the cover of shrubs (mostly broom snakeweed) and consumed litter that had accumulated on the soil surface. This finding is similar to that reported elsewhere in the region (Boyd, 1999). Burning during the growing season, when vegetation was physiologically active, resulted in the direct mortality of many forbs and a steep decline in buffalograss. The tissue of fire-killed plants that was not consumed by growing-season fire subsequently contributed to the increase in litter cover on these plots.

Although able to tolerate burning in times of above-average moisture (Trilca and Schuster, 1969; Heirman and Wright, 1973; Wright, 1974), most grass species of the shortgrass prairie are reportedly harmed by fire during dry years (Wright and Bailey, 1980; Ford, 1999). Plants in the buffalograss-blue grama community (Hopkins et al., 1948; Launchbaugh, 1964; Dwyer and Pieper, 1967) and other southwestern grasslands (Reynolds and Bohning, 1956; Cable, 1967; Bock *et al.*, 1976; Bock and Bock, 1992) may require up to 3 years to recover following dry-season fire. However, fire has no apparent long-term deleterious effects upon grasses (Wright, 1980). Forbs are noted to be least affected by dormant-season fire, but actively growing forbs are severely injured by burning during the growing season (Wright and Bailey, 1980). Fire during the spring may be only temporarily detrimental to many forbs (Heirman and Wright, 1973).

Diversity dynamics

Shortgrass prairies are ecosystems dominated by vegetation of low species diversity, that is adapted for survival in an environment characterized by periodic fires, seasonal water deficits, low to moderate soil fertility and grazing by free-roaming native ungulates. While 97 species of vascular plants have been noted in this area, only 43 total were recorded along transects on the study site. The typical one dozen or fewer species present on each plot before burning and <16 observed following fire are indicative of the low plant species diversity on this prairie. Plant species diversity is largely determined by interspecific competition interacting with site productivity, microsite heterogeneity and disturbance regimes (Tilman, 1982). The role of recurrent fire as a major disturbance process in grasslands, that affects species composition and community structure, is widely recognized (Daubenmire, 1968; Risser, 1988; Abrams and Gibson, 1991; McPherson, 1995). The effects of fire on the plant community depend on vegetation attributes (successional stage, biomass, moisture content, fuel contiguity), weather conditions (temperature, humidity, wind velocity) and fire characteristics (season, frequency, intensity, areal extent, fuel consumption), with actual changes in plant species composition being site-specific for the most part (DeBano et al., 1998). Given the inherent variation in these factors, the composition and structure of each plant community are likely influenced by a variety of fire regimes (frequency and extent) that vary by season (Steuter, 1986; Bragg, 1991).

While plant species richness was significantly increased following dormant-season fire, the number of species present was not significantly different from the control and this fluctuation was therefore largely time driven. Modest increases in the cover of blue grama, other grasses and forbs appear to be associated with this general rise. The lack of response following growing-season fire indicates that burning at this time, when vegetation is fully developed, is less beneficial and possibly detrimental to the plant community. Significant declines in the cover of buffalograss, graminoids and forbs are no doubt related to this stagnation in species numbers. Direct visual observation, during the growing-season fire, confirmed that numerous well developed forbs were killed by burning at that time. While forb richness and diversity are typically higher following fire than in long-unburned ecosystems (Collins and Barber, 1985; Brockway and Lewis, 1997), burning during the growing season, when forbs are nearly mature, is less favorable to plant diversity, at least in the short-term, than fire during the dormant season, prior to forb emergence. A similar, though non-significant, trend for the

Shannon index is further evidence of this differential response in species diversity to burning during the dormant season and growing season. The lack of any significant response in species evenness to fire treatment indicates a general absence of short-term change in the relative dominance and resource allocation among the species present.

Periodic burning is known to benefit plant diversity in prairie ecosystems and its exclusion through landscape fragmentation and fire suppression are major causes for the overall decline of species diversity in grasslands (Abrams and Gibson, 1991; Leach and Givnish, 1996; Ostlie et al., 1997). The interaction of recurrent fire with other disturbances, such as grazing by bison, improves plant species diversity and spatial heterogeneity, with plant diversity generally greater on more frequently burned areas (Hartnett *et al.*, 1996). By contrast, cattle grazing has reduced the historical efficacy of fire as a regulator of ecological processes in prairie ecosystems (Hartnett *et al.*, 1997). Although responsible for reduction of fine fuels that facilitate the spread of fire, grazing has also been identified as a process which sustains biological diversity in a variety of grasslands (West, 1993; Frank *et al.*, 1998). Indeed, sustaining ecosystem processes is probably more important to the conservation of biological diversity than protecting randomly selected, but functionally redundant, species (West, 1993).

