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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 C_3 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 C_3 plant production could be due to increased soil temperature, reduced soil moisture, or direct negative effects on C_3 plant meristems, although fuel loads and fire temperatures were low relative to other grasslands. Triennial burning had intermediate effects on N availability and C_3 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 C_3 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 (Kotanen 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 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 m^2 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