Fire Ecology Volume 14, Issue 1, 2018
doi: 10.4996/fireecology.140132048

Research Article

Dormant-Season Fire Inhibits Sixweeks Fescue and Enhances Forage Production in Shortgrass Steppe

Nickolas A. Dufek[1*], David J. Augustine[1], Dana M. Blumenthal[1], Julie A. Kray[1], and Justin D. Derner[2]

[1] USDA-Agricultural Research Service, Rangeland Resources and Systems Research Unit, 1701 Centre Avenue, Fort Collins, Colorado 80525, USA

[2] USDA-Agricultural Research Service, Rangeland Resources and Systems Research Unit, 8408 Hildreth Road, Cheyenne, Wyoming 82009, USA

*Corresponding author: Tel.: +1-970-492-7138; e-mail: Nickolas.Dufek@ars.usda.gov

ABSTRACT

Semiarid rangelands experience substantial interannual variability in precipitation, which can determine the relative abundance of species in any given year and influence the way that fire affects plant community composition and productivity. Long-term studies are needed to examine potential interactions between fluctuating community composition and the role of fire in these ecosystems. Here, we report on an 11-year (2006 to 2016) study of annual and triennial dormant-season prescribed fires in the semiarid shortgrass steppe of Colorado, USA. Productivity of the dominant C_4 shortgrasses was not reduced by dormant-season burns in any year. The C_3 annual grass, sixweeks fescue (*Vulpia octoflora* [Walter] Rydb.) was rare during the first 7 years (2006 to 2012) but, following drought in 2012, increased dramatically in unburned plots (2013 to 2016). Both spring and autumn annual burns reduced fescue biomass during 2014 to 2016 by an average of 87%. Autumn triennial burns prior to the 2013 and 2016 growing seasons similarly reduced fescue (86%), while spring tri-

RESUMEN

Los pastizales semiáridos experimentan una variabilidad interanual sustancial en precipitación, lo cual puede determinar la abundancia relativa de especies en un año determinado, e influenciar la forma en que el fuego afecta la composición de la comunidad de plantas y la productividad. Se necesitan estudios a largo plazo para examinar las interacciones potenciales entre la composición fluctuante de la comunidad y el rol del fuego en estos ecosistemas. En este estudio llevado a cabo durante 11 años (2006 a 2016), en temporadas de latencia anuales y trianuales, reportamos quemas prescriptas en la estepa semiárida de pastos bajos en Colorado, EEUU. La productividad de los pastos dominantes bajos C_4 no fue reducida por las quemas en la temporada de latencia en ningún año. Los pastos anuales $C_{3,}$ como la festuca de seis semanas (*Vulpia octoflora* [Walter] Rydb.) fue escasa durante los primeros 7 años (2006 a 2012), pero luego de la sequía en 2012, se incrementó en forma dramática en parcelas sin quemar (2013 a 2016). Quemas anuales tanto de primavera como de otoño redujeron la biomasa de festuca durante 2014 y hasta 2016 en un promedio del 87%. Las quemas trianuales de otoño antes de las estaciones de crecimiento de 2013 y 2016 redujeron en forma similar la festuca (86%), ennial burns implemented prior to the 2012 and 2015 growing seasons did not. Results indicate that burning during fescue establishment can prevent proliferation, but burning two years later when fescue had reached peak abundance was ineffective. All three burn treatments that suppressed fescue subsequently enhanced C_4 grass production. We suggest that rangeland managers be aware of the potential for sixweeks fescue germination and establishment during warm, wet winters that follow drought years, and consider the use of dormant-season prescribed fire to adaptively reduce negative impacts on forage production.

mientras que las quemas trianuales de primavera implementadas antes de las temporadas de crecimiento en 2012 y 2015 no tuvieron ese efecto. Los resultados indican que las quemas durante el establecimiento de la festuca pueden prevenir su proliferación, pero realizadas dos años más tarde, cuando la festuca alcanza un pico en su abundancia, fueron inefectivas. Los tres tratamientos de quema que suprimieron la festuca, favorecieron la producción de pastos C_4. Nosotros sugerimos que los gestores de pastizales tengan en cuenta el potencial de la festuca de germinar por 6 semanas y de establecerse durante inviernos cálidos y húmedos que siguen a años secos, y considerar el uso de quemas prescriptas en la temporada de latencia para reducir en forma adaptativa sus impactos negativos en la producción de forraje.

Keywords: annual prescribed fire, *Bouteloua gracilis*, grassland, rangeland management, semi-arid, *Vulpia octoflora,* western Great Plains

Citation: Dufek, N.A., D.J. Augustine, D.M. Blumenthal, J.A. Kray, J.D. Derner. 2018. Dormant-season fire inhibits sixweeks fescue and enhances forage production in shortgrass steppe. Fire Ecology 14(1): 33–49. doi: 10.4996/fireecology.140132048

INTRODUCTION

Fire plays an important role in the maintenance, restoration, and management of many rangeland ecosystems worldwide. In the Great Plains of central North America, fire effects on vegetation productivity can vary considerably along an east-to-west gradient of declining mean annual precipitation and aboveground plant productivity (Oesterheld *et al*. 1999, Schientaub *et al.* 2009, Wonkka *et al.* 2017). Across this gradient, substantial regional variation occurs in the historic frequency and seasonality of fires, and in the present-day use of prescribed fire as a management tool for rangelands. In the eastern, mesic tallgrass prairies of the Great Plains, historic fire return intervals are generally estimated to be <4 yr (Guyette *et al*. 2012), and in portions of the tallgrass prairie today, frequent spring prescribed fire is employed to enhance livestock forage quality and maintain dominance of desired forage grasses (Svejcar 1989, Engle and Bidwell 2001, Fuhlendorf and Engle 2004). In the western, semiarid grasslands of the Great Plains, historic fire return intervals were likely >10 yr (Guyette *et al*. 2012). Results from early studies of wildfires in this semiarid region suggested that they had potential negative effects on plant productivity (Oesterheld *et al*. 1999) and little or no benefit to livestock production (Wright and Bailey 1982), and today, prescribed fire is not a widely used management tool in the western Great Plains (Ford and McPherson 1996, McDaniel *et al*. 1997). However, studies of infrequent prescribed fire have identified potential applications for land managers, including suppression of plant species that are unpalatable to livestock (e.g., McDaniel *et al*. 1997, Vermeire and Roth 2011, Strong *et al*. 2013, Augustine and Derner 2015), short-term enhancement of forage quality (Augustine *et al*. 2010, Dufek *et al*. 2014), and improvements in habitat for wildlife species of conservation concern (e.g., Thompson *et al*. 2008, Augustine and Derner 2012).

