

Prescribed fire, soil inorganic nitrogen dynamics, and plant responses in a semiarid grassland



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ABSTRACT

In arid and semiarid ecosystems, fire can potentially affect ecosystem dynamics through changes in soil moisture, temperature, and nitrogen cycling, as well as through direct effects on plant meristem mortality. We examined effects of annual and triennial prescribed fires conducted in early spring on soil moisture, temperature, and N, plant growth, and plant N content in semiarid shortgrass steppe. Annual burning increased soil inorganic N availability throughout the growing season, which was associated with increased soil temperature and a reduction in aboveground N in C₃ plants. Furthermore, the increase in soil inorganic N pools with annual burning was modest and did not facilitate success of ruderal species. Negative fire effects on C₃ plant production could be due to increased soil temperature, reduced soil moisture, or direct negative effects on C₃ plant meristems, although fuel loads and fire temperatures were low relative to other grasslands. Triennial burning had intermediate effects on N availability and C₃ plant production compared to annual burning and unburned controls. Results show that prescribed burns can be used in the management of this semiarid grassland without facilitating annual plant invasion, but excessively frequent burning can reduce production of C₃ plants.

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1. Introduction

Fire is a key driver of the structure and function of many grassland ecosystems due to its pervasive effects on nutrient cycling, vegetation structure and composition, and herbivore distribution (Anderson, 2006; Fuhlendorf et al., 2012; Oesterheld et al., 1999; Van Wilgen et al., 2003). The relationship between fire, nitrogen (N) cycling and plant productivity has been widely studied because fire can influence short-term availability of N for plant uptake (e.g. Blair, 1997), and because frequent fires can influence ecosystem N balance through repeated volatilization of N in aboveground biomass (Ojima et al., 1994; Reich et al., 2001). Although seasonal variation in soil moisture and temperature are typically primary controls over N cycling rates (Austin et al., 2004; Burke et al., 1997), fire has been shown to increase the availability of inorganic N throughout the first post-burn growing season in many arid and semiarid ecosystems. Examples include desert grassland

(Allred and Snyder, 2008), desert shrubland (Esque et al., 2010), Mediterranean grassland and shrubland (Romanya et al., 2001), and sagebrush steppe (Davies et al., 2007; Rau et al., 2007). The implications of such post-burn increases in soil N availability for vegetation dynamics are uncertain. Large increases in post-burn N availability have been implicated in the invasion of annual plants (Esque et al., 2010). In other cases, prescribed fire can enhance production, photosynthesis rates, and/or nutrient content of native herbaceous plants without altering species composition (Allred and Snyder, 2008; Davies et al., 2007; Lu et al., 2011).

In the semiarid shortgrass steppe, interest in the use of prescribed fire to manage wildlife habitat (Augustine and Derner, 2012; Augustine et al., 2007; Thompson et al., 2008) and control plant species that are unpalatable to livestock (Ansley and Castellano, 2007; Augustine and Milchunas, 2009; McDaniel et al., 1997) has led to questions concerning potential impacts of fire on plant productivity and invasion. Oesterheld et al. (1999) originally predicted that fire could have increasingly negative effects on plant production with increasing aridity in the western Great Plains. However, recent experiments in the most arid portions of the Great Plains found that dormant-season burns did not

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negatively affect ANPP (Augustine and Milchunas, 2009; Augustine et al., 2010; Scheintaub et al., 2009) or cover of dominant perennial grasses (Ford and Johnson, 2006), raising questions about how fires affect resources limiting plant growth. To the extent that fire in this system does not affect plant abundance or transpiration rates, changes in bare soil exposure may be one way that fires influence soil temperature, moisture, and nutrient availability. Furthermore, heat-induced release of NH_4 from organic matter or clay interlayers during fires could enhance post-fire soil nitrogen availability (Choromanska and DeLuca, 2002; DeBano et al., 1998). Associations between fire, increased soil N availability, and plant invasion in some arid and semiarid ecosystems (Brooks et al., 2004; D'Antonio and Vitousek, 1992; Esque et al., 2010) have also led to concerns that fire could increase invasion in shortgrass steppe. Given that very high N availability can lead to invasion of this typically invasion-resistant ecosystem (Milchunas and Lauenroth, 1995), a key question is how much, and for how long, does fire influence soil N availability?

Research by Scheintaub et al. (2009) in the shortgrass steppe revealed that aboveground production of both C_3 and C_4 plants was negatively affected by spring burns that occurred when vegetation had already initiated some photosynthetic activity. Following a second year of spring burns that occurred in dormant vegetation, no effects on aboveground production (either C_3 or C_4) were observed (Scheintaub et al., 2009). Their measurements occurred in a drought year (2006) and an average precipitation year (2007); burns did not significantly reduce soil moisture in either year, and soil N responses were not measured. Here, we report on a continuation of the study of Scheintaub et al. (2009). We expand on that work by examining soil N availability, plant N content, ANPP, soil moisture and soil temperature in both annually burned shortgrass steppe (burned each year during 2006–2010) and triennially burned shortgrass steppe (burned in 2006 and 2009), and by examining burn effects during two consecutive years of above-average precipitation. We hypothesized that prescribed burning in the shortgrass steppe would (1) enhance soil inorganic N availability, which in turn would (2) enhance plant production in wet years, when moisture limitation is less severe. Our treatments were motivated by the fact that most previous studies in this ecosystem examined one-time burns (Augustine and Milchunas, 2009; Augustine et al., 2010), and rangeland managers questioned whether frequent burning of the same location for wildlife habitat management would have negative consequences for vegetation and soil. We hypothesized that with above-average precipitation, fire-induced enhancement of soil N availability and soil temperature would outweigh any negative effects on soil moisture, and thereby enhance plant N content and ANPP. We also hypothesized that in wet years, annual burns would prevent litter accumulation to a greater degree and induce greater increases in bare soil exposure, soil temperature, and inorganic N pools compared with triennial burns. This in turn was expected to increase plant N content and ANPP in annual versus triennial burns. We also sought to quantify the magnitude and timing of changes in soil N availability following burns, and evaluate whether increased inorganic N availability was associated with increased abundance of annual grasses or forbs. We predicted that if burning can influence N-availability enough to favor annual species, this would be most likely to occur with annual burning in years with above-average precipitation.

