Chihuahuan Desert Grassland Responds Similarly to Fall, Spring, and Summer Fires During Prolonged Drought

Laura M. Ladwig,¹ Scott L. Collins,² Paulette L. Ford,³ and Laura B. White⁴

Authors are ¹Graduate Student and ²Professor, Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA; ³Research Ecologist, Rocky Mountain Research Station, USDA Forest Service, Albuquerque, NM 87102, USA; and ⁴High School Science Teacher, Albuquerque Public Schools, Albuquerque, NM 87110, USA.

Abstract

Land managers frequently use prescribed burning to help maintain grassland communities. Semiarid grassland dynamics following fire are linked to precipitation, with increasing soil moisture accelerating the rate of recovery. Prescribed fires are typically scheduled to follow natural fire regimes, but burning outside the natural fire season could be equally effective and more convenient for managers, depending on their management objectives. We conducted a field experiment in desert grassland to determine if fire seasonality influenced plant community recovery. Experimental burn treatments occurred in fall, spring, and summer in replicate 0.24-ha plots to determine if fire seasonality affected the rate of recovery of an ungrazed Chihuahuan Desert grassland in central New Mexico. Plant communities were surveyed seasonally for 5 yr after the burns. Grassland community structure responded to fire but not fire seasonality. Grass cover in all burned treatments remained lower than unburned controls for 3 yr after the burns. Community change through time was largely influenced by low rainfall, as grass cover in burned and unburned communities converged during a year with severe drought. In conclusion, fire seasonality did not influence rate of community recovery, but extended drought was possibly more influential than fire on grassland dynamics.

Key Words: black grama, Bouteloua eriopoda, fire seasonality, semiarid grassland

INTRODUCTION

Grasses are a critical component of rangeland function. Both natural phenomena and poor management practices can compromise grassland integrity, and maintaining semiarid grassland vegetation remains a challenge for rangeland managers. Fire frequently shapes and maintains grass-dominated communities (Pausas and Ribeiro 2013) and is often used as a management tool due to its affordability, effectiveness, and speed of treatment (Teague et al. 2001, 2008). Prescribed fires are effective in mesic grasslands where fire stimulates productivity (Knapp and Seastedt 1986), yet in semiarid grasslands lower water availability leads to decreased, patchy fuel loads and longer fire-return intervals. As aridity increases, the magnitude of ecosystem benefits of fire decrease, and often semiarid plant communities are neutrally or negatively impacted by fire (Scheintaub et al. 2009). Several years might be necessary for semiarid vegetation recovery (Gosz and Gosz 1996; Parmenter 2008), and many impacts of fire on semiarid grasslands can be unpredictable (Scheintaub et al. 2009; Pastro et al. 2011). A better understanding of community response to prescribed fire is needed to help managers create optimal fire management practices within semiarid rangelands.

Water availability greatly influences desert grassland recovery (Drewa and Havstad 2001; Scheintaub et al. 2009; Pastro et al. 2011), and higher soil moisture after fire leads to faster grass recovery (Drewa et al. 2006). Total precipitation is low and variable within and between years in semiarid systems (Dettinger et al. 2011), therefore recovery from fire is frequently inconsistent between years or sites. Because response to fire is linked to variable precipitation patterns and fire can negatively impact semiarid systems (Gosz and Gosz 1996; Scheintaub et al. 2009), studying the intricacies of semiarid community response to fire is critical for effective fire management.

The timing of fire with regard to the growing season can impact community response. Within semiarid grasslands of the southwestern United States, perennial grasses predominantly grow during the monsoon season (Muldavin et al. 2008) and natural wildfires generally occur in early summer before the monsoon, when lightning ignites dry grasses (Parmenter 2008). In more mesic (mean annual precipitation [MAP] 665 mm) southern prairie grasslands of northern Texas, species respond differently to the timing of fire, with summer fires stimulating long-term growth of several codominant grass species and winter fires favoring others (Ansley et al. 2006; Ansley and Castellano 2007). Meanwhile, studies have found negative effects of fires during the growing season on Bouteloua eriopoda (Torr.) Torr., a dominant grass of more xeric (MAP 250 mm) Chihuahuan Desert grasslands (Cable 1965; Drewa and Havstad 2001; Parmenter 2008; Killgore et al. 2009). However, it is unclear how prescribed fires during different times of the year affect B. eriopoda, particularly because a related species, Bouteloua gracilis (Willd. ex Kunth) Lag. ex Griffiths, is affected by timing of prescribed fire. Cover of B. gracilis, a dominant grass of the shortgrass steppe, showed little

Research was funded in part by an NSF grant to the University of New Mexico for Long-Term Ecological Research and by a grant from the USDA Forest Service National Fire Plan.