The shortgrass steppe of the western Great Plains (corresponding to the driest and warmest climate in the region) is dominated by perennial C_4 shortgrasses, primarily blue grama (*Bouteloua gracilis* [Willd. ex Kunth] Lag. ex Griffiths) and buffalo grass (*B. dactyloides* [Nutt] Englm.) (Lauenroth *et al.* 1999). Despite the dominance of these species and their importance to livestock production, a diverse suite of subdominant plants influence the structure and function of these rangelands, and contribute in varying ways to their value for livestock and native wildlife species. The abundance and distribution of subdominants such as perennial C_3 graminoids, annual grasses, cacti, subshrubs, and forbs are often strongly influenced by the variable and unpredictable precipitation inputs that characterize this region, with wet springs enhancing C_3 graminoids (Milchunas *et al*. 1994, Derner *et al.* 2008); droughts enhancing cactus abundance (Lauenroth *et al*. 2009); and warm, wet winters facilitating establishment of winter annual grasses (Hylton and Bement 1961). Although previous studies indicate that C_4 shortgrass productivity and dominance are relatively insensitive to fire (Ford 1999, Scheintaub *et al*. 2009, Augustine *et al*. 2010), fires can potentially affect subdominant plants, depending on their timing, intensity, and frequency in relation to weather patterns. For example, burning in the autumn (Oct to Nov) can suppress prickly pear cactus (*Opuntia polyacantha* Haw.; Augustine and Derner 2015), while spring (Mar to Apr) burning has little effect (Augustine and Milchunas 2009). Long-term studies of fire effects in shortgrass steppe are rare (Ford and Johnson 2006), but are necessary to examine variation in the magnitude of fire effects and post-fire recovery under a range of precipitation patterns and the associated responses of different plant functional groups and species.

Here, we report on an 11-year study examining plant responses to variation in the timing and frequency of prescribed fire in the shortgrass steppe of eastern Colorado. Results published from the first five years of this study focused on the contrast between annual and triennial burns conducted in early spring during 2006 to 2010, and showed that burning when dominant perennial grasses have already initiated growth in the spring can reduce their productivity (Scheintaub *et al*. 2009), while burning when dominant grasses are still dormant does not (Scheintaub *et al*. 2009, Augustine *et al*. 2014*a*). Our objective was to build upon their work by examining both the seasonality (autumn versus spring) and frequency (annual versus triennial) of prescribed fire effects on four plant functional groups: 1) C_4 perennial grasses; 2) C_3 perennial graminoids; 3) forbs; and 4) the annual C_3 grass, sixweeks fescue (*Vulpia octoflora*). We focused in particular on patterns of sixweeks fescue and C_4 shortgrass productivity that emerged during the last four years of the experiment, and which have important implications for how fire can be used to enhance forage availability for livestock in shortgrass steppe.

Annual fire and, to a lesser extent, triennial fire represent extreme fire scenarios in shortgrass steppe, but are still considered to be options for wildlife habitat management and short-term enhancement of forage quality for livestock. The inclusion of these fire frequencies allows us to address concerns that land managers have regarding potential negative impacts on forage production and plant community composition. In particular, one hypothesized reason that fire could affect certain plant species (i.e., subdominants other than the C_4 grasses) in semiarid grasslands is through a reduction in spring soil moisture retention due to increased bare soil exposure in burned areas (Vermiere *et al.* 2005, Schientaub *et al.* 2009).

In addition, species that have already initiated growth when the dominant C_4 grasses are still dormant could be directly injured by flames during dormant-season burns (Schientaub *et al.* 2009, Vermiere *et al.* 2011, Russell 2013). Based on these mechanisms, we hypothesized that fire would have more severe negative effects on C_3 graminoids, forbs, and the annual grass, sixweeks fescue, than on C_4 grasses.

METHODS

Study Area and Plant Community

We studied native shortgrass steppe at the USDA-Agricultural Research Service's Central Plains Experimental Range, a Long-Term Agroecosystem Research (USDA 2017) network location, approximately 12 km northeast of Nunn, Colorado, USA (4050'N, 104°43'W). Mean annual precipitation is 340 mm and topography is characterized by gently undulating plains. The study site was located on fine sandy loam soils associated with the Loamy Plains ecological site (NRCS 2007). Two C_4 perennial grasses, blue grama and buffalo grass, dominate the vegetation (typically >70 % of annual net primary production). C_3 perennial graminoids consisted primarily of needleleaf sedge (*Carex duriuscula* C.A. May) and western wheatgrass (*Pascopyrum smithii* [Rydb.] A. Love). The most common forbs were the perennial scarlet globemallow (*Sphaeralcea coccinea* [Nutt] Rydb.), the annual prairie pepperweed (*Lepidium densiflorum* Shrad.) and the annual prairie evening primrose (*Oenthera albicaulis* Pursh). The only annual grass species in the experiment was sixweeks fescue (*Vulpia octoflora* [Walt] Rydb), which is a C_3 winter annual that germinates and initiates growth either in autumn or early spring, outside of the typical growing season of the dominant perennial grasses (Hylton and Bement 1961). Growth of sixweeks fescue is episodic because optimum temperatures (15 °C to 25 °C) along with extended periods (>7 days) of increased soil moisture occur only intermittently (Hylton and Bement 1961).

Prescribed Burns

Twenty 20 m × 20 m plots were established in a relatively flat, homogenous, upland shortgrass steppe site. Study plots had not been grazed by cattle for 5 years prior to the start of the experiment in 2006 and remained ungrazed throughout the experiment. We used a completely randomized design with five treatments (annual spring burn, annual autumn burn, triennial spring burn, triennial autumn burn, and unburned control) and four replicates per treatment. The annual burn treatments began in 2006 and continued through 2016. The triennial spring and autumn burns were conducted in 2006, 2009, 2012, and 2015. Note that spring and autumn burns conducted in the same calendar years precede different growing seasons. Spring burns conducted in a given calendar year were examined for effects on vegetation in that same calendar year, whereas effects of autumn prescribed burns were evaluated in the following calendar year. Due to this delay in the initiation of the autumn burn treatment, the weather conditions during the first post-burn growing season in the triennial spring burn treatment were different from those in the triennial autumn burn treatment, and hence we did not compare these two treatments. Spring burns in 2006 were conducted when perennial grasses had initiated green-up (Scheintaub *et al*. 2009), while all subsequent spring burns occurred when the dominant perennial grasses were dormant. Autumn burns were implemented in October to December after complete senescence of C_4 grasses. For each burn, we established a wetline (a wetted line along the burn area boundary) on the two downwind boundaries, initiated back burns to create 1 m to 2 m blacklines (~2 m boundary area that was backburned prior to implementing the headfire) on these boundaries, and then burned the remainder of the plot with a head fire lit with hand-held drip torches. All plots were burned within a period of approximately two hours. In years in which both annual and triennial burns occurred, all eight plots were burned on the same afternoon. For details on weather conditions, fuel loads, fire temperatures, and heat dosage that the plots experienced during the burns, see Augustine *et al*. (2014*b*). Burns were implemented as planned in all years of the study with two exceptions: 1) the burns conducted in the autumn of 2012 and spring of 2013 involved low fuel loads following the 2012 drought year (Figure 1), such that fires burned in a patchy manner across the plots (Augustine *et al*. 2014*b*); and 2) the planned annual burns were not conducted in the autumn of 2014 due to the lack of an adequate burn window as the vegetation did not senesce prior to snow coverage.