2. Materials and methods

2.1. Study site

Research was conducted in native shortgrass steppe at the USDA-Agricultural Research Service's Central Plains Experimental

Range (CPER) approximately 12 km northeast of Nunn, Colorado, USA (40°50'N, 104°43'W). The shortgrass steppe is dominated by perennial, C_4 shortgrasses (*Bouteloua gracilis*, *Bouteloua dactyloides*) that are characterized by high belowground biomass allocation and are well-adapted to aboveground disturbances from grazing, fire and periodic drought (Augustine et al., 2010; Milchunas et al., 2008). The plant community also includes a diversity of C_3 perennial grasses, sedges and forbs. Although C_3 plants typically comprise <30% of ANPP, their productivity is more sensitive to precipitation, temperature and grazing management (Derner et al., 2008; Milchunas et al., 2008), and may be more strongly affected by other disturbances such as fire. C_3 plants at the site consist primarily of the perennial graminoids *Carex duriuscula* and *Pascopyrum smithii*, the perennial forb *Sphaeralcea coccinea*, and the annual forb *Lepidium densiflorum*. The most common annual grass is *Vulpia octoflora*, which typically comprises less than 5% of ANPP (Milchunas et al., 2008). The exotic annual grass *Bromus tectorum* is present along disturbed roadsides throughout CPER, but only rarely occurs in undisturbed shortgrass steppe (Kotani et al., 1998). Nomenclature follows the USDA Plants database (www.plants.usda.gov). Mean annual precipitation at the site is 340 mm and topography is characterized by gently undulating plains. Precipitation during the study was substantially above average in 2009 (437 mm) and slightly above average in 2010 (361 mm). All research was conducted in grassland that had not been grazed by cattle for 5 years prior to the initiation of the experiment in 2006, and remained ungrazed throughout the experiment.

2.2. Experimental design

We established 12 20 × 20 m plots in a relatively flat, homogenous, upland shortgrass steppe site, with ≥3 m buffer strips separating each plot. Four were randomly assigned to an annual, early-spring burning treatment, four to a triennial, early-spring burning treatment, and 4 served as unburned controls. Annual burns began in 2006 and continued through 2010. The triennial burning treatment was burned in 2006 and 2009. Burns occurred in late March or early April each year. Burns in 2006 were implemented when vegetation was in the early stage of greenup (Scheintaub et al., 2009), while all subsequent burns occurred in dormant vegetation prior to greenup. Burns were implemented by creating a blackline on the two downwind boundaries of each plot, and then lighting headfires on the two upwind boundaries. Despite the low fuel loads, fuels were spatially contiguous and burns were homogenous. During each burn in 2009 and 2010, fire temperatures were measured at 1 s intervals with six type J thermocouples placed at 1 cm above ground level within the planned burn area. We measured temperature at this height because it corresponds to the approximate height of grass crowns, and is directly relevant to the potential effect of heat on plant meristem mortality (Strong et al., 2013; Vermeire and Roth, 2011). Burns in 2009 were implemented with average ambient air temperature of 18.5 °C, relative humidity of 9% and average wind speed of 5.2 m sec⁻¹. Burns in 2010 were implemented with average ambient air temperature of 17 °C, relative humidity of 10% and average wind speed of 2.7 m sec⁻¹. Prior to each burn, fuel loads were measured by harvesting all standing plant biomass within two randomly-located 0.25 m² quadrats in each plot.

2.3. Soil measurements

We collected soil cores from each treatment periodically throughout the growing season in order to characterize the size and dynamics of soil inorganic N pools. In 2009, we sampled soil cores in order to measure inorganic N pools twice per month from April

to August, with sampling approximately during the first and third week of each month. In 2010, we sampled soils once per month from April to August, with sampling during the first week each month. Cores were collected at random locations, and were 12 cm deep and 5 cm in diameter. On each sampling date in 2009, we collected four cores per plot. In 2010, we collected eight cores per plot and then pooled pairs of cores into four samples per plot. Soils were stored on ice or refrigerated until they were sieved, subsampled, and analyzed for gravimetric moisture and inorganic N within 12–36 h of collection. Gravimetric moisture was measured by drying 30–80 g wet soil at 110 °C for 24 h. A 15–30 g subsample was extracted with 1 M KCl, with samples thoroughly mixed at 0 and 18 h and filtered at 24 h. KCl extracts were analyzed colorimetrically for inorganic N (NH_4^+ -N and NO_3^- -N).

We measured available soil inorganic N with Plant Root Simulator (PRS)TM resin probes (Western Ag Innovations, Saskatoon, SK, Canada). The 17.5 cm² resin membranes of the probes were inserted vertically into 4-cm-wide slits in the soil in the presence of plant roots at a depth of 2–8 cm, the zone of maximum root activity (LeCain et al., 2006). Eight cation and eight anion probes were installed in each plot the day after the burns were implemented each spring, and left in the soil until June 2 of each year. A second set of probes (placed in new, randomly-selected locations) replaced the first set on June 2, and was left in the soil until the end of July. The April–May incubation period lasted 53 days in 2009 and 62 days in 2012. The June–July incubation period lasted 58 days in 2009 and 61 days in 2010. Probes were cleaned with deionized water immediately after being removed from the soil. Probes were grouped into sets of 4 cation and 4 anion probes (2 sets per plot), eluted with 17.5 mL of 0.5 M HCl for 1 h, and inorganic N (NH_4^+ -N and NO_3^- -N) was determined colorimetrically (Hangs et al., 2004).