Plant biomass

Application of dormant-season and growing-season prescribed fire caused dramatic near-term reductions in the standing biomass of herbaceous plants on this shortgrass prairie. These findings are similar to those reported for other southwestern grasslands burned during the dry season (Hopkins *et al.*, 1948; Launchbaugh, 1964; Dwyer and Pieper, 1967; Wright and Bailey, 1980). While productivity losses do not occur following fire in times of above-average moisture (Trilca and Schuster, 1969; Heirman and Wright, 1973; Wright, 1974), herbaceous biomass may require as long as 3 years to recover from dry-season fire (Launchbaugh, 1964). But overall, fire has no lasting adverse effects on perennial and annual grasses (Wright, 1980) and the benefits of fire in controlling woody plant encroachment far outweigh such short-term reductions in grass production (Ffolliott, 1990). In like fashion, the short-term decline in herbaceous biomass noted for this shortgrass ecosystem can be expected to recover over a similar time frame.

Compared to the herbaceous biomass on control plots (-1800 kg/ha), that following dormant-season fire (~1200 kg/ha) represented a substantial 33% decline and that after growing-season burning (-600 kg/ha) was an even greater 67% decrease. This result was not unlike that reported for southern pine-grass ecosystems, where spring fire produced 2-4 times more herbaceous biomass than burning during the fall (Lewis, 1964). Seasonality has a major influence on the effects of fire on vegetation (Wright and Bailey, 1982; Waldrop et al., 1992), often affecting flowering (Platt *et al.*, 1988), seed production (Biswell and Lemon, 1943; Patton et al., 1988; Outcalt, 1994) and herbaceous plant productivity (Lewis, 1964; Hilmon and Hughes, 1965; Lewis and Hart, 1972; Wade and Lewis, 1987; Bragg, 1991; Mitchell *et al.*, 1996; Boyd, 1999). Fire season and frequency are thought to have a stronger influence on the effects of fire in semiarid grassland communities than fire behavior (Steuter and McPherson, 1995). Findings elsewhere indicate that resource values and herbaceous productivity are not diminished in good-condition grasslands, when burned at intervals of 5-10 years (Robinett and Barker, 1996).

Although fire can lead to decreases in the biomass of some grassland plants such as little bluestem *(Schizachyrium scoparium)*, burning can also be beneficial to the growth of others like sand bluestem *(Andropogon hallii)* and switchgrass (*Panicum virgatum*), resulting under some circumstances in a net increase in herbaceous production (McIlvain and Armstrong, 1966; Wright and Bailey, 1980). Burning in forests, woodlands and shrub-dominated communities normally results in increases in herbaceous productivity, which are attributed to decreases in competition for light, water and nutrients between understory and overstory plants (Brockway and Lewis, 1997; DeBano *et al.*, 1998). While those dynamics are not typical of shortgrass prairie ecosystems, grasslands often benefit from fire that (1) facilitates solar warming of the soil and allows plant growth to start earlier in the season, (2) consumes accumulated litter and reduces the interception of light and water, (3) releases nutrients previously immobilized in litter and plant tissue and (4) promotes vigorous plant growth by removal of senescent shoots and foliage (Kozlowski and Ahlgren, 1974; Woodmansee and Wallach, 1981a; Abrams and Gibson, 1991; Daowei and Ripley, 1997; DeBano *et al.*, 1998).

Plant nutrients and soil chemistry

While litter serves as a reservoir for nutrients that have accumulated in the organic detritus of terrestrial ecosystems, nutrient availability to support plant growth is dependent upon the rate of litter decomposition, which is influenced by litter characteristics and environmental conditions (Jenny et al., 1949; Wiegert and Evans, 1964; Melillo *et al.*, 1982; Yin and Huang, 1996). The process of decomposition is often slow and frequently the rate limiting step for nutrient cycling, as in the nitrogen cycle (Ojima *et al.*, 1994). In arid and semiarid environments, where microbes cannot readily breakdown accumulated plant materials, periodic fire acts as the principal decomposing agent (DeBano *et al.*, 1998). Thus, nutrients cycling through grassland ecosystems largely move in pulses following pyric disturbance. Since both dormant-season and growing-season fire effectively consumed the accumulated litter and aboveground biomass on this shortgrass prairie, it was not surprising that the short-term responses of foliar nutrient levels and soil chemical properties were relatively similar.

