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REGULAR ARTICLE

# Fire history as a key determinant of grassland soil $CO_2$ flux

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**Abstract**
*Aims* Fire regimes are key drivers of ecosystem dynamics and are changing worldwide. Uncertainty about how fire history affects responses to individual fires hampers predictions of fire impacts on important ecosystem functions such as C cycling. Thus, we assessed how fire and fire history affect soil $CO_2$ flux and aboveground net primary production (ANPP).
*Methods* We utilized a 35-year fire frequency experiment in a mesic grassland to quantify how two aspects of fire history, long-term fire frequency (fire every one, two, or four years, or no fire) and number of years elapsed since the most recent fire, affect soil $CO_2$ flux. We used long-term annual records from the same grassland to compare this to the effect of fire history on ANPP.
*Results* Historic fire frequency altered the soil $CO_2$ flux response to fire, with greater post-fire stimulation in grassland burned annually than in grassland burned less frequently (~100% vs. ~44% increase over long-term unburned grassland). The flux increase persisted for up to two years after fire. Though fire also stimulated ANPP, this increase did not vary by long-term fire frequency and did not persist into later years.
*Conclusions* Fire history modifies the soil $CO_2$ flux response to individual fires in this grassland. Predicting the dynamics of this important C flux will require considering not only the presence vs. absence of fire, but also fire history.

**Keywords** Fire · Grassland · Soil $CO_2$ flux · Soil respiration · Aboveground net primary production · Carbon cycling · Ecosystem

**Abbreviations**
(ANPP) Aboveground net primary production
(KPBS) Konza Prairie Biological Station

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## Introduction

Recurring fires are integral disturbances for most biomes on Earth and are known to influence ecosystem structure and function (Bond 2005; Bond et al. 2003, 2005; Bowman et al. 2009). Changes in climate and land use have altered fire regimes from historic levels globally, and such changes are predicted to continue (Andela et al. 2017; Flannigan et al. 2009; Knorr et al. 2016; Westerling et al. 2006). It is important to understand how this will impact ecosystem dynamics and the global terrestrial carbon (C) cycle. Fires are known to affect ecosystem C cycling and sequestration (Beringer et al. 2007; Pellegrini et al. 2018; Richards et al. 2011; Williams et al. 2004), and C fluxes to the atmosphere from plant combustion have been well-characterized (Ellicott et al. 2009; Kaiser et al. 2012; Kasischke and Penner 2004; Seiler and Crutzen 1980; Shi et al. 2015; van der Werf et al. 2017). However, the effects of fire on soil C fluxes are not as well understood. For example, though ecosystem history is known to affect responses to disturbances (Buma 2015; Hughes et al. 2019; Johnstone et al. 2016), the relative influence of various aspects of historical fire regimes on grassland soil $CO_2$ flux (a.k.a. soil respiration) is not well understood. Determining how fire history (i.e., long-term fire frequency and years elapsed since the last fire) affects grassland soil $CO_2$ flux and its response to fire has value for improving earth system models, C accounting, and management outcomes.

The long return interval of disturbances, including fires, in many ecosystems can make it difficult to assess impacts of different historical regimes and how history may modify disturbance responses. However, fires occur relatively often in productive, grass-dominated ecosystems (Bragg 1982; Mouillot and Field 2005) and are easily manipulated. Consistent with other biomes, numerous characteristics of fire (e.g., frequency, seasonality, spatial extent, intensity, etc.) have changed from historic levels in grasslands and savannas, due to a variety of land-use/land management practices, climate and environmental conditions, and socio-ecological factors (Archibald et al. 2010a, b, 2012, 2013; Bowman et al. 2011; Frost 1999; Guiterman et al. 2019; Guyette et al. 2002; Laris 2002; Le Page et al. 2010; Probert et al. 2019). Grass-dominated systems are ecologically and economically important, covering much of Earth's terrestrial surface (Dixon et al. 2014) and playing an important role in the global C cycle (Pendall et al. 2018). For these reasons, grass-dominated ecosystems are ideal for assessing the impacts of fire history on ecosystem C dynamics.