Plant Measurements

Aboveground net herbaceous plant production was measured in late July or early August of each year, which corresponds to peak standing crop and the point in the season when measurements best approximate aboveground net production (Milchunas and Lauenroth 1992). Aboveground biomass was clipped in five 0.25 m^2 quadrats (2006 to 2010) or ten 0.10 m^2 quadrats (2011 to 2014) randomly located in each plot. During harvest, we separated biomass into functional groups consisting of C_3 perennial graminoids, C_4 perennial grasses, forbs, annual grass, and standing dead biomass. Biomass of cacti and subshrubs, both rare in the study plots, was not sampled. We defined standing dead biomass as plant tissues that were produced in the prior growing season. Plant tissues that grew in the current growing season but were partly or wholly senescent at the time of harvest were still included in their respective functional group. On the same date as the biomass harvest each year, we also visually estimated the basal cover of bare soil in 25 0.1 m^2 quadrats randomly located in each plot. Following harvest, biomass samples were sorted in the lab to ensure effective separation of standing dead biomass from

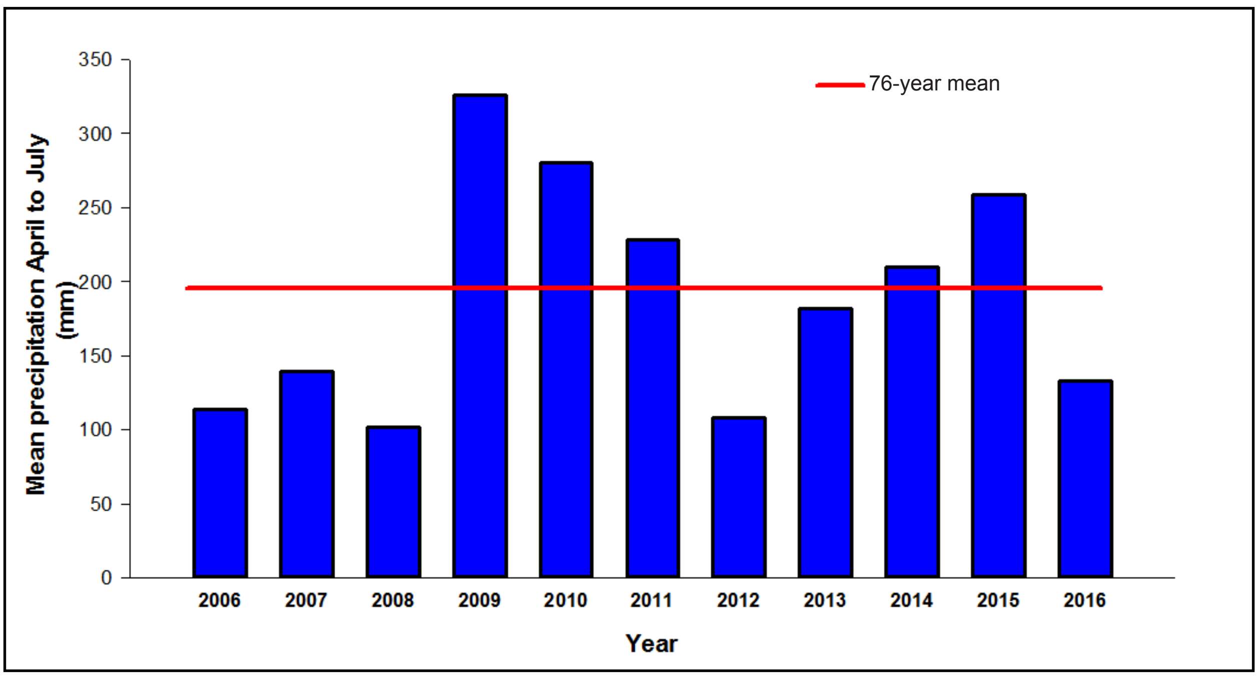

Figure 1. Mean precipitation (mm) for April to July for Central Plains Experimental Range, Colorado, USA, from 2006 to 2016. Red line represents the 76-year mean.

current-year production of each functional group, oven dried at 55 °C, and weighed. Biomass estimates were averaged at the plot level for analysis. The C_4 and C_3 perennial graminoids and the forb functional group all consist of species that are palatable to cattle, whereas the annual grass, sixweeks fescue, is avoided by grazing cattle (Hyder and Bement 1964, Milchunas *et al.* 2008). Throughout this paper, we use the term "forage production" to refer to the summed productivity of C_3 and C_4 perennial graminoids plus forbs.

Soil Moisture Measurements

We measured soil volumetric water content (VWC) at the 0 cm to 10 cm depth hourly using Decagon 5TE® probes and EM50® data loggers (Decagon Devices Inc., Pullman, Washington, USA). We focused on the surface soil layer because it was most likely to be influenced by fire-induced changes in bare soil exposure. A single probe was placed vertically in each plot at least 2 m from the outside edge. During burns, probes were left in place and protected from heat by a 4 cm wide metal pipe lined with a 2 cm wide PVC pipe. We used factory calibrations based on the Topp equation (Topp *et al*. 1980), which are expected to yield VWC measurements within ±3 % of true soil volumetric water content in mineral soils. Soil VWC records were averaged daily prior to analysis.

Data Analyses

We analyzed the effect of prescribed burn treatments on (1) total aboveground herbaceous biomass, (2) total forage production (the sum of perennial C_3 graminoids, perennial C_4 grasses, and forbs), (3) C_3 forage production (the sum of perennial C_3 graminoids, and forbs), (4) C_4 forage production, and (5) annual grass production (consisting entirely of sixweeks fescue). We used generalized linear mixed models that included burn treatment (unburned, annual spring burns, triennial spring burns, annual autumn burns, and triennial autumn burns), year, and burn treatment × year interaction as fixed effects, and accounted for the repeated-measures design by including a random term identifying individual plots as subjects that were measured repeatedly across years (SAS v9.4; SAS Institute Inc., Cary, North Carolina, USA). We inspected residual plots and log-transformed response variables as necessary to address heteroscedasticity. For response variables with significant year × treatment interactions, our focus was on six within-year contrasts. We did not consider contrasts between spring versus autumn burn treatments (either for annual or triennial) because, for a given year of sampling, spring burns had already received the burn treatment whereas autumn burns occurred after biomass harvests. Therefore, we focused on contrasts consisting of unburned controls versus the four burn treatments, annual spring burn versus triennial spring burn, and annual autumn burn versus triennial autumn burn.

We analyzed treatment effects on soil VWC during three seasonal plant growth windows for seven years of the study (2009 to 2016). These six-week intervals represented critical growth periods for (1) C_3 perennial graminoids (spring, 1 May to 15 June), (2) C_4 perennial grasses (summer, 16 June to 31 July), and (3) winter-annual grasses (autumn, 1 September to 15 October). Gaps in soil water content data due to sensor failure occurred in only 4.3 % of 21 920 daily VWC observations. We filled gaps with predicted values from regression equations based on data from all other plots of the same treatment during the 10 days preceding and 10 days following the period of missing data (Boden *et al*. 2013). A few gaps, representing 1.8 % of daily data points, were left as missing data due to insufficient contextual information to create a regression.

Soil moisture mixed models included treatment, year, season, and associated interactions as fixed effects and accounted for the repeated-measures design by including a random term identifying individual plots as subjects that were measured repeatedly across years. To account for plot-level variation in soil texture and microtopography, these models also included maximum soil water content for each plot as a covariate. Maximum VWC occurred shortly after periods of high rainfall, when soils in all plots were saturated, and was thus not influenced by burning treatments.