The lack of change in foliar N status following fire was likely the result of N loss from the site through volatilization. While wind erosion of the nutrient-rich ash layer may have also contributed to this loss as NH_4-N (Neary et al., 1996; DeBano *et al.*, 1998), the enhanced assimilation of several other nutrients is evidence to the contrary. Up to 90% of the aboveground N may be volatilized during grassland fires (Sharrow and Wright, 1977). As in numerous other terrestrial ecosystems, grasslands are N limited and the plant species of tallgrass and shortgrass prairies respond positively to N addition (Fresquez *et al.*, 1990; Benning and Seastedt, 1995; Redente et al., 1995; White et al., 1997). However, little of the N previously immobilized in litter was likely retained onsite and available for plant assimilation following fire. Studies elsewhere indicate that most N (81–99%) in terrestrial ecosystems is resident in the mineral soil (DeBano and Conrad, 1978; DeBano and Klopatek, 1987; Tiedemann, 1987), where fire intensities typical of grasslands have little effect on the microorganisms that regulate its availability (Woodmansee and Wallach, 1981a; Fritze *et al.*, 1992; Neary et *al.*, 1996; DeBano et al., 1998). Therefore, nutritional benefits to plants emerging following fire would be most expected from nutrients other than N.

Significant increases in foliar concentrations of P, K, Ca, Mg and Mn following prescribed burning were indicative of the beneficial effect fire has on releasing nutrients that had become immobilized in accumulated aboveground plant tissue. Residual ash found on the soil surface is typically enriched with P and cations that are normally retained onsite and available for subsequent assimilation by emerging vegetation (Woodmansee and Wallach, 1981b; Wright and Bailey, 1982; Debano and Klopatek, 1988; Riggs *et al.*, 1996). Not only do these enhanced chemical conditions encourage plant growth, but the improved nutritional status of emerging herbaceous plants increases the forage value of vegetation consumed by herbivores (Pearson *et al.*, 1972; Hobbs and Spowart, 1984; DeByle *et al.*, 1989; Carreira and Niell, 1992). The only difference between fire treatments was the generally higher levels of foliar Mg on plots burned during the dormant season than on those burned in the growing season, This increase may have been related to the generally greater response of plant cover, growth and diversity to dormant-season burning than growing-season fire. Evidence from other grasslands indicates that a positive relationship exists between increasing nutrient resource use and increasing plant diversity (Hooper and Vitousek, 1998). It was not surprising that soil chemical properties were unaffected by prescribed fire. The primary effects of fire on this shortgrass prairie were to volatilize most of the aboveground N and deposit a nutrient-rich ash on the soil surface. Available nutrients were rapidly assimilated by emerging vegetation and thus not available for translocation deeper into the soil profile.

Restoring fire in the ecosystem

Although the close association of shortgrass prairie ecosystems with periodic fire has been long recognized (Wright and Bailey, 1980; Axelrod, 1985; Anderson, 1990), fire suppression efforts and domestication of this landscape through road construction, conversion to cropland and systematic heavy grazing by livestock have prevented fire from sweeping across these grasslands during the 20th century as it did so commonly in previous times (Hart and Hart, 1997). These changes and the increasing prevalence of non-native plant species have transformed the shortgrass prairie into an ecosystem of decreased biological diversity and reduced size, now occupying only 23% of its original extent (Ford and McPherson, 1996; Ostlie *et al.*, 1997). Reintroduction of fire to long-unburned shortgrass prairies is an essential step in reversing these ecologically negative trends and ultimately achieving some measure of ecosystem restoration. But given the shifts in species abundance, changes in climate, atmospheric increases in greenhouse gases and other environmental changes occurring during the past 100 years, fire may be unable to recreate ecological conditions similar to those existing in the past (Weltzin and McPherson, 1995).

Restoration efforts typically focus on the reintroduction or recovery of individual species or species assemblages and re-creation of a community that is physiognomically similar to that thought to be prevalent during pre-settlement times (Covington *et al.*, 1997). Considering the now widespread occurrence of non-native species, extirpation of native species and lack of reliable detailed information concerning the community composition, structure and function during these early times, many restoration efforts are best regarded as generalized attempts to improve ecosystem health without overlooking key components and processes. As defined by the National Research Council, 'Merely re-creating the form without the functions, or the functions in an artificial configuration bearing little resemblance to a natural resource, does not constitute restoration; the goal is to emulate a natural, functioning, self-regulating system that is integrated with the ecological landscape in which it occurs' (Cairns, 1995). Although restoring biological diversity is thought to be the greatest challenge to restoration efforts, with even the best examples able to restore only a fraction of the natural species richness (Allen, 1995), unless the essential functional processes that regulate community development and maintenance are restored, individual species will continue to be at risk and the ecosystem cannot be considered sustainable over the long-term. Thus, restoring periodic fire as an essential ecological process in the shortgrass prairie is important to the long-term sustainability of this ecosystem.