The flux of $CO_2$ from the soil to the atmosphere is a large, and increasing, component of the global terrestrial C cycle (Adachi et al. 2017; Bond-Lamberty 2018; Bond-Lamberty and Thomson 2010; Bond-Lamberty et al. 2016; Hashimoto et al. 2015; Jian et al. 2018; Le Quéré et al. 2017; Xu and Shang 2016; Zhao et al. 2017). Globally, soils contain at least twice as much C as the atmosphere (Köchy et al. 2015; Scharlemann et al. 2014). Temperate grasslands in particular allocate substantial primary production to roots and store most C belowground (Hui and Jackson 2006; Risser et al. 1981; Silver et al. 2010; Smith et al. 2008; Soussana et al. 2004). The $CO_2$ flux from soils is thus an especially important component of the annual C cycle in these ecosystems (Gale et al. 1990; Ham et al. 1995; Kim et al. 1992).

Previous work in productive grasslands has shown that most of the annual soil $CO_2$ flux occurs during the growing season, and that soil $CO_2$ flux tends to increase with increased precipitation/soil moisture and soil temperature during this time (Bremer et al. 1998; Harper et al. 2005; Knapp et al. 1998b; Mielnick and Dugas 2000). Fire has also been shown to affect temperate grassland soil $CO_2$ flux, generally increasing flux rates relative to unburned grassland (Jia et al. 2012; Johnson and Matchett 2001; Knapp et al. 1998b; Pujia et al. 2013; Strong et al. 2017; Xu and Wan 2008). However, these past studies often quantified the effects of fire in a binary manner, by comparing burned vs. unburned sites, and did not explicitly consider the effects of differences in historic fire regimes. It thus remains unclear how different fire return intervals can impact soil $CO_2$ flux and its response to fire, or how soil $CO_2$ flux changes in the years after fire. There is some evidence that fire stimulates grassland aboveground net primary production (ANPP) more following a longer fire return interval (e.g., >12 vs. 1–2 years; Knapp et al. 1998a). Though it is not known if the same is true of other ecosystem functions, fire does have both immediate and cumulative effects on a variety of grassland properties that may affect soil C fluxes (Bond and Keeley 2005; Carson and Zeglin 2018; Gill 1975; Pellegrini 2016; Pellegrini and Jackson 2020; Pellegrini et al. 2015). Thus, in addition to the direct effects of fire, differences in fire history may alter the soil $CO_2$ flux response to fire.

The objective of this study was to assess how different historic fire regimes affect soil $CO_2$ flux from a productive, mesic grassland. We took advantage of a long-term (35-year) fire manipulation experiment to assess the impact of fire history and how it may modify the response to fire. This experiment includes adjacent plots with distinct fire histories (different long-term fire frequencies and number of years since last fire). In addition, we quantified the impacts of fire history on ANPP and its response to fire in the same grassland using a long-term (31-year) annual ANPP record from sites with different historic fire frequencies. We compared ANPP and soil $CO_2$ flux responses to assess differences between a major ecosystem C input (ANPP) and output (soil $CO_2$ flux), which are both important in understanding ecosystem function and C cycling, and to link plant and soil impacts for a broader perspective on ecosystem dynamics.

## Materials and methods

*Study site* We conducted this study at the Konza Prairie Biological Station (KPBS), a 3487 ha native, unplowed tallgrass prairie in northeast Kansas, USA (39°05'N, 96°35'W). The KPBS is a USA Long-Term Ecological Research (LTER) site. Recurring fires are a historical feature of this grassland and are key for its existence and for reducing woody plant encroachment (Briggs et al. 2005; Knapp et al. 1998a). The climate is temperate mid-continental with cold, dry winters and warm, wet summers. The mean annual temperature is 13 °C (Knapp et al. 1998a) and the mean annual precipitation is 851 mm, almost 70% of which occurs during the growing season. We performed our research in a lowland site with deep, nonrocky, silty clay loam soils that are part of the Tully series (Collins and Calabrese 2012; Ransom et al. 1998).

