Rangeland Ecology & Management 68 (2015) 40–47

Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: http://www.elsevier.com/locate/rama

Patch Burn Grazing Management in a Semiarid Grassland: Consequences for Pronghorn, Plains Pricklypear, and Wind Erosion☆

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ARTICLE INFO

Article history:
Received 25 March 2014
Accepted 11 September 2014

Keywords:
Antilocapra americana
conservation grazing
Opuntia polyacantha
prescribed fire
pyric herbivory
shortgrass steppe

ABSTRACT

Management strategies that allow for spatiotemporal interactions between fire and herbivores can potentially achieve multiple management goals related to livestock production and wildlife conservation, but little is known about such interactions in semiarid grasslands where fire has traditionally been viewed as having few management applications. We studied patch burn grazing management in the shortgrass steppe of northeastern Colorado, comparing unburned pastures to pastures where 25% of the area was burned in October or November each year over 4 years. Our objective was to examine the interactive effects of patch burns and the subsequent response by pronghorn *(Antilocapra americana)* on plains pricklypear *(Opuntia polyacantha)* and wind erosion rates. We monitored abundance of plains pricklypear and wind erosion rates throughout the experiment and quantified seasonal pronghorn densities and postburn damage to plains pricklypear cladodes during the latter 2 years of the study. Pronghorn density was 26 times greater in winter and 7 times greater in spring on patch burns compared with unburned pastures. By late winter, densities of bitten or uprooted plains pricklypear cladodes were five times greater on patch burns compared with unburned pastures. Patch burns, as well as the subsequent response of pronghorn, reduced plains pricklypear density by 54–71% during the first year after the burns, and density remained suppressed for up to 6 years after burns. Wind erosion rates on patch burns were greater compared with unburned pastures but were two orders of magnitude lower than rates measured on fallow croplands in the region. Autumn patch burns can be a valuable means to suppress plains pricklypear and thereby increase grass available for livestock consumption in the shortgrass steppe. These outcomes can be achieved without increasing wind erosion in a manner that threatens long-term soil sustainability and without negative consequences for livestock weight gains.

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Introduction

Fire and large mammalian herbivores often have interactive effects on ecosystem dynamics because fires alter the quantity and quality of forage available to herbivores and thereby influence the distribution and intensity of herbivory in time and space (Archibald et al., 2005; Fuhlendorf et al., 2009; Knapp et al., 1999). In grasslands, enhanced digestibility of postburn vegetation typically occurs due to increased nutrient availability and uptake by plants and/or because the regrowth is not intermingled with dead stems and leaves from the prior growing season (Allred et al., 2011; Augustine et al., 2010; Fuhlendorf et al., 2009), which affects livestock behavior and diet selection (e.g., Ganskopp et al., 1992). Rangeland management strategies that 1) apply prescribed fires in a spatially and temporally variable mosaic and 2) allow livestock and native herbivores to select among burned and unburned patches in the landscape, often referred to as "patch burn grazing management," have been advocated as a means to restore disturbance processes that historically shaped rangeland ecosystems and sustained native biodiversity (Fuhlendorf and Engle, 2004). Studies in mesic grasslands of the eastern Great Plains of North America have shown that patch burn grazing management can strongly influence livestock distribution (Vermeire et al., 2004; Allred et al., 2011), diversify habitats for native fauna (Fuhlendorf et al., 2006, 2010; McGranahan et al., 2012), and enhance livestock production compared with strategies that use (or suppress) fire in a homogenous manner (Allred et al., 2014; Limb et al., 2011).

☆ Funding for this study was provided by the USA Department of Agriculture's Agricultural Research Service (USDA-ARS), an equal opportunity/affirmative action employer, and all agency services are available without discrimination. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the USA government.

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http://dx.doi.org/10.1016/j.rama.2014.12.010
1550-7424/Published by Elsevier Inc. on behalf of Society for Range Management.

In the western, semiarid regions of the Great Plains, fire was historically viewed as having few rangeland management applications (Wright and Bailey, 1982), and most early studies of the effects of fire were based on post hoc measurements from wildfires (reviewed by Wright and Bailey, 1982 and Scheintaub et al., 2009). Over the past 2 decades, rangeland managers have increasingly recognized the potential value of prescribed fire in the western Great Plains of North America for management of unpalatable plant species (Ansley and Castellano, 2007; McDaniel et al., 1997, 2000; Strong et al., 2013; Vermeire and Roth, 2011) and wildlife habitat (Augustine and Derner, 2012; Augustine et al., 2007; Thompson et al., 2008). These studies have primarily focused on the direct effects of prescribed fires but have not addressed potential interactive effects of fires and large herbivores.