We measured 0–10 cm-deep soil volumetric water content and temperature hourly with Decagon 5TE probes and EM50 data loggers (Decagon Devices Inc., Pullman, WA, USA). We focused on the surface soil layer because this layer was most likely to be influenced by fire-induced changes in bare soil exposure. A single probe was placed in each plot at least 2 m from the outside edge. Probes were inserted vertically, with tips 10 cm below the soil surface. 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 volumetric water content measurements within $\pm 3\%$ of true soil volumetric water content in mineral soils.

2.4. Plant measurements

We measured plant foliar cover and biomass in each plot in late July or early August each year, which corresponds to peak standing crop and the point in the season when measurements best approximate ANPP (Milchunas and Lauenroth, 1992). Functional groups consisted of C₄ perennial grasses, C₃ perennial graminoids, C₃ annual grasses, and forbs. We measured plant cover by visually estimating foliar cover of each plant species in 25 50 × 20 cm quadrats randomly located in each plot, using cover classes consisting of 0–1%, 2–5%, 6–15%, 16–25%, 26–40%, 41–60%, and >60%. We clipped aboveground biomass in 5 50 × 20 cm quadrats randomly located in each plot, and separated biomass into functional groups consisting of C₃ perennial graminoids, C₄ perennial graminoids, forbs, annual grass, and standing dead biomass, which was then oven-dried and weighed. For each quadrat, the biomass of all plant functional groups other than standing dead biomass was combined and ground with a Wiley mill to pass a 0.85 mm sieve, and a subsample was analyzed for plant N concentration using a nitrogen analyzer (LECO Corporation, St. Joseph, MI).

2.5. Statistical analyses

To facilitate comparisons among measurements collected at different time intervals, we averaged soil temperature, soil moisture, and inorganic N pools (NH_4^+ -N and NO_3^- -N) within months. Therefore, monthly inorganic N pools we report represent the mean of the two sampling dates during each month in 2009, and a single sampling date each month in 2010. Soil temperature and moisture represent the mean of daily measurements across all dates within each month. Because soil temperature, moisture and inorganic N pools were measured repeatedly within and among growing seasons, these data were analyzed using a two-way, repeated-measures ANOVA for each of the two years separately, accounting for repeated monthly measurements with plot as the subject. For ANPP, plant cover, and plant N measurements (not repeated within a given growing season) data were analyzed using two-way, repeated-measures ANOVA, accounting for repeated yearly measurements with plot as the subject. All statistical analyses were performed with SAS v9.2 (SAS Institute Inc., Cary, NC, USA).

3. Results

Prescribed burns in the spring of 2009 occurred with mean residual standing dead biomass of 42–53 g m⁻², and generated mean maximum fire temperatures of 126 and 148 °C for annual and triennial burns respectively (Table 1). Due to above-average precipitation during the 2009 growing season, residual standing dead biomass was substantially greater for the prescribed burns in 2010 (91 g m⁻²). Mean maximum fire temperature was 136 °C for annual burns in 2010. Although the 2010 burns had greater fuel loads, burns in 2010 occurred with notably lower wind speed (2.7 m sec⁻¹) compared to 2009 (5.2 m sec⁻¹).

3.1. Inorganic nitrogen

In 2009 (first post-burn growing season for both annual and triennial burns), extractable NH_4^+ pools were significantly influenced by burn treatment ($F_{2,45} = 3.88$; $P = 0.028$) and declined significantly across months ($F_{4,45} = 59.02$; $P < 0.001$), but burn effects did not vary by month (Month × Treatment Interaction; $F_{8,45} = 0.97$; $P = 0.47$; Fig. 1A). Pairwise comparisons showed NH_4^+ was significantly greater in soils of annually burned compared to unburned grassland (Tukey HSD, $P = 0.024$), whereas NH_4^+ in grassland burned every 3 years (and burned in the spring of 2009) was intermediate between and not significantly different from NH_4^+ in annually burned or unburned grassland ($P = 0.67$ and 0.16 for respective pairwise comparisons; Fig. 1A). Extractable NO_3^- pools were also strongly affected by burning in 2009 ($F_{2,45} = 10.8$; $P = 0.001$), and declined significantly with sampling date ($F_{4,45} = 99.8$, $P < 0.001$), with no significant date × treatment

Table 1

Fuel loads, maximum fire temperatures, and duration of fire temperatures greater than 50 °C for prescribed burns conducted in ungrazed shortgrass steppe at the Central Plains Experimental Range in northeastern Colorado. Burns occurred on April 8th in 2009 and March 30th in 2010. Temperature measurements were at 1 cm above ground level. Values in parentheses are 1 standard error.

Treatment	Year	Standing dead biomass (g m ⁻²)	Mean maximum fire temp (°C)	Mean duration of temp >50 °C (seconds)
Annual burns	2009	42.0 (3.4)	126.3 (8.4)	66 (6)
Triennial burns	2009	53.0 (3.3)	147.7 (14.1)	76 (2)
Annual burns	2010	90.9 (10.2)	135.6 (12.2)	70 (4)
Triennial burns	2010	No burns	No burns	No burns