*Study design* We used experimental plots established in 1981 to evaluate the effects of fire on tallgrass prairie ecosystems. The plots (10 m × 25 m) have been burned in the spring at one-, two-, or four-year intervals, or left unburned since their establishment. The experiment includes annually burned plots first burned in 1981, plots burned once every two years starting in 1981 and in 1982, and plots burned once every four years starting in 1981, 1982, 1983, and 1984. Thus, both years of a two-year fire cycle and all four years of a four-year fire cycle are available for sampling every year. This results in a total of eight fire frequency × years since last fire treatments that we included in our study. The experiment includes two replicate plots of each of these treatments (i.e., 16 plots total, Fig. 1). At the time of our study, both of the annually burned plots that we sampled had been burned 36 times, all four of the plots burned every two years had been burned 18 times, all eight of the plots burned every four years had been burned 9 times, and both of the unburned plots had been protected from fire for >35 years (Table 1).

This unique design allowed us to assess the impact of different fire frequencies and different numbers of years since the most recent fire on soil $CO_2$ flux within a single growing season and in adjacent plots. We were thus able to minimize differences in other variables known to affect soil $CO_2$ flux (e.g., precipitation amount and distribution, temperature, soil characteristics, etc.) and focus on the effects of fire history.

*Soil field measurements* We measured soil $CO_2$ flux in situ approximately once per week throughout the 2016 growing season (April – September) using a LiCOR 8100 portable gas exchange system (LiCOR Inc., Lincoln, NE, USA). In most plots, we installed four polyvinyl chloride (PVC) collars (10 cm diameter × 8 cm tall, buried 6 cm into the soil) >1 m from the edge of the plot and > 1 m apart from each other, two in a representative area of herbaceous vegetation (typically dominated by *Andropogon gerardii*) and two in a representative area of woody vegetation (typically dominated by *Cornus drummondii*; Briggs et al. 2005). The exception to this was plots burned annually or every two years, which were uniformly grass-dominated and did not contain woody plant communities. In these plots, we installed two collars in an area of herbaceous vegetation. A preliminary study indicated that this was sufficient to capture within-plot variation in soil $CO_2$ flux (online resource, Fig. S1). We measured soil $CO_2$ flux from 24 collars (all spaced ~1 m apart) six times throughout the previous growing season in a frequently burned area adjacent to the fire experiment, and the difference in growing season soil $CO_2$ flux between all collars vs. any two randomly selected collars (~0.5 μmol $CO_2$ $m^{-1}$ $s^{-1}$) was below the expected threshold for detectable treatments differences, based on previous research at the KPBS. We installed collars in the space between plant tillers/stems, and carefully removed (via clipping with scissors or by hand if loose) any litter and vegetation within the collar so that measurements included only $CO_2$ flux from the soil. Flux measurements required about 1 min and were taken around midday, between 1000 and 1500 Central Daylight Time. We focused on the period of highest soil $CO_2$ flux during the year (June – August), based on previous research at the KPBS (Knapp et al. 1998b). We took additional measurements in 2017 to confirm patterns from 2016. Patterns were consistent, and we include only the earliest measurement from 2017, taken in April (measurements in 2016 began in May). Soil $CO_2$ flux at that time was low, and