Correspondence: Laura M. Ladwig, Dept of Biology, University of New Mexico, Albuquerque, NM 87131, USA. Email: LLadwig@sevilleta.unm.edu

Manuscript received 2 September 2013; manuscript accepted 2 May 2014.

^{© 2014} The Society for Range Management

Table 1. Climate and fire conditions during experimental burns. Climate measures are from 1100 through 1400 hours.

		Mean air temp	Relative	Mean wind speed	Max wind speed	Wind	Mean fire temp	Within-plot standard
Season	Date	(°C)	humidity	$(m \cdot s^{-1})$	$(m \cdot s^{-1})$	direction	(°C)	deviation of fire temp
Fall	29 October 2007	20.9	20	3.4	7.1	S to SSW	322	69
Spring	28 March 2008	16.6	24.7	5.0	9.3	E	317	97
Summer	2 June 2008	31.3	6.8	2.6	5.8	N, WSW	370	181

response to prescribed fire during the dormant season, whereas growing-season fires negatively impacted grass cover (Brockway et al. 2002; Ford and Johnson 2006). Current knowledge of *B. eriopoda* response to fire seasonality is based on a mix of single experimental burns and observations following natural fires; therefore, a controlled experiment examining *B. eriopoda* and grassland community response to fires in different seasons is needed.

The timing of fires not only influences biotic response, but also interacts with management goals and logistics. Currently, human control or manipulation of most rangeland fires and changing socioeconomics (e.g., Dubinin et al. 2011) can indirectly influence fire regimes. In areas with an active burn crew, scheduling managed burns outside the natural fire season allows crews the ability to also deal with naturally occurring fires, yet it remains unclear if burning during other seasons influences community recovery. Understanding grassland response to a more varied seasonal burn regime could allow managers to choose the most economically and ecologically effective time for prescribed burns.

This research was conducted to provide land managers of semiarid grasslands with information about plant community recovery from fire in different seasons. Plant community response was measured for 5 yr following a single spring, summer, or fall burn. Our specific research objective was to examine how fire seasonality influenced grass and forb cover, species richness, and community composition. We hypothesized that grassland communities and the dominant grass, *B. eriopoda*, would respond most favorably to summer burns, because that is when natural fires occur and soil moisture is most reliable because of the summer monsoons.

METHODS

Study Site

This research was conducted on the Sevilleta National Wildlife Refuge (SNWR) located in central New Mexico (lat 34.33° N, long 106.83° W). Mean (± 1 SE) annual precipitation is 240 (± 14) mm, with roughly 60% falling during the summer monsoon season from July to September. Regional precipitation patterns in this area result in two growing seasons: a spring season following winter melt and a late-summer season aligned with monsoon precipitation. Perennial grasses form the majority of aboveground net primary productivity (ANPP) and common grasses include *B. eriopoda*, *Pleuraphis jamesii* Torr., *Aristida* spp., and *Sporobolus* spp. Forb composition is interannually variable, but commonly includes *Chamaesyce* spp., *Sphaeralcea* spp., *Hoffmannseggia drepanocarpa* A. Gray, and *Machaeranthera pinnatifida* (Hook.) Shinners. Prescribed burns are an active management practice at SNWR, and many biotic responses to summer fires have been documented (Gosz and Gosz 1996; Parmenter 2008; Ravi et al. 2009, 2010b; Parmenter et al. 2011; White 2011) but the response of grassland communities to prescribed burns during different seasons in the northern Chihuahuan Desert is unknown.

Experimental Layout

Experimental burn treatments were established in a *B.* eriopoda-dominated grassland located near the Deep Well area of McKenzie Flats at SNWR. The grasslands are known to have remained unburned for at least 20 yr and likely were unburned for decades longer due to overgrazing during the 20th century, but fire records do not occur prior to 1989. In 2007, twenty 40 m \times 60 m plots were established in a 4 \times 5 grid with a 10-m firebreak between plots. Fire treatments included unburned controls and a one-time fire in either fall, spring, or summer (n=5). Replicates were randomly assigned to the 20 treatment plots. Prescribed burns occurred in



Figure 1. Annual precipitation for the extent of the experiment. Each bar represents total annual precipitation (mm) for the corresponding water year (October–September), with the portion of monsoon precipitation (July–September) indicated in black. The dashed line indicates long-term (22 yr) average mean annual precipitation for the site. Arrows above the graph indicate when the seasonal burns occurred.