In the semiarid shortgrass steppe, prescribed fires could potentially benefit livestock production by enhancing the quality of herbaceous forage early in the growing season (Augustine et al., 2010) and by suppressing the abundance of cactus (*Opuntia* spp.) species (Vermeire and Roth, 2011). Plains pricklypear cactus (*O. polyacantha* Haw.) is one of the most abundant nongraminoid species in the shortgrass steppe (Milchunas et al., 1989), and although plains pricklypear has not been found to suppress forage production, it can substantially reduce accessibility of forage to grazing livestock (Bement, 1968). Clusters of plains pricklypear cladodes create refugia from livestock grazing, and these refugia are characterized by an increased plant species diversity and seed production within cladode interspaces (Rebollo et al., 2005). Prescribed fires can cause direct, heat-induced mortality to plains pricklypear depending upon fire conditions and temperatures, but short-term mortality rates measured after late-winter or spring burns are relatively low (Ansley and Castellano, 2007; Augustine and Milchunas, 2009). However, burns conducted in other seasons could potentially differ in their effects on plains pricklypear and short-term, postburn measurements may underestimate mortality rates due to longer-term responses of insect or mammalian herbivores to burned plants (Ansley and Castellano, 2007; Bunting et al., 1980; Vermeire and Roth, 2011). Burns that remove spines from plains pricklypear at a time of year when other forage sources are in short supply can create a valuable forage source for wild or domestic ungulates (Courtney, 1989; Sawyer et al., 2001; Shoop et al., 1977). Such a combination of burning and herbivory could also potentially induce higher rates of mortality than expected from direct fire effects alone.

Because patch burn grazing management allows herbivores to graze in recently burned areas, often significantly increasing bare soil exposure, one concern is whether this management strategy could increase wind erosion rates (Vermeire et al., 2005). Concerns regarding wind erosion from prescribed burns may reflect the fact that wind erosion from fallow or drought-affected croplands in the western Great Plains can be widespread and substantial (e.g., Fryrear, 1995; Fryrear et al., 1991; Merrill et al., 1999; Stout and Zobeck, 1996). Croplands, however, often have bare soil exposure exceeding 80%, whereas burned rangeland maintains cover from perennial grass crowns (Augustine and Derner, 2012). A key question is whether burning in autumn, when plant regrowth may not occur for 5–6 months after the burn, results in substantial soil loss due to wind erosion.

The objective of this study was to examine relationships among patch burn grazing management, pronghorn antelope *(Antilocapra americana)* and cattle distribution, plains pricklypear abundance, and wind erosion. We originally hypothesized that patch burns would affect the distribution of cattle and pronghorn antelope during the growing season (typically April–September) and that pronghorn would be most strongly attracted to burns in the spring (April–May) due to earlier onset of plant growth and increased forage quality. During the first 2 years of the study, we therefore measured plant and herbivore responses during April–October. Cattle response to patch burns was primarily determined by the phenology of herbaceous plants, with selective grazing on patch burns during periods of rapid herbaceous plant growth and no selection for burns when plant biomass was stable or declining (Augustine and Derner, 2014). During the first 2 years, we also observed surprising numbers of pronghorn using the patch burns during autumn and winter, when these patches were largely devoid of green vegetation. Direct observations indicated they were feeding on burnt pricklypear cladodes, as well as the bases and roots of uprooted pricklypear plants. A similar pronghorn response to late-summer wildfires was reported in mixed-grass prairie in Canada (Courtney, 1989; Stelfox and Vriend, 1977). Therefore, during the latter years of the study, we conducted year-round measurements of pronghorn density on patch burned and unburned pastures and quantified pronghorn-induced damage to pricklypear cladodes at the end of the winter. Here, we examine the degree to which patch burns implemented in autumn (October–November), combined with the subsequent response of pronghorn to those burns: 1) suppress plains pricklypear populations and 2)increase wind erosion rates in the shortgrass steppe.

Methods

Study Area

Research was conducted at the Central Plains Experimental Range (CPER) approximately 12 km northeast of Nunn, Colorado, USA (40°50′N, 104°43′W). Mean annual precipitation is 340 mm. Soils consisted of very deep, well-drained, fine sandy loams on convex alluvial flats and upland plains. Two C_4 grasses (blue grama, *Bouteloua gracilis* [Willd. Ex Kunth] Lag. ex Steud and buffalograss, *B. dactyloides* [Nutt.] J. T. Columbus) dominate the vegetation (>70% of ANPP), plains pricklypear is the dominant succulent plant, and scarlet globemallow (*Sphaeralcea coccinia* [Nutt] Rydb.) is the dominant forb (Lauenroth and Burke, 2008). Plains pricklypear is one of the most abundant plant species after blue grama, with mean basal cover of 2–5% (Milchunas et al., 1989). Pronghorn in the region are nonmigratory but may exhibit seasonal distribution shifts in response to forage availability and weather; landscape-scale aerial surveys indicate densities of ~1–1.5 pronghorn · km^{-2} (Pojar et al., 1995).