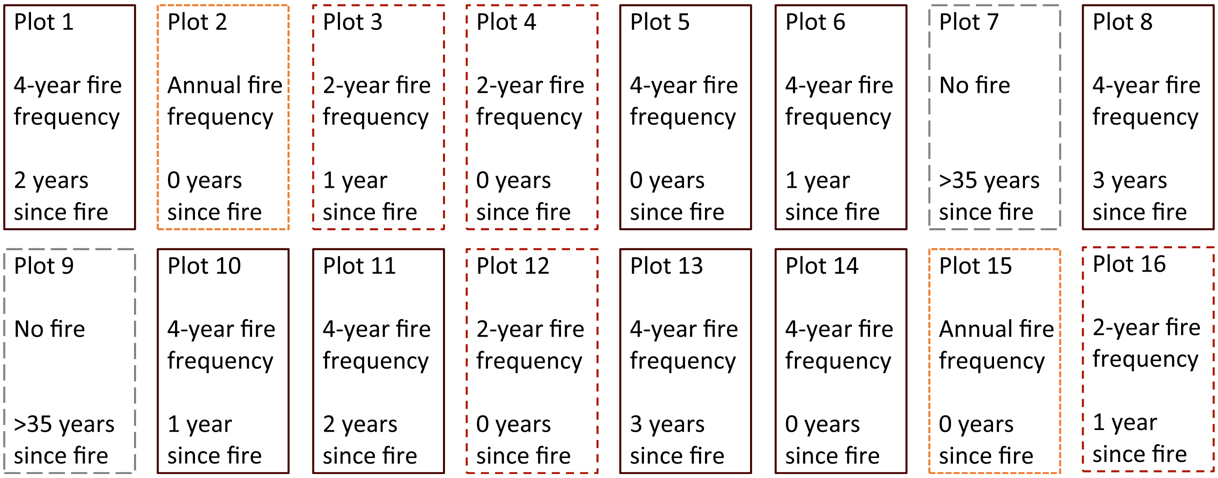


**Fig. 1** Schematic representation of the experimental design. Each plot is labeled with its unique ID number, its randomly assigned fire frequency, and the number of years since it was last burned. Not drawn to scale. Adjacent plots are separated by several meters. Plot outlines match the lines indicating fire frequency in Fig. 2

differences among treatments were minimal. We placed the April 2017 measurement at the beginning of the Fig. 2 time series, to easily visualize a complete seasonal pattern. This earliest measurement that we took was approximately two weeks after the plots were burned. In total, we measured soil $CO_2$ flux in all plots 15 times.

We measured soil moisture and soil temperature concurrently with soil $CO_2$ flux. We measured soil moisture in the top 0–20 cm of the soil using a portable soil moisture probe (HydroSense II, model CS658, Campbell Scientific Inc., Logan, UT, USA). We measured soil temperature at a depth of 10 cm using a portable temperature probe (LiCOR attachment, LiCOR Inc., Lincoln, NE, USA). We took soil moisture and temperature measurements adjacent to each collar each time that we measured soil $CO_2$ flux.

At the end of the growing season, we collected soil samples for pH, total nitrogen (N), and total organic C analysis. We collected two soil cores from near each collar, to a depth of 10 cm, and air-dried them at room temperature. We combined the two cores taken from near each collar, removed large roots and pieces of litter, and homogenized each composite sample via sieving. We determined soil pH via saturation paste pH tests and analyzed soil C and N content via dry combustion on a LECO Tru-Spec CN analyzer (Leco Corp. St. Joseph, MI, USA).

**Table 1** Treatment characteristics, including average (standard error) soil composition, growing season average (standard error) soil moisture, and growing season average (standard error) soil temperature for each fire treatment. See Methods for details, including sample size. The asterisk signifies the only significant difference in soil characteristics ($p < 0.05$) among treatments

| Fire frequency | Years since last fire | Total fires | Soil pH | Total soil N (%) | Soil organic C (%) | Soil moisture (% vwc) | Soil temperature (°C) |
|---|---|---|---|---|---|---|---|
| Annual | 0 | 36 | 6.15 (0.15) | 0.365 (0.01) | *4.25 (0.20) | 34.3 (1.44) | 23.7 (0.85) |
| 2 years | 0 | 18 | 6.30 (0.20) | 0.305 (0.05) | 3.42 (0.26) | 35.8 (1.51) | 23.4 (0.93) |
| 2 years | 1 | 18 | 6.20 (0.20) | 0.323 (0.01) | 3.45 (0.20) | 36.4 (1.51) | 22.4 (0.96) |
| 4 years | 0 | 9 | 6.35 (0.15) | 0.363 (0.01) | 3.70 (0.13) | 32.5 (1.65) | 22.9 (1.43) |
| 4 years | 1 | 9 | 6.25 (0.15) | 0.380 (0.01) | 3.81 (0.15) | 32.6 (1.62) | 22.4 (1.02) |
| 4 years | 2 | 9 | 6.15 (0.05) | 0.355 (0.01) | 3.83 (0.03) | 35.4 (1.48) | 21.7 (1.02) |
| 4 years | 3 | 9 | 6.30 (0.30) | 0.367 (0.02) | 3.81 (0.01) | 37.5 (1.28) | 21.9 (1.16) |
| No fire | >35 | 0 | 6.40 (0.40) | 0.381 (0.02) | 3.76 (0.09) | 32.1 (1.50) | 22.3 (1.01) |