Shortgrass plants, particularly blue grama, are extremely resilient and can recover from highly destructive disturbances (McGinnies *et al.*, 1991). Fire during times of abundant moisture does not depress the growth of prairie vegetation (Trilca and Schuster, 1969; Heirman and Wright, 1973; Wright, 1974) and plant recovery from dry-season fire typically requires no longer than 3 years (Launchbaugh, 1964). Since burning shortgrass prairies has no lasting negative effects on annual and perennial grasses (Wright, 1980), enhances nutrient cycling, stimulates seed production and improves species diversity, the major issue yet in question is identification of fire regimes appropriate for achieving the multiple objectives of land managers. Dormant-season fire can be employed as a means of producing several beneficial results without endangering plants that are vulnerable to harm by fire during the growing season, while growing-season fire may be used to achieve other ecological and economic benefits (Suijendorp, 1981; McPherson, 1995; Daowei and Ripley, 1997). Once prescribed burning is chosen as the means by which recurrent fire will be restored as an ecological process in the shortgrass prairie, selection of appropriate regimes (season, frequency, size and configuration of areas burned) is best left to the land manager, who must consider social and economic imperatives in addition to ecological factors.

Conclusion

Prescribed fire during the dormant season and growing season caused substantial changes in plant cover, diversity, biomass and nutrient status within several months of burning a long-unburned shortgrass prairie ecosystem. Fire during both seasons consumed the accumulated aboveground litter and reduced the cover of shrubs, primarily broom snakeweed. Dormant-season fire increased the cover of blue grama, graminoids and forbs, the richness of plant species, the foliar concentrations of P, K, Ca, Mg and Mn and decreased herbaecous biomass by -33%. Growing-season burning led to declines in the cover of buffalograss, grasses and forbs, a decrease in herbaceous biomass of -67% and increases in litter cover and the foliar levels of P, K, Ca and Mn. Increases in litter cover resulted in part from the mortality of forbs killed but not completely consumed by the growing-season fire.

Although this long-term experiment was initiated with the intent of evaluating fire effects over a time period of two decades, these results at the end of the first post-treatment season provide useful insight concerning the short-term influence of dormant-season and growing-season fire on this shortgrass prairie, where fire has been long excluded. Our findings are particularly germane and timely, now that land managers have recently begun to implement programs intended to reintroduce periodic fire in long-unburned shortgrass prairie ecosystems. Prescribed fire in the growing season appears to be a more severe disturbance in this environment than fire during the dormant season. Growing-season fire causes significant reductions in buffalograss and forbs by direct action at the time of burning. The forbs are killed in place never to resprout and the regrowth of buffalograss is likely inhibited during this initial year by internal mechanisms which do not allow for the rapid reallocation of carbohydrate reserves to foliar production. Thus, no benefits to plant species diversity are realized in the short-term. In addition, growing-season fire very likely stresses the carbohydrate reserves of other grasses, thereby impeding their regrowth and resulting in a large decrease in the standing biomass of herbaceous plants. By contrast, dormant-season fire was beneficial in at least modestly increasing the cover of grasses and forbs and improving plant species richness. Herbaceous plant biomass declined much less following dormant-season fire, being approximately twice that measured after growing-season fire.

While conclusions can be offered with greater certainty as additional data accumulate during the ensuing years of this study, short-term results indicate that burning shortgrass prairies during the growing season appears to place the plant community at greater risk of decline or stagnation. The risk of growing-season fire having adverse impacts on this ecosystem would be particularly high during dry years when plant species are already under increased physiological stress. Prescribed fire during the dormant season appears to diminish this risk to the ecosystem and provides several immediate benefits to the plant species present. Therefore, while recognizing the historical occurrence of fire in both dormant and growing seasons, understanding that fire during either or both seasons may prove sustainable over the long-term and mindful of the very preliminary nature of these findings, we recommend that managers wishing to proceed cautiously with restoring fire in the shortgrass prairie ecosystem emphasize use of dormant-season burning, especially during dry periods when available moisture is very limited.

Acknowledgements

The authors express their appreciation to Pam Brown of the Kiowa-Rita Blanca National Grasslands for administrative support and Jerome MacDonald of the Cibola National Forest for coordination of prescribed fire treatments. We also thank Lawrence Abeita and Bill Wilmoth for assistance in data collection. We are also grateful to Roy Jemison, Sam Loftin and two anonymous reviewers for comments quite useful in improving this manuscript.

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