Experimental Design

We studied three replicate 65-ha pastures that each received the patch burn grazing management treatment and three replicate 65-ha pastures that received no burning treatment. All pastures were grazed by crossbred yearling cattle from approximately May 15–October 1 each year at a moderate stocking rate of 0.6 Animal Unit Months (AUM) ha^{-1}, which results in approximately 40% forage utilization (Hart and Ashby, 1998). In the patch burn treatment, prescribed burns were applied to one quarter of each pasture per year for 4 years such that all areas of a given pasture were burned once over the course of the study. No portion of control pastures were burned during the study. Burned areas were square (16.25 ha), and burns were implemented in autumn (October or November) of 2007–2010 when vegetation was dormant. Despite low fuel loads (549–1175 kg ha^{-1}), fuels were spatially contiguous and the burns were relatively homogenous in all 4 years (Augustine et al., 2014a). For details on weather conditions, peak fire temperatures, and heat dosages during the burns, see Augustine et al. (2014a). For details regarding experimental design, growing season conditions, and cattle responses to the patch burn treatment, see Augustine and Derner (2014).

Pronghorn Response

We measured the number of pronghorn in each quarter of six pastures (three patch burn pastures and three unburned control pastures) by driving established roads and counting the number of pronghorn. Each pasture quarter was 16.25 ha and the topography was gently rolling, such that an observer could view each target area from one or two elevated locations along the established survey route. A 3-m tall metal pole painted white was placed in the center of each of the three patch burn pastures to facilitate observers determining which pasture quarter the pronghorn were located within when first observed. Pronghorn were counted two to three times per week, with surveys occurring between 0800 and 1000 hours. We did not quantify the detection rate, but given the small size of the pastures and the fact that pronghorn could be seen at distances much greater than the typical flight distance, we assumed that detection was near 100%. On any given day, two different observers conducted the survey (one on the eastern and one on the western half of the study area) at the same time and in a short time frame (~15–25 min); notes were maintained on herd movement directions to minimize any possibility of animals being counted twice in the same day. Data were analyzed seasonally, where "spring" was defined as counts occurring during March 1–May 20, "summer" as May 20–October 1 (which coincided with the timing of cattle grazing in these pastures), and "winter" as the period between the date of the autumn burns (occurring in October or November each year) and the end of February.

We did not conduct counts during the winters of 2007–2008 or 2008–2009 because we did not anticipate pronghorn using burns at this time of year. Because we observed substantial pronghorn use of burns in both of these winters, we conducted winter counts (i.e., 2–3 counts per week from the time of the burn until the end of February) during 2009–2010, 2010–2011, and 2011–2012. In addition, during the first growing season of the study (spring and summer of 2008), we only counted pronghorn in the three patch burn pastures (i.e., no counts in unburned pastures); counts of unburned pastures began in the spring of 2009 and continued through the remainder of the study. Each year during 2008–2012, we conducted a total of 23–30 instantaneous counts of pronghorn at each study site during spring and 46–55 counts during the summer. During the winters of 2009–2010, 2010–2011, and 2011–2012, we conducted 49–57 counts each winter.

Plains Pricklypear Response

We monitored the number and condition of plains pricklypear cladodes in each of the four, 16-ha quarters of the patch burned pastures and in one 16-ha quarter of each control pasture. Within each 16-ha area, we established a randomly located 50-m transect. Along this transect, we placed a 0.25 m^2 circular quadrat every 2 m. If the quadrat contained at least one live cladode, the center was marked with a nail and 3-cm-diameter washer to facilitate future relocation of the same point, and we recorded the number of live and dead cladodes. Live cladodes were defined as flattened stem segments (pads) that had any visible green or yellow color on the surface. We continued adding new 50-m transects parallel to and 10 m away from the first transect until we attained 20 marked quadrats containing one or more live pricklypear cladodes. We used this approach to ensure the same number of quadrats were monitored in each 16-ha site regardless of spatial variation in pricklypear density within and among the sites. Across sites, two to seven transects were required to obtain 20 quadrats containing live pricklypear cladodes. We report our results in units of cladodes 0.25 m^{-2} quadrat, but note that these numbers cannot be extrapolated to pasture-scale pricklypear densities because they do not account for the density of unmarked quadrats where pricklypear was absent.

In August of 2007, we used the previously described procedure to establish 20 permanently marked pricklypear quadrats in the unburned control pastures and in the 16-ha quarter of the treatment pastures that were scheduled for burning in the autumn of 2007. In August of each year during 2008–2010, we established new permanently marked quadrats in the quarter of the treatment pastures that were scheduled to be burned in the subsequent October or November of that year. Thus quadrats in the control pastures and the patches burned in autumn of 2007 were measured throughout the 7-year period (2007–2013), while patches burned in later years were only measured during the August preceding the burn and each subsequent August until 2013.

During 2007–2009, we only counted cladodes in the permanently marked quadrats in August each year. In order to quantify the kind and amount of overwinter damage caused by pronghorn, we also visited the quadrats in March of 2010 and 2011. At this time we recorded 1) the number of cladodes that were green (alive with burn, insect, or disease-related damage on < 10% of cladode surface), injured (burn, insect, or disease-related damage on > 10% of surface) or dead; 2) the number of cladodes with a bite removed by an ungulate herbivore; and 3) the number of cladodes that were rooted versus uprooted. We recorded rooted versus uprooted cladodes because our observations of pronghorn during the winter indicated that much of their damage to pricklypear resulted from uprooting of cladodes with their hooves and/or while feeding on a cluster of cladodes, which appeared to be related to their feeding on pricklypear roots or bases of the cladodes.