RESULTS

Spring and summer (April to July) precipitation varied from 101 mm to 325 mm (Figure 1), characteristic of long-term variation in growing season precipitation during 1939 to 2016 (mean = 196 mm, standard deviation = 63 mm, range = 53 mm to 453 mm). Annual variation in April to July precipitation was strongly correlated with mean soil VWC during May to July ($r^2 = 0.92$, $P < 0.001$), which in turn was a primary driver of annual variation in herbaceous plant production ($r^2 = 0.53$, $P = 0.04$).

Standing Dead Biomass, Bare Soil Exposure, and Soil Moisture

In all years except 2013, annual fire treatments reduced standing dead biomass by an average of 93 % (Figure 2a and 3a). Signifi-

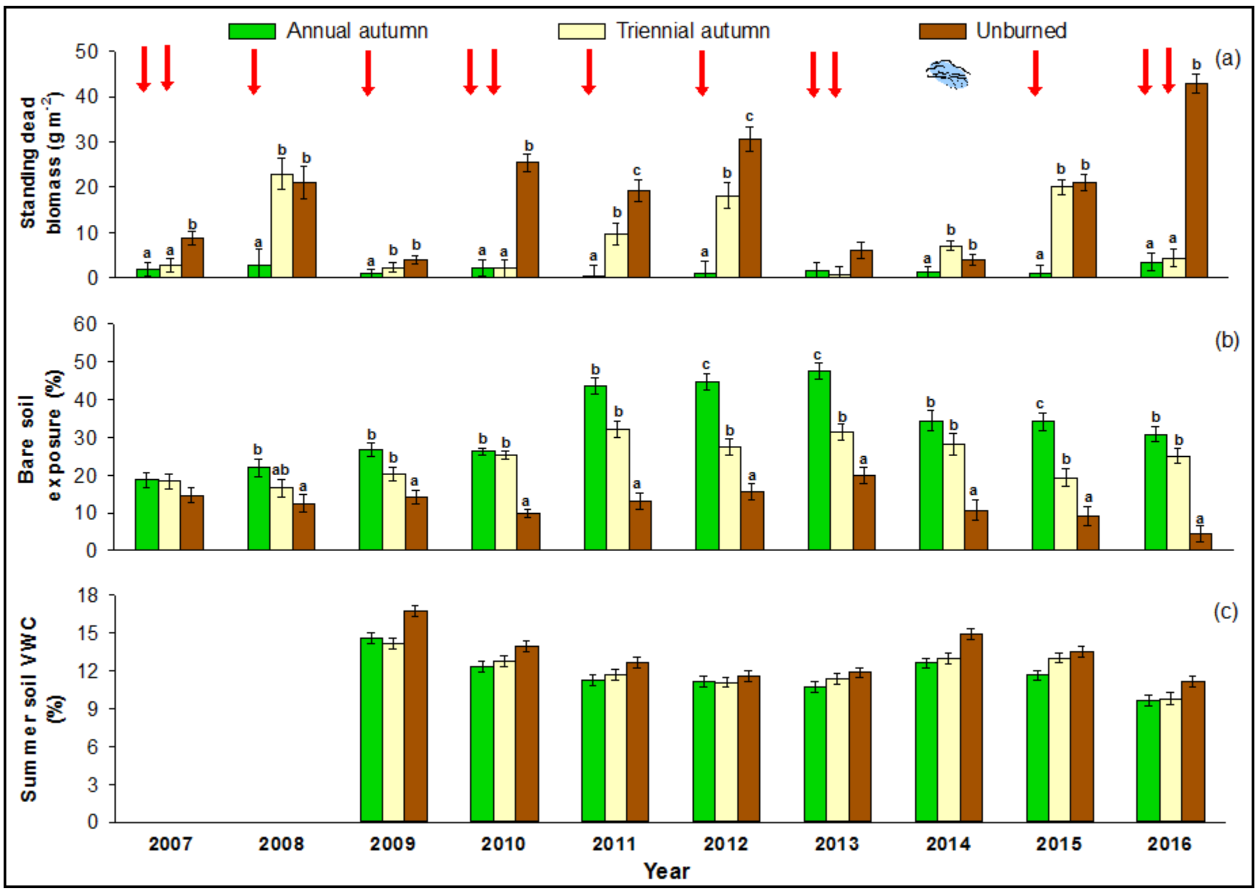

Figure 2. Least squares means ± standard error of the mean for autumn fire treatment × year for (a) standing dead biomass (g m^{-2}) and (b) bare soil exposure (%) collected in late summer from 2007 to 2016, and (c) summer soil volumetric soil water content (%) collected from 16 June to 31 July in 2009 to 2016. Means with different subscripts differ ($P < 0.05$). Red arrows point to measurements taken in the growing season following burning. The rain cloud is above the year when precipitation patterns prevented burning.