Figure 2. Percent cover of grasses (top) and forbs (lower) during spring (left) and fall (right) throughout the experiment. Burn treatments are depicted with different symbols, and mean percent cover is graphed with error bars representing ± 1 SE. Arrows indicate when the burn treatments occurred (fall, dashed; spring, grey; summer, black).

November 2007 (fall), March 2008 (spring), and June 2008 (summer; Table 1). During each burn, fire temperature was measured at 7 to 12 points across each plot using metal tags coated in temperature-sensitive paint that changed color to indicate the maximum fire temperature. Precipitation was measured at the Sevilleta Long-Term Ecological Research (LTER) Deep Well Meteorological station (sev.lternet.edu/ data).

Ten permanent 1 m \times 1 m quadrats were established within each plot to monitor plant communities. Vegetation surveys were conducted in both spring (April to June) and fall (September to October) when plant cover was highest. Prefire vegetation surveys on all plots occurred in 2007 and percent cover of all plants occurring within each quadrat was assessed twice yearly through 2012, with the exception of spring 2009 and fall 2010 when surveys were not conducted.

Several soil parameters were measured before and after fires. Pretreatment soil samples were collected in August 2007 and postfire samples collected in August 2008. Three 2-cm-diam by 10-cm-deep soil samples were collected from each plot with a soil auger. Each soil sample was analyzed separately and averaged for mean plot measurements. Soil moisture was measured by drying soils to constant weight and organic matter content (SOM) via combustion. Field available nitrogen (NO₃ and NH₄) was measured via extraction with 2M KCl and analyzed with a Technicon AutoAnalyzer (Crenshaw et al. 2008). The timing of sampling can influence the soil parameters measured, because time since fire varied between treatments: 2 mo since summer burns, 5 mo since spring burns, and 9 mo since fall burns.

Statistical Analysis

Changes in grass and forb cover through time were analyzed with a separate repeated measure analysis of variance (RMANOVA) for spring and fall data to determine if seasonal cover varied among burn treatments between years. Some plants could only be identified to genus when individuals were very small or not flowering; therefore, taxa richness is reported because our measure of richness was primarily based on species with a few genus-level identifications. Taxa richness at the quadrat (1 m^2) and plot scale (combined 10 quadrats; 10 m²) were analyzed with separate RMANOVAs. Differences in annual cover of the four most abundant grasses through time were assessed with a RMANOVA. Changes in community composition through time were evaluated with nonmetric multidimensional scaling (NMS) ordinations using a Bray-Curtis distance matrix and two dimensions. A separate NMS was run for spring and fall using average percent cover of taxa within each treatment, and similar NMS were run for each year. A Permutational MANOVA (PERMANOVA) was run to determine if data groupings from each NMS were statistically different between treatments and years. To determine which species abundances varied between burn treatments, a Similarity Percentages (SIMPER) for species contributions to compositional variation between treatments was run for each year. Soil properties (SOM content, % moisture, NO₃, NH₄ content), pre- and postfire and between burn treatments, were compared with a separate ANOVA for each soil property. All ANOVAs were run in SAS v.9.3 (SAS Institute Inc, Cary, NC) with an α =0.05. NMS, PERMANOVA, and SIMPER analysis



Figure 3. Annual percent cover of the four most abundant grasses. Burn treatments are depicted with different symbols with error bars representing \pm 1 SE. The dominant grass was *B. eriopoda* (top) and the horizontal grey bar within the graph denotes the range of mean percent cover for the next most abundant grasses (lower graphs). Arrows indicate when the burn treatments occurred.

were preformed using PRIMER v.6 (PRIMER-E Ltd, Lutton, Ivybridge, UK).

RESULTS

Above-average monsoon precipitation in 2006 stimulated grass production (Ladwig et al. 2012), increasing fuel loads prior to the experimental burns. Annual precipitation was also aboveaverage in 2007, the year of the fall experimental burns. During all recovery years, annual precipitation was below average (Fig. 1). Monsoon season precipitation was also below average from 2009 to 2012, with only half the average amount of monsoon rainfall occurring in 2010 and 2011.