Wind Erosion

We measured wind erosion rates using Big Spring Number Eight (BSNE) field samplers (Fryrear et al., 1991). We selected these samplers because they are widely used in studies of wind erosion on croplands (Zobeck et al., 2003) and have also been used to measure wind erosion associated with patch burn grazing management in mixed-grass prairie (Vermeire et al., 2005). BSNE samplers are designed with a wind vane to orient the 2 × 5 cm opening into the wind to collect blown soil. At each site, we installed a pair of samplers placed approximately 1.5 m apart so that they could rotate completely in the wind without contacting each other. Samplers were mounted on conduit such that the bottom of the openings of both samplers was 20 cm above ground level, with tall vegetation in the immediate vicinity removed if necessary to ensure full rotation. Saltation is the primary form of wind erosion measured at this height. Each year, we installed a pair of samplers in the center of each 16-ha burned patch and in the center of the unburned control pastures.

Table 1
Amounts of wind-blown soil collected by samplers mounted 20 cm above ground level on patch burns ($n = 3$) and unburned control sites ($n = 3$) in shortgrass steppe of northeastern Colorado during 2007–2011.

			Controls		Patch Burns	
Start	End	Days	Mean	1 SE	Mean	1SE
Dormant Season						
11/15/2007	4/18/2008	155	0.13	0.02	1.88*	0.47
11/25/2008	4/23/2009	149	0.42	0.15	0.75	0.09
11/6/2009	4/21/2010	166	0.06	0.01	1.09*	0.50
11/2/2010	4/12/2011	161	0.05	0.00	0.58*	0.06
4-Yr Mean	**158**	**0.16**	**0.04**		**1.07***	**0.11**
Growing Season						
4/18/2008	11/25/2008	221	1.04	0.43	2.57*	0.31
4/23/2009	11/6/2009	197	0.46	0.12	0.47	0.02
4/21/2010	11/2/2010	195	0.33	0.09	0.68	0.17
4/12/2011	11/18/2011	220	0.61	0.27	1.13	0.24
4-Yr Mean	**208**	**0.61**	**0.21**		**1.21***	**0.03**

All values are grams of soil collected per sampler, which is equivalent to kg soil · m^{-2} of sampler opening. * indicates patch burn values that are significantly greater than controls at the $P < 0.05$ level.

Samplers were installed in October or November each year after implementation of the burns (or left in place in unburned control pastures), and soil was collected periodically from the traps until the next set of burns occurred the subsequent year. Collected soil was stored in metal cans and weighed after drying at 105 °C. During the livestock grazing season (May–October), a small exclosure was erected around the samplers to prevent livestock damage; exclosures were removed during the nongrazing season to prevent buildup of debris or snow. For analyses, we examined the amount of soil collected by the samplers during November–April (corresponding to the overwinter period of plant dormancy) and April–October (corresponding to the growing season; see Table 1 for exact sampling dates).

Data Analyses

For analyses of pronghorn density, we converted the instantaneous counts of pronghorn numbers in each 16-ha area to units of pronghorn $\cdot$ km^{-2} and then calculated the mean density in each site on the basis of all counts that occurred in each season each year. We examined variation in relation to five treatments consisting of recent burns (patches burned in the preceding October or November), 2-year-old burns (patches burned 1 year before recent burns), 3-year-old burns (patches burned 1 year before recent burns), adjacent unburned sites (unburned patches within the patch burn pastures), and unburned control pastures (whole pastures that received no burning treatment). Adjacent unburned areas were 0.0–0.56 km distant from the burned patches, whereas unburned control pastures were 0.56–4.4 km distant from burns. We first conducted a full three-way analysis of variance (ANOVA) that included treatment, year, and season plus their interactions. Given the complexity of the three-way interaction and relatively consistent seasonal effects of burn treatments across years (see results), we examined the effects of burn treatments within each season using a model that included treatment, year, season, and a treatment x year interaction term. For both analyses, densities were log-transformed before analysis to meet assumptions of normality, and we report the back-transformed means for each treatment. We examined effects of burn treatments on the density of overwinter damage to pricklypear cladodes using a two-way (treatment × year) ANOVA. We examined patch burn effects on long-term trends in pricklypear density with a repeated-measures ANOVA and then examined specific contrasts between the unburned control pastures and each yearly set of patch burns (controls vs. 2007 burns for 7 yr; controls vs. 2008 burns for 6 yr, controls vs. 2009 burns for 5 yr, and controls vs. 2010 burns for 4 yr). For the repeated-measures ANOVA, we considered five different types of covariance structures, and following the procedure of Littell et al. (2000), we selected and used the Toeplitz (banded) covariance structure for the final model. We examined effects of burn