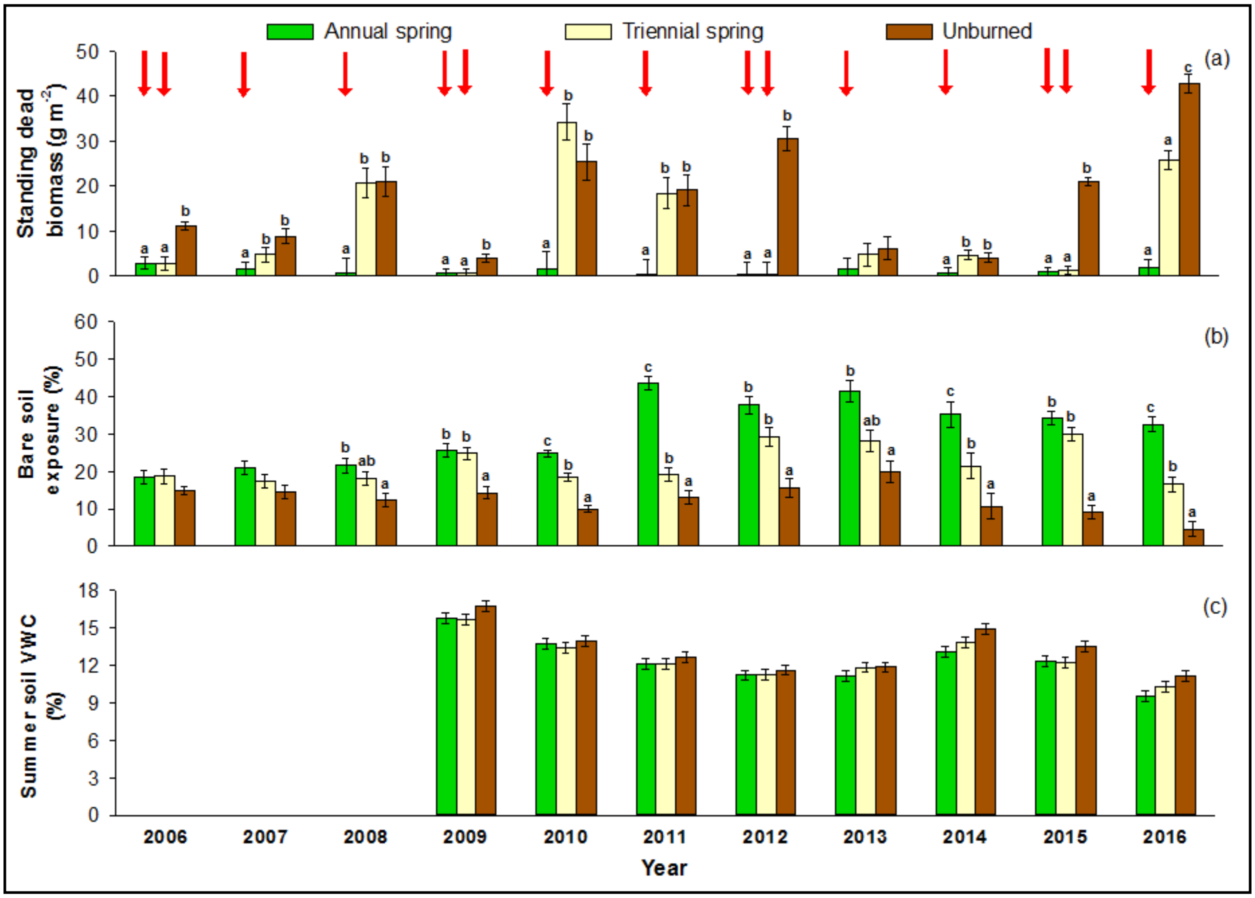

Figure 3. Least squares means ± standard error of the mean for spring fire treatment × year for (a) standing dead biomass (g m^{-2}) and (b) bare soil exposure (%) collected in late summer from 2006 to 2016, and (c) summer soil volumetric soil water content (%) collected from 16 June to 31 July in 2009 to 2016. Means with different subscripts differ ($P < 0.05$). Red arrows point to measurements taken in the growing season following burning.

cant fire effects on standing dead biomass and bare soil exposure were clear throughout this experiment (year × treatment: $F_{32, 120} = 13.54$, $P < 0.001$; year: $F_{8,120} = 26.82$, $P < 0.001$; treatment: $F_{4,15} = 26.85$, $P < 0.001$; Figures 3 and 4). Triennial burn treatments significantly reduced standing dead biomass in the first post-burn year (average reduction: 90%), with the exception of the triennial autumn burn in 2013. Two years following the triennial treatment, standing dead biomass was still lower in the 2011 autumn triennial treatment (50%) and the 2016 spring triennial treatment (40%) relative to the unburned plots. Standing dead biomass did not differ between the third year post-burn plots and unburned controls. Due to low fuel loads and patchy burns, burning did not affect standing dead biomass in 2013. From 2008 to 2016, annual burns increased bare soil exposure by an average of 177%. Following 2008, the triennial spring fire treatment increased bare soil exposure relative to unburned controls every year except 2013. The mean increase in bare soil exposure in the first, second, and third years post treatment for the triennial spring burns was 116%, 145%, and 70% of the unburned treatment, respectively. From 2009 to 2016, triennial autumn burns increased bare soil exposure in the first, second, and third years post treatment by averages of 139%, 152%, and 72%, respectively.

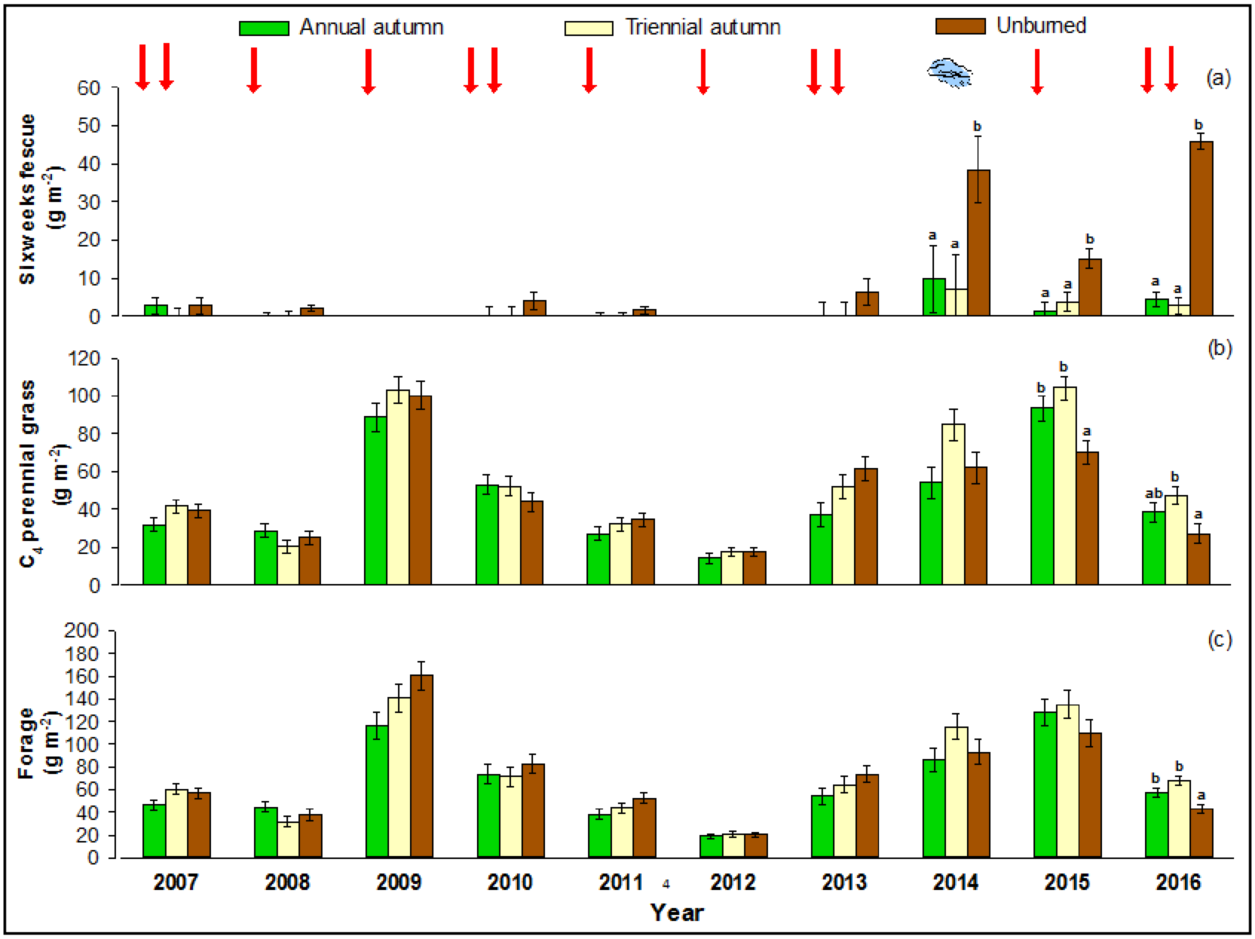

Figure 4. Least squares means ± standard error of the mean for autumn fire treatment × year for (a) sixweeks fescue (g m^{-2}), (b) C_4 perennial grass (g m^{-2}), and (c) forage (g m^{-2}) biomass collected in late summer from 2007 to 2016. Means with different subscripts differ ($P < 0.05$). Red arrows point to measurements taken in the growing season following burning. The rain cloud is above the year when precipitation patterns prevented burning.