*Aboveground net primary production measurements* We also quantified the effect of fire on ANPP, to compare to our assessment of the effect of fire on soil $CO_2$. We used annual estimates of ANPP from 1984 to 2015 from permanent sampling transects at the KPBS, located in the lowlands of three different watersheds, each with a different long-term fire frequency: annual fire, fire once approximately every four years, and no fire (no data were available for a two-year fire frequency). These ANPP transects are not a part of the experimental plots that we used for soil $CO_2$ flux measurements (where no destructive sampling has occurred), but they are located in areas with similar topography and soil characteristics. We have no reason to think that fire history would alter ANPP differently at these transects than at the plots where we measured soil $CO_2$ flux. Each year, end-of-season aboveground biomass has been harvested to the soil surface (via clipping with scissors) within each of five 0.1 $m^2$ quadrats spaced along every transect, dried at 60 °C for at least 48 h and weighed. Litter and previous years' biomass were removed from samples to estimate annual ANPP.

*Statistical analysis* We analyzed the effects of fire history on soil $CO_2$ flux, soil temperature, soil moisture, and ANPP via repeated measures mixed-effects analyses of variance models using the nlme package in R (R Core Team 2018; Pinheiro et al. 2020). We averaged within-plot replicates for each sampling date prior to analysis. We included plot as a random effect in the models. We focused on analyzing the effects of fire and fire history on soil $CO_2$ flux, soil moisture, and soil temperature at the time scale of the growing season, rather than on analyzing differences on any individual sampling date. Several previous studies have already assessed temporal patterns of soil $CO_2$ flux at the KPBS (e.g., Bremer et al. 1998; Knapp et al. 1998b; Mielnick and Dugas 2000). In addition, analyzing differences on any one particular sampling date would have consisted of only two true replicates, a limitation of the number of plots included in the original 1981 experimental design. We thus included data from all sampling dates, and a repeated measures structure, in our statistical models (n for each of the eight fire frequency × years since last fire treatments = two replicate plots per treatment, on each of the 15 sampling dates throughout the growing season). The repeated measures structure ensured that values from the same plot on different sampling dates were not treated as independent replicates. For ANPP, we analyzed the impact of fire frequency using the average annual herbaceous ANPP for each of the three frequencies (annual fire, fire every two years, and no fire) for each year for 32 years, and we analyzed the impact of the number of years since the most recent fire using the average annual herbaceous ANPP from the watershed burned every four years (n = approximately eight for each of the four years of the fire cycle). For each dependent variable, we ran a model to assess differences among all of the treatments. When necessary, we performed pairwise comparisons with Holm adjustment to assess which treatments differed from each other. In addition, to assess the impact of woody encroachment on soil $CO_2$ flux, we ran models using data from both herbaceous- and woody plant-dominated areas (when both were present, weighted by estimated % cover), as well as using only data taken from herbaceous-dominated areas. Adding an autocorrelation structure to the model did not change the output, and we present the results of the models without autocorrelation here. We collected soil samples for C, N, and pH analysis only once, and thus did not include a repeated measure structure in the statistical analysis of those data. We treated the composite soil samples from near each collar as replicates (n = two or four per plot × 2 plots per treatment combination = four or eight per treatment combination). We consider $p$-values <0.05 significant.

## Results

*Seasonal averages of soil $CO_2$ flux* Fire treatment significantly affected soil $CO_2$ flux (df = 7, F = 15.90, $p < 0.0001$, online resource Table S1). Soil $CO_2$ flux responded positively to fire, it was higher in all treatments burned in the year of the study than in long-term unburned plots (Fig. 2 inset, $p < 0.0001$, $p < 0.0001$, $p = 0.003$ for annual, 2-year, and 4-year fire frequencies vs. long-term unburned plots, respectively). However, historic fire frequency altered the magnitude of this response. Of the plots burned in the study year, average growing season soil $CO_2$ flux was higher in annually burned plots than in plots burned every two ($p < 0.0001$) or four years ($p < 0.0001$). Soil $CO_2$ flux from plots burned every two or four years did not differ from each other ($p = 0.99$). The growing season average soil $CO_2$ flux was 10.7 ± 0.52 μmol $CO_2$ $m^{-2}$ $s^{-1}$ under an annual fire frequency, 7.9 ± 0.46 μmol $CO_2$ $m^{-2}$ $s^{-1}$ and 7.5 ±