In the year after fire, fall grass cover significantly decreased and forbs increased in all burned plots (grasses, P=0.002, F_{12,64}=3.04; forbs, P=0.0004, F_{12,64}=3.57; Fig. 2). Compared to the unburned control, grass cover remained significantly lower in burned plots for 3 yr after fire but was generally unaffected by the timing of fire treatments (Fig. 2). Two years after the fires, spring grass cover was also lower in burned plots (P=0.003, F_{12,64}=2.95), and spring forbs were unaffected by fire (P=0.9). The most abundant grass, B. eriopoda, decreased following fire (P=0.05, $F_{15,33.5}=2.01$) and through time (P=0.01, F_{5.12}=4.65; Fig. 2). Sporobolus spp. and Aristida purpurea Nutt. cover decreased with time (P=0.002, $F_{5,12}=8.02$; P=0.008, $F_{5,12}=5.45$, respectively) but was unaffected by the fire treatments over time (P=0.7; P=0.7, respectively). There was no difference in cover of *Pleuraphis jamesii* over time (P=0.4) or among fire treatments through time (P=0.4; Fig. 3). Richness at the 1 m² and 10 m² scale decreased through time (P < 0.001, $F_{5,80} = 101.08$; P < 0.001, $F_{12,80}=73.28$, respectively), but only varied between fire treatments at the 1 m² scale in 2008 (P=0.003, $F_{15,80}=2.58$) and not the 10 m² scale (P=0.1; Fig. 4).

Spring community composition changed and was significantly different between years (P=0.001) and not different between fire treatments or the year * fire interaction (P=0.1,P=0.9; NMS stress=0.16; Fig. 5). Fall communities varied between both years (P=0.001) and fire treatments (P=0.001) but not the year * fire interaction (P=0.9; NMS stress=0.19). In particular, after summer burns, fall plant communities were the most different (farthest) from unburned control communities, with fall and spring burned communities being similar and generally occurring between summer and control communities (Fig. 5). The most abundant forbs throughout the extent of the experiment were Dalea nana Torr. ex A. Gray, Kallstroemia parviflora J. B. S. Norton, Machaeranthera pinnatifida, Hoffmannseggia drepanocarpa, and Yucca glauca Nutt. The species that contributed the most to community dissimilarity following fire was B. eriopoda, specifically contributing 31-35% of the variation between burn and control plots (Table S1). B. eriopoda also contributed the most to community differences between years, contributing 21-33% of the variation between fall communities and 38-45% of the variation between spring communities (Table S1). Fire treatments or time did not significantly influence NH₄ (P=0.5) or NO₃ concentrations (P=0.4; Table 2). Soil organic matter content remained low, but a significant fire * interaction indicated that SOM was only significantly different in summer plots before and after the fire (model, P=0.03, $F_{7,39}=2.55$, $r^2=0.36$; Fire, P=0.2, Year, P=0.07, Fire * Year, P=0.04; Table 2).

DISCUSSION

Fire alters plant communities, lowering grass cover and increasing forb cover regardless of when the burn occurred.



Figure 4. Average (\pm 1 SE) annual richness at the 10-m² (top) and 1-m² (bottom) scale. Each burn treatment is represented with a separate line: fall burn (long dashed), spring burn (solid grey), summer burn (solid black), and unburned control (short dashed). Arrows indicate when seasonal burn treatments occurred (fall, dashed; spring, grey; summer, black).

In water-stressed systems, grass cover frequently decreases during the first year postfire (Scheintaub et al. 2009), increasing resource availability for forbs. Also, forb abundance increased in a *B. eriopoda* removal experiment, suggesting a general competitive interaction between these dominant grasses and forbs (Peters and Yao 2012). Indeed, forb cover peaked initially following fire while grasses required several years to recover, leading to different recovery trajectories for fall and spring communities. Rather, fall-burned communities dominated by perennial grasses took longer to converge than communities burned in spring, which contained more forbs. Prescribed burns can increase grassland diversity through increases in species richness (Drewa and Havstad 2001), and within this grassland, changes in richness are largely dictated by forbs (Báez et al. 2006). Richness slightly increased the first year following summer and fall burns at the 1 m^2 but not the 10 m^2 scale. Forbs were presumably more evenly distributed across plots after summer and fall fires, leading to one or two more species at the 1 m² scale, but ultimately the same number of taxa remained within the larger plots. Forb abundance can be unrelated to number of taxa (Xia et al. 2010) and in this experiment increased forb cover was due to larger or more numerous individuals instead of more species.