For soil volumetric water content (0 cm to10 cm layer) we observed a treatment × season interaction ($F_{14, 203} = 374$, $P = 0.009$). Burning had no effect on soil moisture in either spring ($P > 0.74$) or autumn ($P > 0.24$). In the summer, there was a significant treatment effect ($F_{4,15} = 5.92$, $P = 0.005$), with both annual autumn and triennial autumn burns having significantly lower soil moisture than control plots (Figures 2c and 3c). Averaged across years, mean summer soil VWC was 13.3 % in unburned plots, 11.8 % in annual autumn burn plots, and 12.1 % in triennial autumn burn plots.

Productivity of Plant Functional Groups

The most productive plant during our study was the annual grass, sixweeks fescue. Biomass averaged only 1.8 g m^{-2} (range: 0 g m^{-2} to 2.8 g m^{-2}) in the unburned treatment during 2006 to 2012, but then increased dramatically in abundance to an average of 26.4 g m^{-2} (range: 6.4 g m^{-2} to 45.9 g m^{-2}) during the four-year period from 2013 to 2016 (Figures 4a and 5a). Both spring and autumn annual burning treatments reduced sixweeks fescue biomass during 2014 to 2016 by an average of 87 % (Figures 4a and 5a). During the same time period, a reduction of similar magnitude

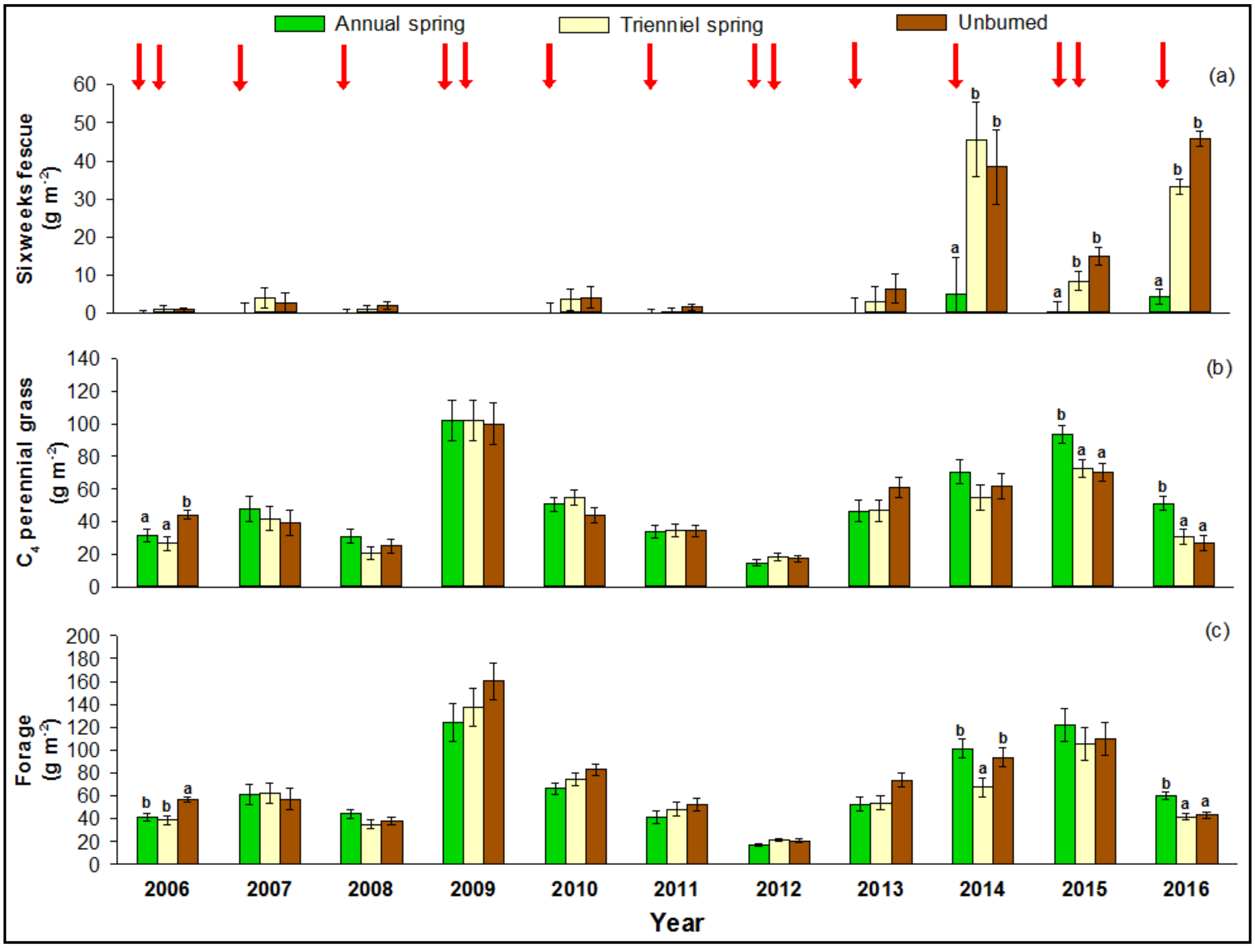

Figure 5. Least squares means ± standard error of the mean for spring fire treatment × year for (a) sixweeks fescue (g m^{-2}), (b) C_4 perennial grass (g m^{-2}), and (c) forage (g m^{-2}) biomass collected in late summer from 2006 to 2016. Means with different subscripts differ ($P < 0.05$). Red arrows point to measurements taken in the growing season following burning.

(86 %) occurred in the autumn triennial treatment, which was burned prior to the 2013 and 2016 growing seasons, relative to unburned controls (Figure 4a). In contrast, we found no significant effect of the spring triennial burn treatment, which was burned prior to the 2012 and 2015 growing seasons, on sixweeks fescue production relative to unburned controls (Figure 5a). This latter result was not surprising during the years of 2013 and 2014. However, even though the spring triennial plots were burned in spring of 2015, sixweeks fescue production was not suppressed in this treatment either in 2015 or 2016 (Figure 5a).

For C_4 perennial grass production, burn effects varied among years and changed in direction of effect from the first year (2006) as compared to the last two years of the experiment (2015 and 2016; year × treatment interaction, $F_{40,150} = 2.21$, $P = 0.0003$; Figures 4b and 5b). We tested for contrasts between the unburned controls and each of the four burn treatments in those years with significant ($P < 0.05$) yearly effects. Spring burns significantly reduced C_4 grass production in the first year of the experiment, likely because burns occurred after C_4 growth was initiated (Scheintaub *et al.* 2009 and Figure 5b). However, plots that burned a second time during the dormant season in 2007 recovered to the same level of C_4 grass production as unburned plots (Schientaub *et al* 2009). From 2008 through 2014, none of the burn treatments affected C_4 grass production (Figures 4b and 5b), despite the fact that precipitation varied widely among these years, from a drought in 2012 to substantially above-average precipitation in 2009. During the 2015 and 2016 growing seasons, however, annual and triennial autumn burning, which suppressed sixweeks fescue (Figures 3a and 4a), also increased C_4 grass productivity (Figures 4b and 5b).