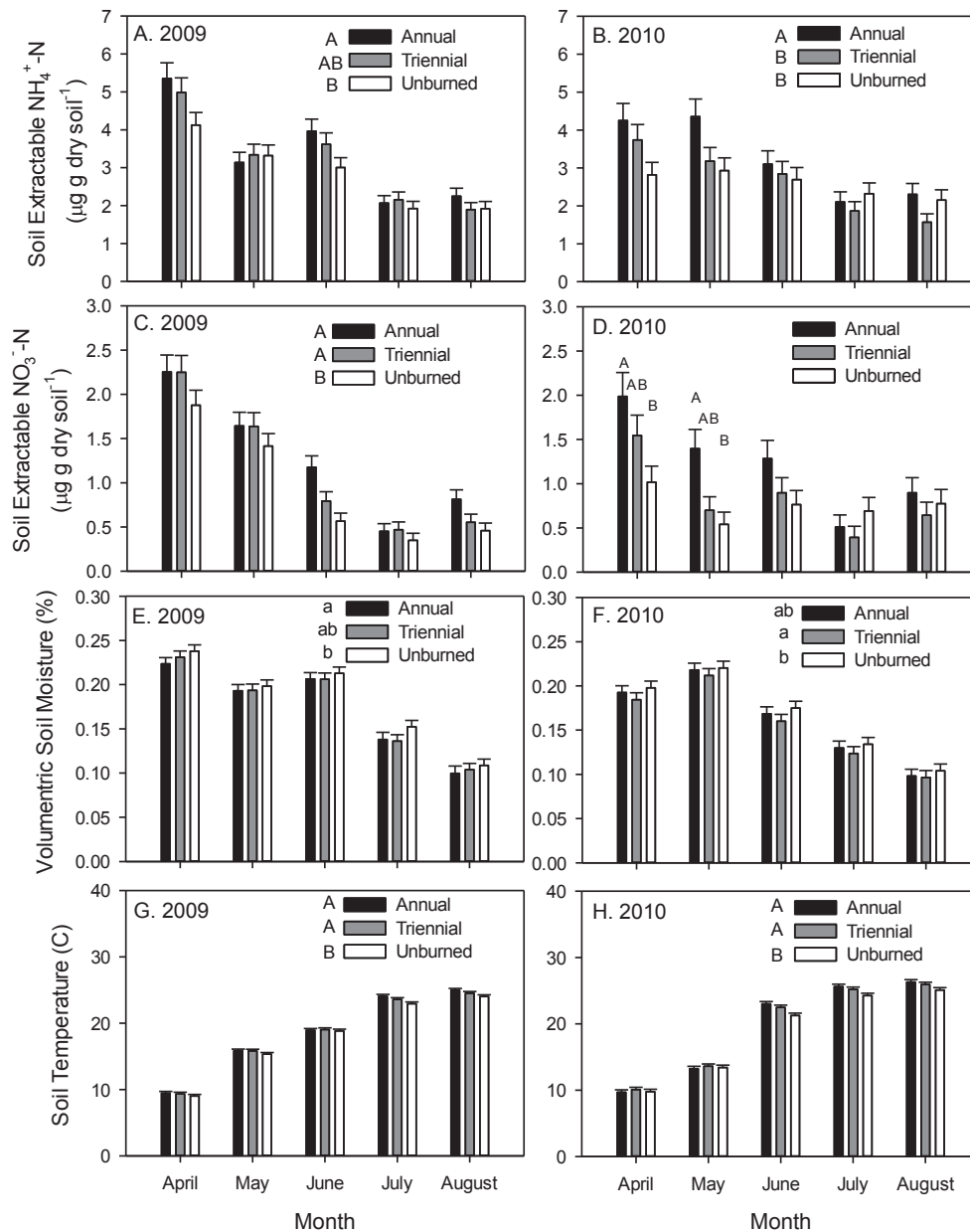


Fig. 1. Variation in soil inorganic N pools (NH_4^+ and NO_3^-), soil moisture, and soil temperature (mean + 1 SE) among prescribed burning treatments and from April to August in ungrazed shortgrass steppe at the Central Plains Experimental Range in northeastern Colorado during 2009 and 2010. In one case where we detected a significant month $\times$ burn treatment interaction (soil extractable NO_3^- -N in 2010), letters above the bars indicate significant differences for those months in which a significant burn effect was detected ($P < 0.05$). In all other cases, no significant month $\times$ burn treatment interactions were detected, and letters to the left of the legend symbols indicate differences among burn treatments. Legend symbols with different letters are significantly different at the $P < 0.05$ level (capital letters) or at the $P < 0.1$ level (lowercase letters).

interaction ($F_{8,45} = 1.12$, $P = 0.37$; Fig. 1B). Pairwise comparisons showed NO_3^- was significantly greater in soils of both the annually burned and triennially burned treatments compared to unburned grassland (Tukey HSD; $P = 0.0001$ and 0.023 respectively), and did not differ between annually vs. triennially burned treatments ($P = 0.16$).

In 2010 (first and second post-burn growing season for annual and triennial burns respectively), extractable NH_4^+ pools were significantly influenced by burn treatment ($F_{2,45} = 5.23$; $P = 0.009$) and declined significantly with sampling date ($F_{4,45} = 17.33$; $P < 0.001$), but burn effects did not vary by month (Month $\times$ Treatment Interaction; $F_{8,45} = 1.61$; $P = 0.15$; Fig. 1E). Pairwise comparisons showed that NH_4^+ was significantly greater in soils of annually burned grassland compared to both the triennially

burned (not burned in 2010) and unburned grassland (Tukey HSD, $P = 0.006$ and 0.009 respectively), whereas extractable NH_4^+ did not differ between the triennially burned and unburned treatments ($P = 0.89$; Fig. 1F). For extractable NO_3^- pools in 2010, we detected a marginally significant burn $\times$ month interaction ($F_{8,45} = 2.02$, $P = 0.065$), so we analyzed burn effects by month. Burning strongly and significantly affected extractable NO_3^- in April ($F_{2,45} = 5.23$, $P = 0.009$) and May ($F_{2,45} = 7.24$, $P = 0.002$), but not during June–August ($F_{2,45} < 2.4$, $P > 0.1$; Fig. 1E); the only significant differences in April and May were between annual burns and the unburned controls.