Grass dynamics were largely attributed to the response of the dominant grass of the Chihuahuan Desert grassland, *Bouteloua* eriopoda. B. eriopoda exhibits a variable response to fire

(Drewa and Havstad 2001; Parmenter 2008; Killgore et al. 2009). Natural fire-return intervals can directly relate to the length of dominant grass recovery (Cable 1967), estimated around 10 yr in B. eriopoda-dominated grasslands (Parmenter 2008), but remain highly variable based on moisture availability. B. eriopoda often shows slow or negative responses to fire (Parmenter 2008; Killgore et al. 2009; Vargas et al. 2012) and requires adequate soil moisture for full recovery (Drewa and Havstad 2001). If ample precipitation follows a fire, B. eriopoda can recover in one growing season (Drewa et al. 2006). During this study, drought conditions occurred throughout all years of recovery, presumably resulting in the slow recovery of B. eriopoda. Within mixed grasslands at SNWR, grass species respond differently to fire, and B. eriopoda recovers slower than neighboring grasses, including B. gracilis, Sporobolus contractus Hitchc., and Muhlenbergia arenicola (Buckley) Hitchc. (Gosz and Gosz 1996; Ford 1999; Parmenter 2008; Augustine et al. 2010). Other grass taxa (Pleurapis jamesii, Aristida spp., and Sporobolus spp.) were unresponsive to fire and could have filled the niches made available by low *B. eriopoda* cover, but these subdominant grasses maintained low cover (1-5%), and likely contributed minimally to community recovery.

Fire seasonality had a limited influence on grassland recovery. During the first year postfire, grass cover was lower and forbs were more abundant following summer burns, but



Figure 5. Fall (top) and spring (lower) communities based on separate nonmetric multidimensional scaling (NMS). Treatments are depicted with different symbols and years indicated in different shades of grey. The pretreatment (2007) data points are white and outlined in black, and subsequent years are increasingly darker shades of grey, with the final year (2012) in black.

this difference did not persist. This seasonal pattern was contrary to our hypothesis that grasses would respond more favorably to summer fires, because summer is the natural fire season (Parmenter 2008). Although plant communities were not responsive to fire seasonality, the timing of fires could influence other factors related to grassland function. Fire can homogenize soil resources by dispersing nutrient concentrations associated with islands of fertility (White 2011; Sankey et al. 2012). Additionally, several ecosystem benefits of plant

Table 2. Average preburn (2007) and post burn (2008) soil properties.

 Asterisks indicate the values that were significantly different from each other at the 0.05 level.

Fire	Organi (g · g⁻	c matter ⁻¹ soil)	N (Nmg•)	IH ₄ kg ^{—1} soil)	NO_3 (N mg · kg ⁻¹ soil)	
treatment	Preburn	Postburn	Preburn	Postburn	Preburn	Postburn
Fall	0.013	0.013	0.82	1.36	1.64	1.84
Spring	0.014	0.013	1.049	1.18	1.56	1.76
Summer	0.013*	0.015*	1.14	0.86	1.79	1.66
Control	0.013	0.014	1.38	1.013	1.82	1.54

cover are based on the physical presence of plant material. Standing dead or live biomass can trap soil particles and debris to help stabilize surface soil (Turnbull et al. 2008) and decrease wind (Ravi et al. 2010a) and fluvial (Bhark and Small 2003; Turnbull et al. 2008) erosion. Altered plant cover following fire can increase runoff, lower infiltration, and lead to overall losses of water, soil, and nutrients from the system (Ludwig et al. 2005; White et al. 2006). Given that standing dead plant cover is important in many abiotic processes, the ecosystem benefits to allowing dead cover to overwinter and burning closer to the growing season can be important to consider when scheduling fires in Chihuahuan Desert grasslands.

The plant community was not influenced by fire seasonality, but community composition changed through time in both burned and unburned plots. Natural fire regimes in southwestern United States are predicted to change as a result of global climate change. Increased temperatures and decreased humidity can lead to fires starting earlier in the spring, overall longer fire seasons, and an increased number of fire danger days (Weiss et al. 2009; Abatzoglou and Kolden 2011). Although fire had an immediate effect on plant communities, precipitation, particularly drought, had a larger overarching influence (White et al. 2006). Precipitation, the dominant driver of ecological processes in semiarid regions (Ludwig et al. 2000; Austin et al. 2004; Reynolds et al. 2004; Collins et al. 2008), influences community trajectories during fire recovery (White et al. 2006; Scheintaub et al. 2009; Vargas et al. 2012). Precipitation was low when burning occurred and remained below-average in all subsequent years, at one point reaching less than half mean annual precipitation. Drought conditions not only slowed recovery from fire but also affected the unburned controls as all grassland communities changed, regardless of fire history. Convergence of burned and unburned communities occurred during the severe drought year. Although fire is an influential disturbance in these semiarid grasslands, soil moisture availability remains the ultimate driver of community dynamics.