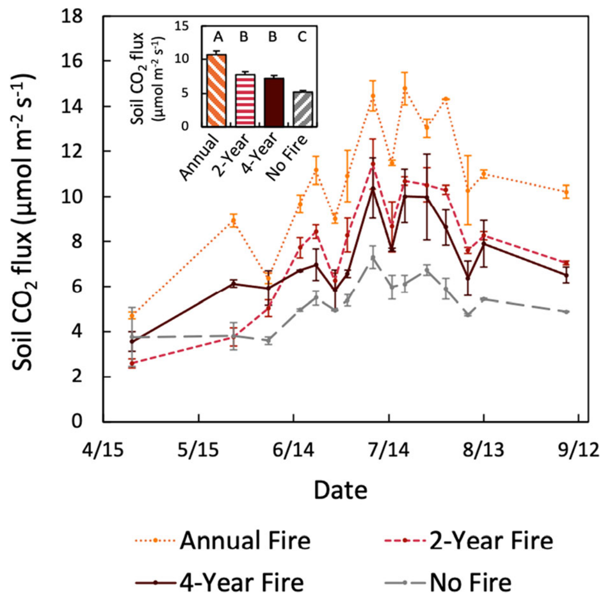


**Fig. 2** Soil $CO_2$ flux dynamics throughout the growing season. Average ± one standard deviation soil $CO_2$ flux from plots burned in the year of the study, by long-term fire frequency, and from long-term unburned plots (n = two plots for each date, for each fire frequency). **Inset** Growing season average soil $CO_2$ flux + one standard error from plots burned in the year of the study, by long-term fire frequency, and from long-term unburned plots (n = two plots per treatment and 15 sampling dates). Different letters (A-C) signify differences among treatments ($p < 0.05$)

0.36 µmol $CO_2$ m$^{-2}$ s$^{-1}$ under two-year and four-year fire frequencies (respectively) in plots that were burned in the year of the study, and 5.3 ± 0.25 µmol $CO_2$ m$^{-2}$ s$^{-1}$ in long-term unburned plots. These values are generally similar in magnitude to previously reported growing season average values for productive grassland (Harper et al. 2005; Hoover et al. 2016; Knapp et al. 1998b).

Stimulation of soil $CO_2$ flux in the year of a fire persisted through following growing seasons. Under a two-year fire frequency, soil $CO_2$ flux was higher than in long-term unburned plots in plots burned in the current year ($p < 0.0001$) and plots burned in the previous year ($p = 0.0008$, Fig. 3), and soil $CO_2$ flux in plots burned in the current year did not differ from that in plots burned in the previous year ($p = 1.00$). Under the four-year fire frequency, fire stimulation of soil $CO_2$ flux had completely abated by the third year after fire. That is, soil $CO_2$ flux in plots burned three years ago was significantly lower than in plots burned in the current year ($p = 0.005$) and did not differ from long-term unburned plots (p = 1.00).

*Seasonal dynamics of soil $CO_2$ flux* As a general pattern, soil $CO_2$ flux tended to be higher with annual fire than with other fire frequencies throughout the growing season, though the magnitude of the difference among treatments varied (Fig. 2). Soil $CO_2$ flux was lowest, and the differences among treatments were the smallest, at the beginning of the growing season. As expected, soil $CO_2$ flux generally increased early in the season as soils warmed and fluctuated with precipitation, generally increasing following rainfall events and decreasing between events.

*Soil $CO_2$ flux in herbaceous vs. woody plant communities* In plots with both herbaceous and woody plant-dominated communities, soil $CO_2$ flux was about 45% higher in areas dominated by herbaceous vegetation than in areas dominated by woody vegetation (6.8 ± 0.43 µmol $CO_2$ m$^{-2}$ s$^{-1}$ and 4.7 ± 0.33 µmol $CO_2$ m$^{-2}$ s$^{-1}$, respectively, $p < 0.0001$, Fig. 3 inset). However, analyzing only fluxes from herbaceous communities (i.e., removing the effect of woody plant encroachment), did not alter our main findings (Fig. 3). Fire treatment still significantly affected soil $CO_2$ flux (df = 7, F = 14.02, $p < 0.0001$, online resource Table S2). Soil $CO_2$ flux was still higher in all treatments burned in the year of the study vs. long-term unburned plots and responded most strongly under an annual fire frequency (p < 0.0001 for annual fire treatment vs. all other fire treatments). Removing the effect of woody plant encroachment did alter the significance of the relationships between some of the 2-year and 4-year fire frequency treatments not burned in the year of our study.