We found extremely low NH_4^+ on probes during spring and summer incubations in both years (mean of $0.046 \mu\text{g } 10 \text{ cm}^{-2} \text{ day}^{-1}$), hence results were not analyzed statistically or

presented graphically. We note that probe $\text{NH}_4^+\text{-N}$ was more than an order of magnitude lower than probe $\text{NO}_3^-\text{-N}$, despite the fact that soil extractions contained more $\text{NH}_4^+\text{-N}$ than $\text{NO}_3^-\text{-N}$. Resin N probes did measure significant variation among treatments and seasons in terms of soil $\text{NO}_3^-\text{-N}$ availability. Burn effects on resin $\text{NO}_3^-\text{-N}$ varied by season and year ($F_{6,36} = 3.46$, $P = 0.0084$), with significantly greater soil $\text{NO}_3^-\text{-N}$ availability detected in annual burns as compared to triennial burns and unburned plots in the spring of 2009 ($P < 0.001$), but no variation among treatments in the summer of 2009 ($F_{2,36} = 0.05$, $P = 0.95$) or the spring or summer of 2010 ($F_{2,36} < 0.77$, $P > 0.47$; Fig. 2).

3.2. Soil moisture and temperature

In both years, soil moisture varied substantially among months, with greatest levels during April–June, and declining soil moisture from June to August ($F_{4,45} > 112$, $P < 0.001$ in both years; Fig. 1E,F). In both years, burning had only a marginally significant effect on soil moisture ($F_{2,43} = 2.64$, $P = 0.083$ in 2009; $F_{2,45} = 2.50$; $P = 0.093$ in 2010), and burn effects did not vary by month (Month $\times$ Treatment interaction tests: $F_{8,43} = 0.19$, $P = 0.99$; $F_{8,45} = 0.06$, $P = 0.99$; Fig. 1E,F). Annually burned grassland tended towards lower soil moisture compared to unburned controls in 2009 (Tukey HSD, $P = 0.092$), but not in 2010 ($P = 0.59$). Triennially burned grassland tended towards lower soil moisture compared to unburned controls in 2010 ($P = 0.077$), but not in 2009 ($P = 0.20$).

Burning significantly increased soil temperature in both burn treatments and years (2009: $F_{2,43} = 7.45$, $P = 0.002$; 2010: $F_{2,45} = 7.82$, $P = 0.001$). Soil temperature increased from April to August both years ($P < 0.0001$), but burn effects did not vary by month ($P > 0.15$). In 2009, burning increased mean soil temperature (averaged across all months from April to August) by 0.62°C in annual burns compared to controls (Tukey HSD, $P = 0.0016$) and by 0.43°C in triennial burns compared to unburned controls (Tukey HSD, $P = 0.0275$). In 2010, burning increased mean soil temperature by 0.81°C in annual burns ($P = 0.019$) and by 0.69°C in triennial burns ($P = 0.0084$) compared to unburned controls.

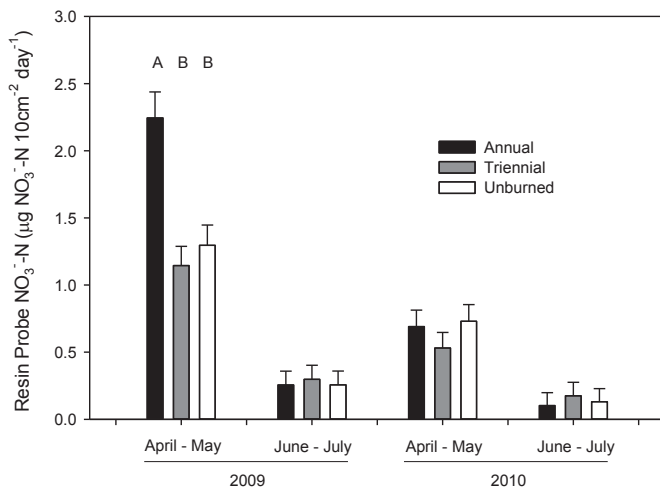


Fig. 2. Soil $\text{NO}_3^-\text{-N}$ availability (mean + 1 SE) measured by PRS resin probes in burned and unburned shortgrass steppe at the Central Plains Experimental Range in northeastern Colorado. See text for the number of days for probe incubations in each season and year. Bars with different letters above them are significantly different at the $P < 0.05$ level.

3.3. Plant responses

In terms of the foliar cover of plant functional groups, burning had no influence on annual grass, perennial forbs or C_4 perennial grasses ($F_{2,18} < 1.92$, $P > 0.17$ for each functional groups; Fig. 3). However, burn treatments significantly reduced cover of annual forbs ($F_{2,18} = 23.1$, $P < 0.001$) and C_3 perennial graminoids ($F_{2,18} = 5.03$, $P = 0.018$; Fig. 3). We found no significant year $\times$ treatment interactions for any functional group ($F_{2,18} < 2.28$; $P > 0.13$). Annual grass consisted only of *V. octoflora*; no invasion of *B. tectorum* occurred during the study. C_4 production was substantially greater in 2009 than 2010 ($F_{1,18} = 45.98$, $P < 0.0001$), reflecting greater precipitation and soil moisture during the 2009 growing season, but neither annual nor triennial burning affected aboveground production of C_4 perennial grasses in either year (Treatment $\times$ Year interaction: $F_{2,18} = 0.12$, $P = 0.89$; treatment main effect: $F_{2,18} = 0.27$, $P = 0.77$). Pairwise comparisons showed that C_3 production was significantly lower on annually burned compared to unburned grassland (Tukey HSD, $P = 0.007$), whereas C_3 production on triennial burns was intermediate between the other two treatments (Triennial vs. Unburned, $P = 0.070$; Triennial vs. Annual, $P = 0.52$). At the time of plant biomass harvesting in early August, residual standing dead was low on the unburned treatment in 2009 (3.9 g m^{-2}), but still significantly greater than the burned treatments (both $< 0.75 \text{ g m}^{-2}$ remaining after the