IMPLICATIONS

This experiment was conducted to determine if fires during the nontraditional burn season (spring and fall) have a different influence on community recovery than traditional summer fires. In general, fire seasonality did not influence plant communities. Burned plots, regardless of seasonal timing, experienced decreased grass cover and increased compositional variation for several years following the fire. Community response to fire was also presumably influenced by several years of drought that followed the experimental burns. Although even following extensive drought, plants respond quickly to adequate precipitation (Pennington and Collins 2007). Unlike aboveground production, belowground production by *B. eriopoda* is not influenced by fire (Burnett et al. 2012). Therefore, roots can immediately utilize available moisture following rain events. Higher soil moisture accelerates the rate of recovery from fire, and previous studies suggest an ideal time for a fire is right before a rain event (e.g., Drewa and Havstad 2001). Given the importance of soil moisture and the unpredictable nature of the timing of precipitation, it might be more feasible to burn within several days after a large rain event, when plants and surface soils are dry but moisture remains in the rooting zone.

Fire did not enhance grass cover or community richness; instead, overall grass cover was lower for several years following fire. Prescribed burns are often conducted to help maintain grassland integrity by returning nutrients to the soil, preventing or managing woody encroachment, or decreasing forb competitors to increase grass vigor, all of which help maintain grass-dominated communities. During fire recovery, grasses were slow to respond and unburned communities changed as much as burned communities in response to several years of drought. Because semiarid grassland communities are already stressed by unpredictable drought conditions, the use of fire, particularly during drought conditions, should be carefully aligned with management goals.

ACKNOWLEDGMENTS

We would like to thank the US Fish and Wildlife burn crew, Sevilleta National Wildlife Refuge for allowing us to conduct this research on their land, A. Swann for data collection, S. Koerner and J. Mulhouse for helpful comments on earlier versions, and Sevilleta LTER staff for logistical and data support.

LITERATURE CITED

- ABATZOGLOU, J. T., AND C. A. KOLDEN. 2011. Climate change in western US deserts: potential for increased wildfire and invasive annual grasses. *Rangeland Ecology & Management* 64:471–478.
- ANSLEY, R. J., AND M. J. CASTELLANO. 2007. Texas wintergrass and buffalograss response to seasonal fires and clipping. *Rangeland Ecology & Management* 60:154–164.
- ANSLEY, R. J., M. J. CASTELLANO, AND W. E. PINCHAK. 2006. Sideoats grama growth responses to seasonal fires and clipping. *Rangeland Ecology & Management* 59:258–266.
- AUGUSTINE, D. J., J. D. DERNER, AND D. G. MILCHUNAS. 2010. Prescribed fire, grazing, and herbaceous plant production in shortgrass steppe. *Rangeland Ecology & Management* 63:317–323.
- AUSTIN, A. T., L. YAHDJIAN, J. M. STARK, J. BELNAP, A. PORPORATO, U. NORTON, D. A. RAVETTA, AND S. M. SCHAEFFER. 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* 141:221–235.
- BÁEZ, S., S. L. COLLINS, D. LIGHTFOOT, AND T. L. KOONTZ. 2006. Bottom-up regulation of plant community structure in an aridland ecosystem. *Ecology* 87:2746–2754.
- BHARK, E. W., AND E. E. SMALL. 2003. Association between plant canopies and the spatial patterns of infiltration in shrubland and grassland of the Chihuahuan Desert, New Mexico. *Ecosystems* 6:185–196.