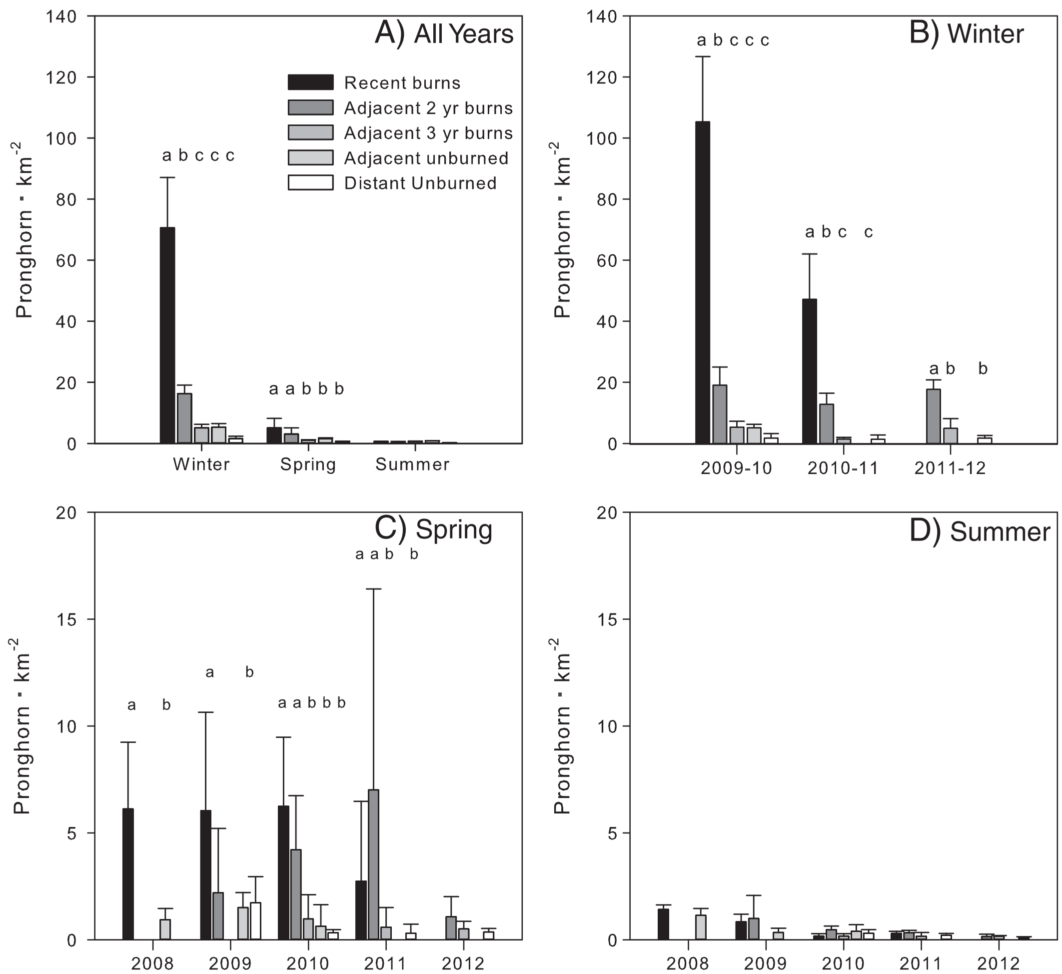

Fig. 1. Seasonal densities of pronghorn in relation patch burn treatments in the shortgrass steppe of northeastern Colorado. Recent burns refer to sites that were burned in October or November and then surveyed for pronghorn in the subsequent winter, spring, and summer. Error bars show ±1 SE. Within a given season (**A**) or year (**B-D**), bars with different letters above them indicate means that differ at the $P < 0.05$ level. Note the difference in scale between panels **A** and **B** versus **C** and **D**.

treatments on wind erosion with a three-way ANOVA that included treatment, year, and season plus their interactions.

Results

Pronghorn Density

Effects of patch burn treatments on pronghorn density varied by season (treatment x season interaction, $F_{8,147} = 9.24$, $P < 0.001$). During winter, pronghorn densities were 26 times greater on recent burns and six times greater on 2-year-old burns compared with unburned pastures (Fig. 1A). During spring, pronghorn densities on burns declined substantially relative to winter densities but still remained significantly greater on recent burns and 2-year-old burns relative to the other treatments ($P < 0.05$; Fig. 1A). In contrast, pronghorn densities were consistently low during the summer and unaffected by burns (Fig. 1A). Analyses of yearly effects of treatments within each season (full model including a treatment x year x season term) showed relatively consistent patterns across years, except the magnitude of effects varied among some years (treatment x season x year interaction, $F_{37,114} = 2.83$, $P < 0.01$; Fig. 1B-D). Burns affected pronghorn density more strongly in the winter of 2010 compared with 2011 (Fig. 1B). Two-year-old burns supported significantly greater pronghorn densities than unburned areas in spring of 2010 and 2011, but not in spring of 2009 (Fig. 1C). Overall, our results show that extraordinarily high densities of pronghorn (averaging 71 animals $\cdot$ km^{-2}) were concentrated on recent patch burns during the winter, when actively growing vegetation was not present on these sites.