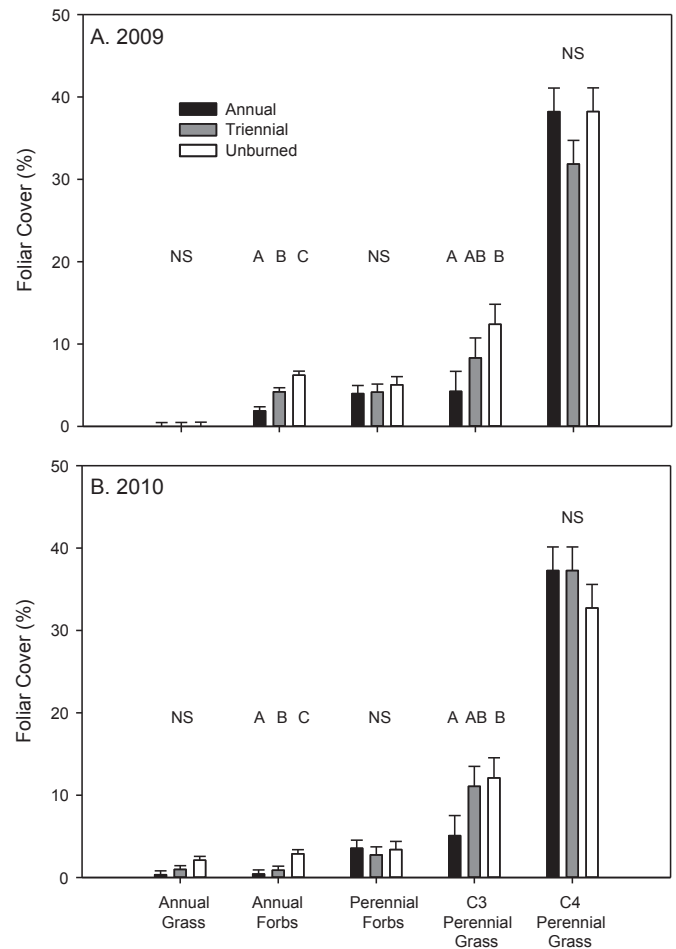


Fig. 3. Effects of annual and triennial prescribed burns on foliar cover of plant functional groups (means + 1 SE) in 2009 and 2010 in ungrazed shortgrass steppe at the Central Plains Experimental Range in northeastern Colorado. Bars with different letters above them differ significantly at the $P < 0.05$ level.

burns in spring of 2009; Fig. 4). In 2010, when the triennial treatment was not burned, residual standing dead in August was higher on the unburned and triennial plots ($>25 \text{ g m}^{-2}$), compared to 1.4 g m^{-2} on the annually burned plots (Fig. 4).

Nitrogen concentration in aboveground plant biomass was not affected by burning treatments in either year (Treatment $\times$ Year interaction: $F_{2,18} = 0.41$, $P = 0.67$; Treatment main effect: $F_{2,18} = 0.88$, $P = 0.43$; Fig. 5). However, total aboveground plant N yield was significantly lower with annual burning compared to unburned grassland in both years (Treatment $\times$ Year interaction: $F_{2,18} = 0.02$, $P = 0.98$; Treatment main effect: $F_{2,18} = 4.24$, $P = 0.031$). Annual burning significantly reduced plant N yield compared to unburned controls (Tukey HSD, $P = 0.024$), whereas N yield in triennially burned grassland was intermediate between and not significantly different from either annually burned or unburned grassland ($P > 0.32$; Fig. 5).

4. Discussion

We found that annual burning in early spring for 5 consecutive years in the shortgrass steppe significantly increased inorganic N pools throughout the growing season, which is consistent with several previous studies of fire in arid and semiarid ecosystems (Allred and Snyder, 2008; Davies et al., 2007; Esque et al., 2010).

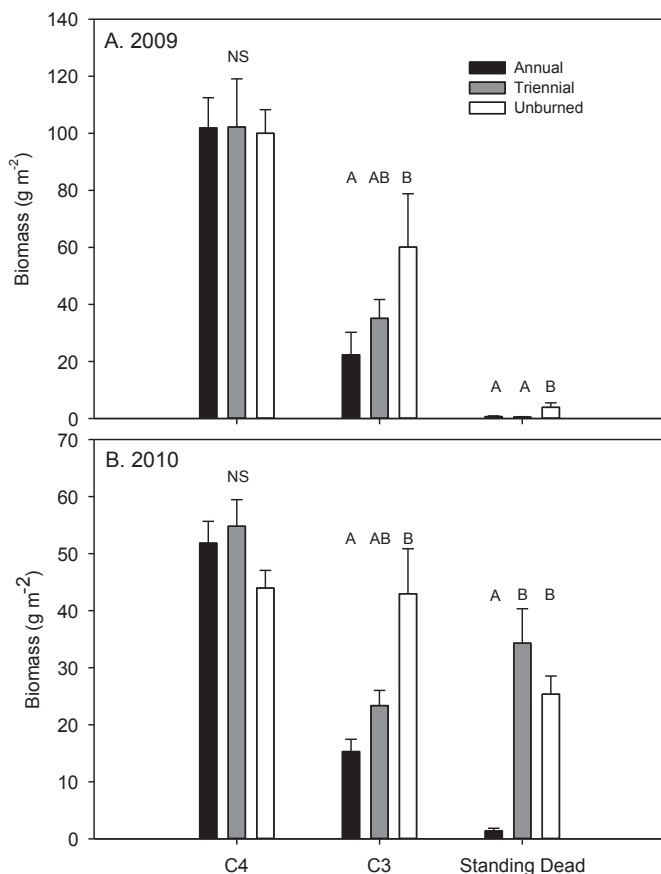


Fig. 4. Effects of annual and triennial prescribed burns on aboveground C₃ and C₄ plant production and residual standing dead biomass (means + 1 SE) in 2009 and 2010 in ungrazed shortgrass steppe at the Central Plains Experimental Range in northeastern Colorado. C₃ plant production included forbs, perennial grasses and sedges, with minimal contribution of annual grasses (<0.5% of total). C₄ plant production consisted entirely of perennial grass. Standing dead represents the amount of standing dead biomass carried over from the prior growing season. Note the difference in scales between 2009 and 2010. Bars with different letters above them differ significantly at the $P < 0.05$ level.