- BROCKWAY, D. G., R. G. GATEWOOD, AND R. B. PARIS. 2002. Restoring fire as an ecological process in shortgrass prairie ecosystems: initial effects of prescribed burning during the dormant and growing seasons. *Journal of Environmental Management* 65:135–152.
- BURNETT, S. A., J. A. HATTEY, J. E. JOHNSON, A. L. SWANN, D. I. MOORE, AND S. L. COLLINS. 2012. Effects of fire on belowground biomass in Chihuahuan desert grassland. *Ecosphere* 3:Article 107.
- CABLE, D. R. 1965. Damage to mesquite (*Prosopis juliflora*), Lehmann lovegrass (*Eragrostis lehmanniana*), and black grama (*Bouteloua eriopoda*) by a hot June fire. *Journal of Rangeland Management* 18:326–329.
- CABLE, D. R. 1967. Fire effects on semidesert grasses and shrubs. *Journal of Range Management* 20:170–176.
- Collins, S. L., R. L. Sinsabaugh, C. CRENSHAW, L. GREEN, A. PORRAS-ALFARO, M. STURSOVA, AND L. H. ZEGLIN. 2008. Pulse dynamics and microbial processes in aridland ecosystems. *Journal of Ecology* 96:413–420.
- CRENSHAW, C. L., C. LAUBER, R. L. SINSABAUGH, AND L. K. STAVELY. 2008. Fungal control of nitrous oxide production in semiarid grassland. *Biogeochemistry* 87:17–27.
- DETTINGER, M. D., F. M. RALPH, T. DAS, P. J. NEIMAN, AND D. R. CAYAN. 2011. Atmospheric rivers, floods and the water resources of California. *Water* 3:445–478.
- DREWA, P. B., AND K. M. HAVSTAD. 2001. Effects of fire, grazing, and the presence of shrubs on Chihuahuan desert grasslands. *Journal of Arid Environments* 48:429– 443.
- DREWA, P. B., D. P. C. PETERS, AND K. M. HAVSTAD. 2006. Population and clonal level responses of a perennial grass following fire in the northern Chihuahuan Desert. *Oecologia* 150:29–39.
- DUBININ, M., A. LUSCHEKINA, AND V. C. RADELOFF. 2011. Climate, livestock, and vegetation: what drives fire increase in the arid ecosystems of southern Russia? *Ecosystems* 14:547–562.
- FORD, P. L. 1999. Response of buffalograss (Buchloe dactyloides) and blue grama (Bouteloua gracilis) to fire. Great Plains Research 9:261–276.
- FORD, P. L., AND G. V. JOHNSON. 2006. Effects of dormant- vs. growing-season fire in shortgrass steppe: biological soil crust and perennial grass responses. *Journal of Arid Environments* 67:1–14.
- Gosz, R. J., AND J. R. Gosz. 1996. Species interactions on the biome transition zone in New Mexico: response of blue grama (*Bouteloua gracilis*) and black grama (*Bouteloua eripoda*) to fire and herbivory. *Journal of Arid Environments* 34:101– 114.
- KILLGORE, A., E. JACKSON, AND W. G. WHITFORD. 2009. Fire in Chihuahuan Desert grassland: short-term effects on vegetation, small mammal populations, and faunal perturbation. *Journal of Arid Environments* 73:1029–1034.
- KNAPP, A. K., AND T. R. SEASTEDT. 1986. Detritus accumulation limits productivity of tallgrass prairie. *Bioscience* 36:662–668.
- LADWIG, L. M., S. L. COLLINS, A. L. SWANN, Y. XIA, M. F. ALLEN, AND E. B. ALLEN. 2012. Above- and belowground responses to nitrogen addition in a Chihuahuan Desert grassland. *Oecologia* 169:177–185.
- LUDWIG, J. A., E. MULDAVIN, AND K. R. BLANCHE. 2000. Vegetation change and surface erosion in desert grasslands of Otero Mesa, Southern New Mexico: 1982 to 1995. American Midland Naturalist 144:273–286.
- LUDWIG, J. A., B. P. WILCOX, D. D. BRESHEARS, D. J. TONGWAY, AND A. C. IMESON. 2005. Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes. *Ecology* 86:288–297.
- MULDAVIN, E. H., D. I. MOORE, S. L. COLLINS, K. R. WETHERILL, AND D. C. LIGHTFOOT. 2008. Aboveground net primary production dynamics in a northern Chihuahuan Desert ecosystem. *Oecologia* 155:123–132.
- PARMENTER, R. R. 2008. Long-term effects of a summer fire on desert grassland plant demographics in New Mexico. *Rangeland Ecology & Management* 61:156–168.
- PARMENTER, R. R., M. KREUTZIAN, D. I. MOORE, AND D. C. LIGHTFOOT. 2011. Short-term effects of a summer wildfire on a desert grassland arthropod community in New Mexico. *Environmental Entomology* 40:1051–1066.
- PASTRO, L. A., C. R. DICKMAN, AND M. LETNIC. 2011. Burning for biodiversity or burning biodiversity? Prescribed burn vs. wildfire impacts on plants, lizards, and mammals. *Ecological Applications* 21:3238–3253.
- PAUSAS, J. G., AND E. RIBEIRO. 2013. The global fire-productivity relationship. Global Ecology and Biogeography 22:728–736.