For C_3 graminoid production, we detected a marginally significant year × treatment interaction ($F_{40, 149} = 1.36$, $P = 0.096$), which led us to investigate individual year slices for potential treatment effects in one or more years. This analysis did not reveal any significant differences between burn treatments and unburned controls in any given year ($P \geq 0.13$ for all years). For forb production, we found no significant year × treatment interaction ($F_{40, 150} = 1.24$, $P = 0.18$) and no main effect of burn treatments ($F_{4, 15} = 0.26$, $P = 0.89$). Thus, fire effects on C_3 graminoids and forbs were consistently absent across a wide range of precipitation conditions, varying from drought to substantially above-average precipitation.

Finally, for total forage production (the sum of forbs plus C_3 and C_4 perennial graminoid production, but excluding subshrubs and annual grasses), effects of burn treatments varied among years (year × treatment: $F_{40, 150} = 2.34$, $P < 0.0001$). Parallel with the results for C_4 grass production, burns in the first spring of the study (2006) negatively affected total forage production (Scheintaub *et al*. 2009; Figure 5c). During the subsequent eight-year period from 2007 to 2013, none of the burn treatments significantly affected total forage production across a wide range of precipitation conditions. In 2014, total forage production on the triennial spring burn treatment (third year post treatment) was 28% lower than production in the unburned and the annual spring burns (Figure 5c), while autumn burn treatments showed no significant differences (Figure 4c). Following the burns in spring of 2015, total forage production in the triennial spring burn treatment returned to a similar level as unburned controls. Additionally in 2015, there was no significant difference in total forage production on any treatment compared to unburned controls despite increases in C_4 grass production on both spring and autumn annual burns and triennial autumn burns. In 2016, all treatments that suppressed sixweeks fescue also enhanced forage production relative to unburned controls.

Time since Burn Analysis

When examining results from 2013 to 2016 in terms of time since fire application (instead of season and frequency of fire), we found that time since burning significantly influenced sixweeks fescue production (main effect, $F_{2,69} = 25.11$, $P < 0.001$), with the magnitude of effect varying by year (year × time since burn interaction: $F_{5,69} = 3.95$, $P = 0.003$; Figure 6). Plots burned in the current year consistently had less sixweeks fescue than plots that remained unburned for >2 yr (Figure 6). Plots burned in the previous year produced more sixweeks fescue than plots burned in the

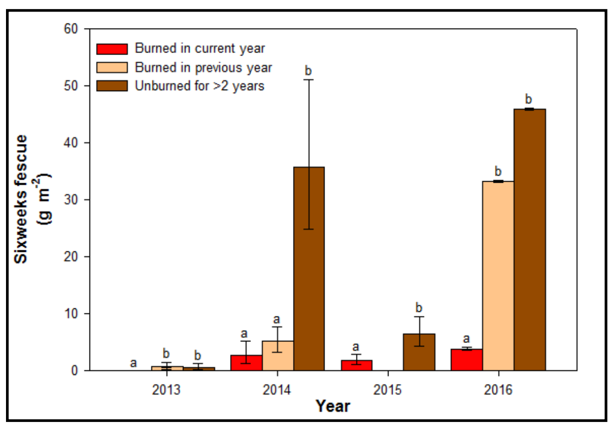

Figure 6. Relationship between time since burning in a given year and productivity of sixweeks fescue. For each time since burn category, we show least square means ± 1 standard error (whiskers) for sixweeks fescue biomass (g m^{-2}) collected in late July in 2013 to 2016. Means with different subscripts within a year differ at the $P < 0.05$ level.

current-year plots in 2013 and 2016, but not in 2014 (Figure 6).

Relationship between Sixweeks Fescue and Total Forage Production

In the last three years of our study, sixweeks fescue production increased dramatically in the unburned and triennial spring burn treatments (Figure 5a). Furthermore, we detected the first significant effect of burn treatments on total forage production compared to the unburned controls since the first year of the study (Figure 4c and 5c). In each of these three years (2014 to 2016), variation in sixweeks fescue production across all plots in the study was inversely related to total forage production (Figure 7). In particular, total forage production was consistently low in all plots in which sixweeks fescue production exceeded 30 g m^{-2} (Figure 7).

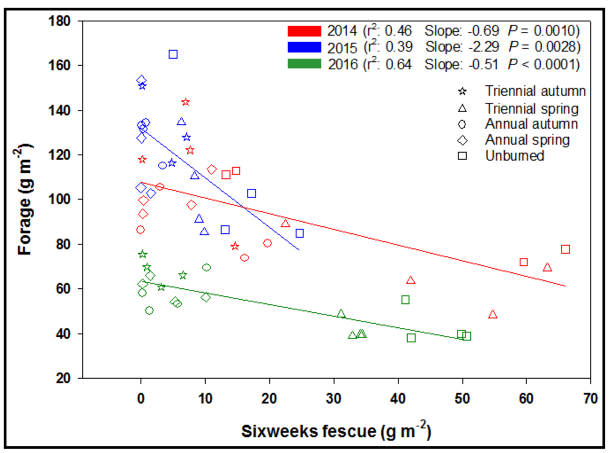

Figure 7. Relationship between time since burning in a given year and productivity of sixweeks fescue. For each time since burn category, we show least square means ± 1 standard error for sixweeks fescue biomass (g m^{-2}) collected in late July in 2013 to 2016. Means with different subscripts within a year differ at the $P < 0.05$ level.

DISCUSSION

In semiarid grasslands of the western Great Plains, accumulating evidence indicates that appropriately timed prescribed fires can reduce the abundance of unpalatable succulents, subshrubs, and annual grasses without negatively affecting productivity of dominant perennial forage grasses (McDaniels *et al.* 1997; Ansley and Castellano 2007; Vermeire *et al.* 2011, 2014; Augustine and Derner 2015). Because these semiarid grasslands experience substantial interannual variability in precipitation, which influences the abundance of subdominant plant species, effects of prescribed fires on plant communities can be contingent on the types of plants that proliferate under a given set of seasonal weather or climatic conditions. We used a long-term (11 yr) experiment employing multiple frequencies and seasons of prescribed burning to assess how fire effects vary across a wide range of seasonal weather or climatic conditions in shortgrass steppe of eastern Colorado. Our findings provided additional support for the conclusion that dormant-season prescribed fires, applied either in autumn or spring and at relatively high frequency (annually or triennially), do not negatively affect the productivity of the dominant forage plants under periods of varying precipitation.