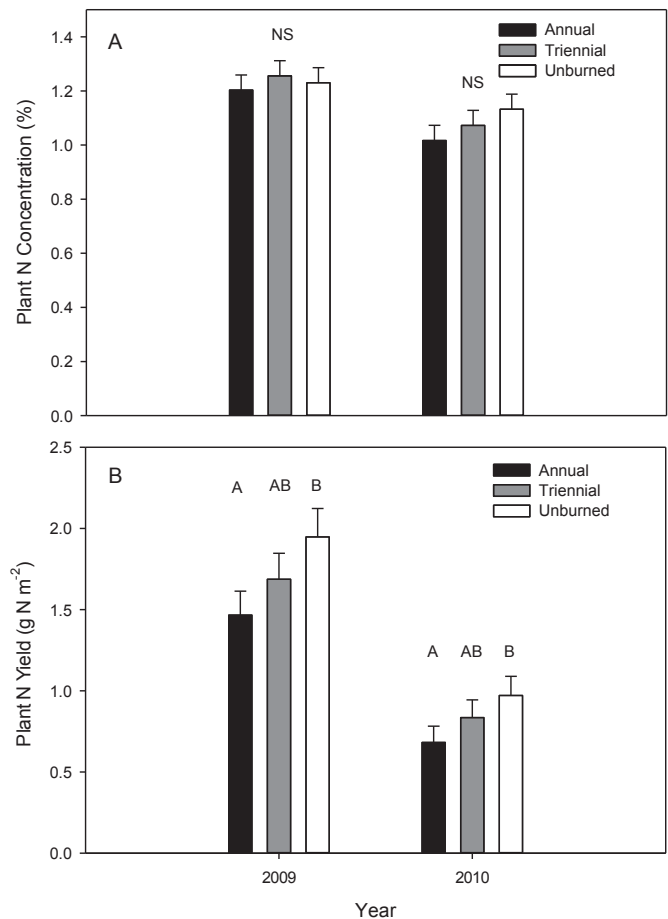


Fig. 5. Effects of annual and triennial prescribed burns on aboveground plant N concentration (A) and N yield (B; means + 1 SE) in 2009 and 2010 in ungrazed shortgrass steppe at the Central Plains Experimental Range in northeastern Colorado. Bars with different letters above them differ significantly at the $P < 0.05$ level.

We also found that soil $[\text{NH}_4^+]$ was greater than soil $[\text{NO}_3^-]$ and increased to a similar degree in response to annual burning. Consistent with McCulley et al. (2009), our results in terms of absolute inorganic N pool sizes and response to the burn treatments indicate that NH_4^+ is the primary form of available N in this system. Resin probes also showed that annual burning substantially increased NO_3^- availability during the spring of 2009, consistent with the NO_3^- pool measurements. However, the greater soil $[\text{NH}_4^+]$ we measured was not tracked by the resin probes, for which accumulated NH_4^+ was too low to be detected in all 4 incubation periods. It might be argued that the uncoupling between soil $[\text{NH}_4^+]$, as measured by KCl extracts, and its availability measured on the resin probes, occurred because NH_4^+ is bound tightly to negatively charged soil particles, and hence is present in the soil but not available to plant roots. However, we suggest that these contrasting results were observed because plants and microbes were more effective than the probes in competing for NH_4^+ in the soil. The latter is supported by ^{15}N tracer experiments (conducted in 2009 at an unburned site adjacent to our prescribed fire experiment) which showed that plants in the shortgrass steppe are just as effective in acquiring NH_4^+ as NO_3^- (Dijkstra et al., 2012).

Our measurements of fire temperatures, soil temperature and moisture, and plant responses to burns provide some insight into mechanisms underlying increased soil inorganic N availability following fire in the shortgrass steppe. Maximum temperatures at

the level of plant crowns and litter during burns were only 126–148 °C, with temperatures above 50 °C only persisting for 66–76 s. Given that fire temperatures at the surface layer were well below 200 °C, a portion of N in the fuel may have been returned to the soil surface in organic and inorganic forms in the ash (DeBano et al., 1998; Neary et al., 1999). For example, field measurements of post-burn residual N in ash and partially combusted material in grassland fires predict that for burns with the fuel loads similar to those we studied, as much as 80% of N in the fuel may remain in ash and partially combusted biomass (McNaughton et al., 1998). N deposition in ash and partially combusted biomass could have provided substrate that led to increased soil inorganic N. Soil heating during burns could also have released NH_4^+ from organic residues or clay minerals in the surface soil layer (e.g. Choromanska and DeLuca, 2002; Klopatek et al., 1990) although the short duration of heating suggests that soil temperatures would only have been elevated to levels that induce NH_4^+ release in the top few millimeters of the profile (DeBano et al., 1998).

Reduced total plant N uptake could also have allowed inorganic N to accumulate in burned plots. Annual burning significantly reduced C_3 plant production, but did not affect C_4 plant production or N concentrations in aboveground plant biomass, such that total plant N yield was reduced on annual burns. We suggest that reduced soil moisture (most notably in the spring of 2009) and increased soil temperatures (due to removal of litter and blackening of the soil) contributed to the reduction in C_3 growth, rather than simply heat-induced mortality of plant meristems, because fire temperatures were well below those observed in other grasslands and below the thresholds that typically cause perennial plant death (Limb et al., 2011; Romanya et al., 2001; Vermeire and Roth, 2011). In addition, increased soil temperature could have contributed to increased soil inorganic N pools through increased microbial activity and N mineralization rates. The largest increase in soil NH_4^+ was evident both early and in the middle of the growing season (Fig. 1, April and June), suggesting the increase was not just the result of ash deposition and soil heating during the burns, but also due to changes in microbial activity or plant uptake later in the growing season.