Plains Pricklypear Response

Surveys in March of 2010 and 2011 showed that autumn patch burns significantly affected the density of pricklypear cladodes that were bitten or uprooted (treatment x year interaction; $F_{3,19} = 3.54$, $P < 0.001$). Analysis of treatment effects within each year showed that in 2010, the density of bitten or uprooted cladodes was eight times greater on recent burns compared with 3-year-old burns and unburned sites, with intermediate densities on 2-year-old burns (Fig. 2). In 2011, the density of bitten or uprooted cladodes was significantly greater on all sites with some history of burning compared with unburned controls, with the greatest density occurring on 2-year-old burns (Fig. 2).

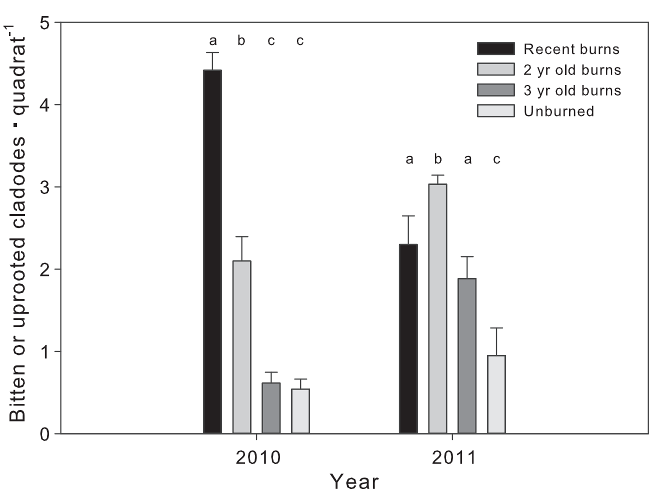

Fig. 2. Densities of plains pricklypear cladodes that were bitten or uprooted in relation to patch burn treatments in the shortgrass steppe of northeastern Colorado. Error bars show ±1 SE. Bars with different letters above them indicate means that differ at the $P < 0.05$ level.

Pricklypear densities declined significantly in burned patches in all 4 years of the study and remained significantly lower compared with control plots for up to 6 years after the burns (Fig. 3). For patches burned in the autumn of 2007, 2008, and 2009, preburn pricklypear densities did not differ significantly from densities in the control pastures ($P > 0.31$ in all three comparisons; Fig. 3A-C). For plots in patches burned in 2007, 2008, and 2009, pricklypear densities declined 54%, 54%, and 62%, respectively, by the subsequent postburn measurement in August, whereas pricklypear density in unburned plots neither decreased nor increased significantly over these same time periods (Fig. 3A-C). For plots in patches burned in 2010, pricklypear cactus densities were marginally lower compared with unburned plots even before conducting the burns (Fig. 3D; $P = 0.068$). Consistent with results from other years, however, pricklypear densities in plots burned in October of 2010 declined by 71% by August 2011, whereas densities in unburned plots remained stable (Fig. 3D). Pricklypear densities on plots burned in 2007 were still 30% lower than unburned plots 6 years later in August 2013. Pricklypear densities showed slightly greater recovery on plots burned in 2008 and 2009, having reached 47% and 42% of control plot densities by August of 2013. Pricklypear density on plots burned in 2010 was only 17% as great as densities on control plots by August of 2013. Although the magnitude of reduction in pricklypear density varied among years, burn treatments from all 4 years had significantly ($P \leq 0.01$) lower pricklypear densities than control plots as of August 2013 (Fig. 3).

Wind Erosion

Averaged across all 4 years of the experiment, erosion samplers collected significantly more wind-blown soil on patch burns compared with unburned control pastures during both the dormant and growing seasons (season x treatment interaction: $F_{1,44} = 2.51$; $P = 0.12$; main effect of burn treatment: $F_{1,44} = 25.11$, $P < 0.0001$). We also found a highly significant year x season x treatment interaction ($F_{10,32} = 3.59$; $P = 0.003$) because wind-blown soil collection rates were significantly greater on patch burns during the dormant season in 3 of 4 years (2007–2008, 2009–2010, and 2010–2011; Table 1) and significantly greater on patch burns during the growing season in only 1 of 4 years (2008; Table 1). Maximum amounts of wind-blown soil were collected on patch burns during the dormant season of 2007–08 (1.9 kg $\cdot$ m^{-2} over 155 days) and the growing season of 2008 (2.6 kg $\cdot$ m^{-2} over 221 days).

Discussion

We documented substantial, long-term reductions in plains pricklypear density in shortgrass rangeland due to a strong interaction between patch burns and pronghorn. Pronghorn showed only a weak attraction to burns in the spring and no attraction during the summer but concentrated on burns at high densities (averaging 71 animals $\cdot$ km^{-2} over the 2 years of measurements) during the winter. Pronghorn in the study area are nonmigratory, with individuals widely distributed in small groups during the growing season and aggregating into larger groups in winter. Our findings suggest that pronghorn density increased in the vicinity of our burn study during the winters relative to summer, but there is no evidence of a migratory component to this. In more than 10 years of field studies on prescribed burns in the shortgrass steppe (e.g., Augustine and Derner, 2012; Augustine et al., 2007), we have not witnessed such large and consistent concentrations of pronghorn on burned areas,