Our long-term study offered a unique opportunity to examine the effect of prescribed fire on the winter annual C_3 grass, sixweeks fescue, which proliferated in this grassland in wet years (2013 to 2016) following a severe drought year (2012). The proliferation of sixweeks fescue in this grassland during the latter four years has important implications for livestock production because this species is unpalatable to cattle, and forms a layer that impedes the ability of cattle to graze on the C_4 shortgrasses (Houston and Hyder 1976; Figure 8). When abundant, sixweeks fescue individuals are finely interspersed within the canopies of perennial grasses. Fescue individuals are uprooted by livestock during grazing, due to their shallow root systems, and grazers either have to expel the sixweeks fescue biomass from their mouths (loss of instantaneous intake rate efficiency) or consume the fescue with its as-

Figure 8. Contrasting vegetation response in the eleventh year (2016) of this study between the annually burned treatment (left) and an unburned portion of the study area (right). The green vegetation in the annually burned treatment is the dominant C_4 shortgrass, blue grama. The amber vegetation on the right is the annual grass, sixweeks fescue, which is unpalatable to cattle and interferes with their consumption of C_4 shortgrasses. The tall, light tan plants are the C_3 perennial bunchgrass, bottlebrush squirreltail (*Elymus elemoides* [Raf] Swezey), which was unaffected by the burn treatments.

sociated root system and soil, which negatively impacts weight gain (Hyder and Bement 1964). From 2013 through 2016, clumps of uprooted sixweeks fescue expelled by grazing cattle were observed throughout grasslands in our study region. Early studies addressing this problem found substantial reductions in sixweeks fescue abundance through autumn and spring herbicide application (Hyder and Bement 1964, Houston and Hyder 1976). Our results indicated that similar reductions can be achieved with appropriately timed prescribed fire. These findings are consistent with studies in more mesic mixed-grass prairie, where carefully timed prescribed fire has also been found to inhibit the introduced winter annual grasses, *Bromus tectorum* L. and *B. arvensis* L. (White and Currie 1983, Harmoney 2007, Vermeire *et al.* 2014).

Given the relatively low temperatures and short duration of fires in shortgrass steppe (Augustine *et al*. 2014*b*), it is unlikely that the mechanism for reduction in sixweeks fescue is heat-induced seed mortality (Odion 2000, Vermeire and Rinella 2009). Burning when the dominant perennial grasses are dormant (typically late October to early April) corresponds to burning during the early vegetative stages of growth of sixweeks fescue, likely leaving the plants vulnerable to the lethal aboveground temperatures created by fire. In turn, fire-induced direct mortality of sixweeks fescue at this early vegetative stage increased the productivity of C_4 perennial grasses. Similarly, in mixed-grass prairie, spring burning killed seedlings of *Bromus arvensis* and *B. tectorum*, and increased productivity of C_4 perennial grasses (White and Currie 1983, Whisenant and Uresk 1990, Vermeire *et al.* 2011).

Annual burning either in the spring or autumn effectively prevented sixweeks fescue proliferation (Figures 4 and 5). In addition, the autumn triennial burn treatment, in which plots were burned only in the autumn preceding the growing seasons of 2013 and 2016 (unburned in 2014 and 2015), also prevented sixweeks fescue proliferation. In contrast, the spring triennial treatment was burned in 2015 (unburned in 2013, 2014, and 2016), and did not suppress sixweeks fescue. These results suggest that burning in 2013, at the early stage of sixweeks fescue proliferation, had a particularly strong suppressive effect that persisted through the 2015 growing season, regardless of whether plots were reburned in 2014 or 2015. We note that burns preceding the 2013 growing season were patchy and of low intensity due to low fuel loads. Because no treatment was burned only in 2014, we cannot assess whether burning in this second year of the proliferation period was effective. Our results do show that waiting until after sixweeks fescue became particularly abundant in 2014, and then burning in the dormant season preceding the 2015 season (i.e., the triennial spring treatment) was ineffective. It remains unclear why this latter treatment had such a limited effect on sixweeks fescue productivity in 2015, as these burns occurred in high fuel loads that accumulated during above-average precipitation in 2014. One possible explanation is that sixweeks fescue had already become so abundant in the triennial spring treatment during the winter of 2014 to 2015 that the dense stand of sixweeks fescue seedlings insulated a portion of individuals from direct mortality effects of the prescribed burns.

Annual and triennial burning regimes represent extreme fire frequency treatments in shortgrass steppe and were used here, in part, as a means to compare results to fire frequency studies in other grassland regions (Knapp *et al.* 1998, Scheintaub *et al*. 2009, Vermeire *et al*. 2011). Annual or triennial burning in the same location may not be a realistic scenario in semiarid rangelands managed for livestock production, as grazing maintains much lower fuel loads in recently burned patches of semiarid grasslands compared to mesic grasslands (Augustine and Derner 2014). However, our findings provide some key insights to potential positive effects of prescribed fire application. Even with grazing excluded from our study plots, fuel loads and fire temperatures were similar to what can occur in moderately grazed shortgrass steppe under average to above-average precipitation (Augustine *et al.* 2014*b*); thus, our results have general application to grazed shortgrass steppe in which fuel loads are similar. In addition, within the temporal scale of a decade, moderate grazing does not alter plant species composition (Klipple and Costello 1960, Augustine *et al.* 2017). Our results are consistent with the idea that infrequent prescribed burning (i.e., at least less frequent than triennial, perhaps on the order of one in 10 or more years) can be used to strategically influence forage quality, subshrub and succulent abundance, and wildlife habitat in an adaptive management approach, without negatively affecting forage production. Furthermore, our findings indicate that, when weather conditions facilitate germination and growth of high densities of sixweeks fescue, dormant-season burns (i.e., burns conducted anytime during October to March when sixweeks fescue is growing but perennial grasses are not) can be used to effectively control sixweeks fescue, and thereby enhance forage accessibility and quantity of dominant and palatable species.

Conditions that facilitate sixweeks fescue proliferation are still not fully understood. Laboratory studies show that germination opportunities are optimized when winter temperatures fluctuate between 15 °C and 20 °C and coincide with adequate soil moisture (Hylton and Bement 1961). We also hypothesize that seasonal weather conditions during the preceding summer months (i.e., the growing season of the dominant perennial, blue grama) may be important because (1) germination is enhanced by increased inorganic nitrogen in the soil solution (Hylton and Bement 1961), which in turn is enhanced by prior summer drought (Evan and Burke 2013); (2) studies in the 1940s and 1950s showed that sixweeks fescue reached peak abundance in 1941 and 1958 (Hylton and Bement 1964), following drought conditions in the late 1930s and 1954 to 1956; and (3) sixweeks fescue proliferation in our study (2013 to 2016) followed a severe drought in 2012. We suggest that rangeland managers be especially aware of the potential for sixweeks fescue germination and establishment during warm, wet winters that follow drought years, and consider the use of dormant-season prescribed fire to adaptively reduce negative impacts of sixweeks fescue on forage production and resultant livestock production. Prescribed fire may provide a valuable alternative to the use of herbicides because it also can benefit wildlife species of conservation concern (Augustine and Derner 2012) and enhance forage quality for livestock early in the growing season (Augustine *et al*. 2010).

ACKNOWLEDGEMENTS

We thank M. Ashby, P. Freeman, T. Kanode, M. Lindquist, P. McCusker, M. Mortenson, R. Pate, D. Smith, T. Smith, J. Thomas, and many Agricultural Research Service (ARS) summer field technicians for assistance in implementing the burn treatments and measuring plant productivity. Funding for this study was provided by USDA-ARS and the USFS Joint Fire Science program (NFP-13-15-GSD-82).

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