- PENNINGTON, D. D., AND S. L. COLLINS. 2007. Response of an aridland ecosystem to interannual climate variability and prolonged drought. *Landscape Ecology* 22:897–910.
- PETERS, D. P. C., AND J. YAO. 2012. Long-term experimental loss of foundation species: consequences for dynamics at ecotones across heterogeneous landscapes. *Ecosphere* 3:Article 27.
- RAVI, S., D. D. BRESHEARS, T. E. HUXMAN, AND P. D'ODORICO. 2010a. Land degradation in drylands: interactions among hydrologic-aeolian erosion and vegetation dynamics. *Geomorphology* 116:236–245.
- RAVI, S., P. D'ODORICO, T. E. HUXMAN, AND S. L. COLLINS. 2010b. Interactions between soil erosion processes and fires: implications for the dynamics of fertility islands. *Rangeland Ecology & Management* 63:267–274.
- RAVI, S., P. D'ODORICO, L. X. WANG, C. S. WHITE, G. S. OKIN, S. A. MACKO, AND S. L. COLLINS. 2009. Post-fire resource redistribution in desert grasslands: a possible negative feedback on land degradation. *Ecosystems* 12:434–444.
- REYNOLDS, J. F., P. R. KEMP, K. OGLE, AND R. J. FERNANDEZ. 2004. Modifying the 'pulsereserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia* 141:194–210.
- SANKEY, J. B., S. RAVI, C. S. A. WALLACE, R. H. WEBB, AND T. E. HUXMAN. 2012. Quantifying soil surface change in degraded drylands: shrub encroachment and effects of fire and vegetation removal in a desert grassland. *Journal of Geophysical Research: Biogeosciences* 117:G02025.
- SCHEINTAUB, M. R., J. D. DERNER, E. F. KELLY, AND A. K. KNAPP. 2009. Response of the shortgrass steppe plant community to fire. *Journal of Arid Environments* 73:1136–1143.

- TEAGUE, W. R., R. J. ANSLEY, U. P. KREUTER, W. E. PINCHAK, AND J. M. McGRANN. 2001. Economics of managing mesquite in north Texas: a sensitivity analysis. *Journal of Range Management* 54:553–560.
- TEAGUE, W. R., W. E. GRANT, U. P. KREUTER, H. DIAZ-SOLIS, S. DUBE, M. M. KOTHMANN, W. E. PINCHAK, AND R. J. ANSLEY. 2008. An ecological economic simulation model for assessing fire and grazing management effects on mesquite rangelands in Texas. *Ecological Economics* 64:611–624.
- TURNBULL, L., J. WAINWRIGHT, AND R. E. BRAZIER. 2008. A conceptual framework for understanding semi-arid land degradation: ecohydrological interactions across multiple-space and time scales. *Ecohydrology* 1:23–34.
- VARGAS, R., S. L. COLLINS, M. L. THOMEY, J. E. JOHNSON, R. F. BROWN, D. O. NATVIG, AND M. T. FRIGGENS. 2012. Precipitation variability and fire influence the temporal dynamics of soil CO₂ efflux in an arid grassland. *Global Change Biology* 18:1401–1411.
- WEISS, J. L., C. L. CASTRO, AND J. T. OVERPECK. 2009. Distinguishing pronounced droughts in the Southwestern United States: seasonality and effects of warmer temperatures. *Journal of Climate* 22:5918–5932.
- WHITE, C. S. 2011. Homogenization of the soil surface following fire in semiarid grasslands. *Rangeland Ecology & Management* 64:414–418.
- WHITE, C. S., R. L. PENDLETON, AND B. K. PENDLETON. 2006. Response of two semiarid grasslands to a second fire application. *Rangeland Ecology & Management* 59:98–106.
- XIA, Y., D. I. MOORE, S. L. COLLINS, AND E. H. MULDAVIN. 2010. Aboveground production and species richness of annuals in Chihuahuan Desert grassland and shrubland plant communities. *Journal of Arid Environments* 74:378–385.