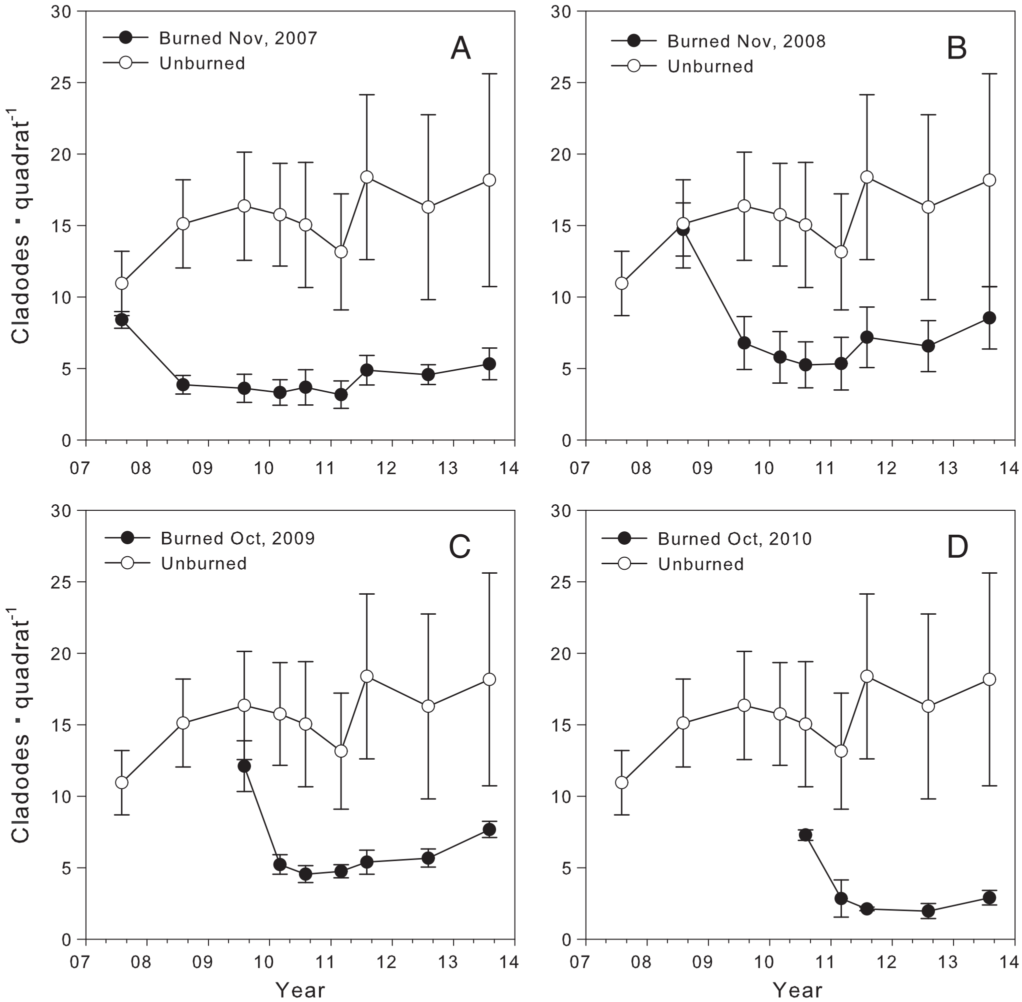

Fig. 3. Temporal changes in plains pricklypear abundance on sites burned in October of November of 2007, 2008, 2009, and 2010 relative to changes on unburned control sites in the shortgrass steppe of northeastern Colorado. In each panel, the first point in the time sequence showing plains pricklypear density in the burn treatment represents the density measured 1–2 months before the burns were implemented. Error bars show ±1 SE.

but all of our prior work focused on burns conducted in late winter or early spring.

Burning in autumn (October or November) removed spines from pricklypear cladodes at a time of year when green forage was limited in availability. We observed pronghorn feeding directly on the burnt pricklypear cladodes, as well as uprooting cladode clusters with their hooves and consuming basal portions of the cladodes and/or roots. Although this was most evident in the recently burned (and still blackened) patches, pronghorn density and the number of bitten or uprooted cladodes also suggested that pronghorn continued to feed on old burnt cladodes and/or newly regrown cladodes in the second winter after a patch was burnt. Densities of bitten or uprooted cladodes were 2.4–8.1 times greater on recently burned and 2-year-old burned patches compared with control pastures. At the time of sampling in March, most of these cladodes were either already blackened or were mostly yellow-brown and desiccated in appearance, indicating that postburn damage induced by pronghorn contributed substantially to pricklypear mortality.

Augustine and Milchunas (2009) found that burns conducted in late winter or early spring reduced pricklypear density by an average of 35% during the first postburn growing season. Burns in shortgrass steppe typically occur with fuel loads < 1000 kg ha^{-1}, such that maximum fire temperature and heat dosage is typically not sufficient to cause direct, fire-induced pricklypear mortality rates exceeding 50% (Vermeire and Roth, 2011; Augustine et al., 2014a). However, we found that autumn patch burns reduced pricklypear densities by 54–71% at the end of the first postburn growing season. Such a large reduction again indicates that the fire-pronghorn interaction, rather than direct fire effects alone, contributed to our results.