Differences in the effects of annual versus triennial burns on inorganic N pools also provide some insights to mechanisms. If the deposition of ash and partially combusted organic matter combined with heating of soils during the burns were primary contributors to increased inorganic N pools, we would expect both burn treatments to increase pools in the year both were burnt (2009), but only the annual burns to increase pools in 2010. We found that results were consistent with these predictions for NO_3^- –N pools (similar responses in both treatments in 2009 but not in 2010; Fig. 1 C,D), but that NH_4^+ –N pools on triennial burns were generally intermediate between annual burns and controls in both years (Fig. 1 A,B). These mixed findings again suggest that burns may be altering soil N dynamics both through direct, short-term effects of combustion and heating during the fire as well as longer-term changes associated with increased bare soil exposure, increased soil temperature, and reduced total plant N uptake over the growing season.

We did not find that increased inorganic N pools or increased NO_3^- –N availability following burns enhanced plant N concentrations or aboveground plant N yield. One consideration is whether plants in the burned treatments increased belowground N uptake and storage, which we did not measure. However, this explanation seems unlikely given that burns suppressed aboveground N yield in two consecutive and relatively wet years (Fig. 5). If increased belowground allocation and N storage in crowns occurred in the first year, we would have expected this to allow for reallocation of stored C and N aboveground in the second year, which did not

occur. If burned plants increased allocation to root production in the first year, we would again expect this to facilitate growth through reduced need for belowground allocation in the second year. We suggest the sustained reduction in aboveground C_3 plant N yield across years reflects reduced N uptake by C_3 plants with annual burning.

While annual burns increased soil inorganic N pools, the magnitude of this change in the shortgrass steppe (+28% for $\text{NO}_3^- + \text{NH}_4^+$ –N averaged over the first post-burn growing season) was small compared to the increase in sagebrush steppe (+58%; Davies et al., 2007), desert grassland (+52%; Allred and Snyder, 2008), and desert shrubland (+109%; Esque et al., 2010). Where the increase is particularly large, as in the desert shrubland example, invasion of annual plants can be facilitated (Esque et al., 2010). Such large increases in soil inorganic N pools are most likely where fire kills dominant plants. For example, in the intermountain region of the western United States, fire and other disturbances that kill shrubs can cause both short-term and long-term increases in N availability, and facilitate invasion by the nitrophilic winter-annual grass *B. tectorum*, particularly in areas with low perennial grass cover (Beckstead and Auspurger, 2004; Blumenthal et al., 2006; Monaco et al., 2003; Young and Evans, 1978). In the shortgrass steppe, experimental N fertilization facilitates invasion of annuals such as *V. octoflora*, *B. tectorum*, *Bassia scoparia*, and *Salsola tragus*, but this requires relatively large N additions (Lowe et al., 2003; Milchunas and Lauenroth, 1995; Paschke et al., 2000). For example, Paschke et al. (2000) showed that fertilization with 10 g m⁻² N, which facilitated annual forbs, increased inorganic N availability by more than an order of magnitude (+1356%) during the growing season. Thus, while it is possible to increase N availability to the point where annuals invade shortgrass steppe, the magnitude of the increase required is far greater than what occurs with annual burning at our study site. We attribute the small effect of fire on soil N in shortgrass steppe to the lack of fire effects on the dominant C_4 perennial grasses, *B. gracilis* and *B. dactyloides*. These grasses have high allocation to root and crown biomass, and are well-adapted to both intense grazing and aridity (Milchunas et al., 2008). These grasses also appear to be highly resistant to the intensity of fires that we studied, and thus continue to take up significant amounts of soil N even with annual burning.

Annual burning represents an extreme fire treatment in the shortgrass steppe. The historic fire return interval in this region is not well known due to the lack of trees, but may be longer than 10 years (McPherson, 1995). Today, the use of prescribed burning on public rangelands in the shortgrass steppe typically involves only infrequent burning at a given location (less than once every 10 years). Given that (1) annual burning for 5 years increased inorganic N pools by a mere 28% and did not result in annual plant invasion, and (2) triennial burning had an even smaller effect on inorganic N pools, again with no effect on plant invasion, our results suggest that infrequent prescribed burning of shortgrass steppe (i.e. less frequently than triennially) will not facilitate annual plant invasion. At the same time, neither burn treatment enhanced N concentrations in aboveground plant biomass. Our measurements occurred during two relatively wet years, with above-average plant production. Under such conditions of high soil moisture availability, we had hypothesized that enhanced soil inorganic N in burns could allow for increased plant productivity. However, our findings indicated that either plants were not limited by N in spite of the above-average precipitation, or that burns affected the plant community and growth environment in a manner that did not allow plants to respond to increased soil N availability on burns. Thus, while burning may enhance forage quality by removing residual standing dead biomass and making green leaves more accessible to grazers, the N content in current-season's growth of the plants, at

least as measured at peak standing crop in August, is not enhanced. Overall, our findings indicate that prescribed burning in this ecosystem will not facilitate annual plant invasion.

Previous studies in shortgrass steppe found that one-time burns conducted when grasses are dormant did not suppress aboveground production of C₃ or C₄ plants, regardless of whether or not the site was grazed by livestock in the first post-burn growing season (Augustine and Milchunas, 2009; Augustine et al., 2010; Scheintaub et al., 2009). Here, we found that annual burning significantly reduced C₃ plant production. With triennial burning, C₃ plant production was intermediate between annual burns and unburned controls, suggesting that infrequent burning (i.e. at intervals longer than every 3 years) may be advisable where grassland managers seek to minimize potential impacts on perennial C₃ plants.

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