Shoop et al. (1977) showed that pricklypear cladodes at our study site have high digestibility and are readily consumed by livestock when the spines are removed by singeing. Tissue of other cactus species in the southern Great Plains, such as cholla (*Cylindropuntia imbricate* [Haw] F. M. Knuth), also have high nutritional value for large herbivores (Sawyer et al., 2001). The strong pronghorn response to our autumn patch burns suggests that burnt cactus provided a valuable forage resource for pronghorn at a time of year when other forages are limited in quantity and quality. Observations by Courtney (1989) also suggested that in mixed prairie of Alberta, plains pricklypear provided a significant portion of the diets of pronghorn in areas with late-summer burns. Although most prescribed burns in the shortgrass steppe are currently conducted in the late winter or early spring, expanding burn prescriptions to include late summer and autumn could be an effective strategy to enhance the availability and quality of forage for pronghorn.

One potential reason to avoid burning in the autumn in shortgrass steppe is to minimize soil losses to wind erosion. We found that wind erosion was indeed significantly greater on autumn patch burns compared with unburned pastures. However, the magnitude of soil erosion rates measured in both burned and unburned patches was minor compared with rates recorded on fallow croplands in the western Great Plains. Our measurement method did not quantify soil loss rates at the patch or pasture scale but did provide an index of soil movement via saltation that is comparable with other studies in agricultural lands. We found that rates of soil capture averaged over the entire dormant season (158 days during Nov–Apr; Table 1) were 0.16 $kg \cdot m^{-2}$ in unburned pastures and 1.07 $kg \cdot m^{-2}$ in patch burns. These rates are substantially lower than the 4.2–19.0 $kg \cdot m^{-2}$ of wind-blown soil collected overwinter on patch burns in mixed grass prairie (Vermeire et al., 2005). These rates are also orders of magnitude lower than rates measured on fallow croplands in the region using the same samplers at the same height above ground level. For example, during an individual 6-hr winter storm event, Stout and Zobeck (1996) recorded a soil capture rate of 43 $kg \cdot m^{-2}$ on fallow cropland in eastern Colorado, and Fryrear et al. (1991, 1995) recorded single-day soil capture rates of 100 to 300 $kg \cdot m^{-2}$ on fallow cropland in Texas. Wind erosion rates measured on these fallow croplands are likely to be nonsustainable from a soil erosion and formation perspective (e.g., Blanco-Canqui et al., 2013; Merrill et al., 1999), whereas the rates we documented on patch burns were more than two orders of magnitude lower and were not associated with observations of blowouts, drifting soil, or soil pedestals associated with perennial grass crowns. Wind erosion rates were also similar during the dormant season compared with the growing season, both for burned and unburned sites, suggesting that overwinter cover associated with grass crowns was important in minimizing soil loss.

Implications

Our collective findings show that patch burn grazing management can achieve multiple production and conservation objectives in this semiarid grassland. Patch burns applied in autumn to 25% of the pasture area each year created a forage resource for pronghorn when alternative forages were limited in availability and substantially reduced pricklypear densities 6 years postburning. Furthermore, Augustine and Derner (2012) showed that autumn patch burns were effective in creating breeding habitat for the mountain plover (*Charadrius montanus*), which is a grassland bird of significant conservation concern in this region. Moreover, recently burned patches were selected by cattle during those portions of the growing season when vegetation was rapidly growing (Augustine and Derner, 2014). In 1 of 4 years of the study, patch burning increased average daily weight gains of cattle stocked at moderate rates and had no negative effect on weight gains for the other 3 years. In a fifth year following the patch burns (but in which no burns were implemented), the area experienced a severe drought. The patch-burned pastures still yielded the same average daily cattle weight gains as unburned pastures (Augustine and Derner, 2014). Overall, these results show that autumn patch burns can benefit pronghorn and mountain plovers, reduce pricklypear densities, and have minimal negative consequences for soil loss or livestock production.

Finally, we note that uncertainty still exists concerning the effects of varying fire frequencies in semiarid grasslands. The historic fire return interval in this region is not well known due to the lack of trees for fire scar analysis but may be longer than 10 years (McPherson, 1995). Today, the use of prescribed burning on public rangelands in the region typically involves only infrequent burning of a given location (e.g., less than once every 10 years). Prescribed burns conducted annually or triennially in the same location can begin to alter plant community composition and productivity (Augustine et al., 2014b), suggesting that a conservative (e.g., ≥ 10-year) fire return interval may be more appropriate for sustaining resources related to soils, plants, wildlife, and livestock.

Acknowledgements

We thank Patrick McCusker, David Smith, Mary Ashby, Jeff Thomas, and Troy Smith for their assistance with cactus surveys and Mary Ashby, Jeff Thomas, Troy Smith, and Tammy Kanode for conducting the pronghorn counts. We thank Matt Mortenson for his assistance measuring wind erosion rates. We thank Crow Valley Livestock Cooperative, Inc., for providing the cattle involved in this study.

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