*Soil responses to fire and fire history* Fire treatment did not significantly affect soil moisture or soil temperature (df = 7, F = 0.201, $p = 0.89$ and df = 7, F = 0.078, $p =$ 0.97, respectively, online resource, Figs. S2-S5). Soil

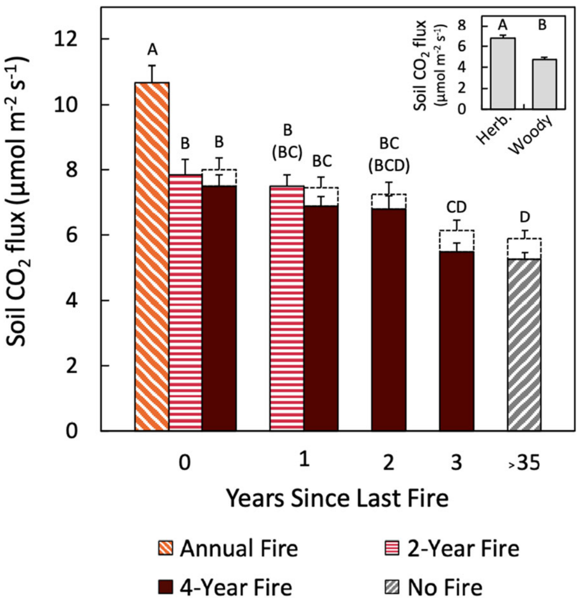


**Fig. 3** Soil $CO_2$ flux by long-term fire frequency and the number of years since the last fire. The filled, solid-outlined bars show overall growing season average from both herbaceous and woody plant communities (when both were present, weighted by estimated % cover + one standard error). The unfilled, dashed-outlined additions show the increase in soil $CO_2$ flux when only data from herbaceous plant communities is considered (+ one standard error); i.e., dashed bars represent how much higher soil $CO_2$ flux is if the effect of woody plant encroachment is removed/ignored. Different letters, A – D, signify a significant difference ($p < 0.05$) among treatments in overall soil $CO_2$ flux, letters in parenthesis indicate where and how significance changed when we analyzed only soil $CO_2$ flux from herbaceous-dominated areas. **Inset** Soil $CO_2$ flux from communities dominated by herbaceous vs. woody vegetation, from plots that contained both community types (growing season average + one standard error). The different letters, A – B, signify a significant difference between the two (p < 0.05)

moisture and temperature did not differ significantly from long-term unburned plots in any of the plots burned in the year of the study, regardless of historic fire frequency ($p > 0.05$ in all pairwise treatment comparisons). Under a four-year fire frequency, there was a trend toward higher average soil moisture and lower average soil temperature as the number of years since fire increased, but this was not statistically significant (p > 0.05 in all treatment comparisons). Soil moisture changed with precipitation, but the magnitude of change did not vary among treatments (online resource, Fig. S4). Soil temperature increased during the first half of the growing season and then remained fairly constant, and the magnitude of these changes did not vary among treatments (online resource, Fig. S5).

Fire frequency significantly affected soil organic C (df = 3, F = 9.06, $p = 0.002$, Table 1); soil organic C was higher with an annual fire frequency than with any of the other three fire frequencies tested ($p < 0.05$ in all cases). There were no statistically significant differences in total soil N or soil pH among fire frequencies (Table 1, F = 4.61, $p = 0.23$ and F = 0.233, $p = 0.91$, respectively). There were also no statistically significant effects of the number of years since the most recent fire on soil organic C, total N, or pH (F = 0.20, $p = 0.94$; F = 0.44, $p = 0.78$; and F = 0.23, p = 0.91, respectively).

*ANPP responses to fire and fire history* Fire treatment significantly affected total herbaceous ANPP (df = 5, F = 21.2, $p < 0.0001$, Fig. 4, online resource Table S3). We focus on herbaceous ANPP as there is very little woody plant biomass along these transects. Compared to long-term unburned grassland, ANPP was higher in the years of a fire under both an annual ($p < 0.0001$) and a four-year fire frequency ($p = 0.001$; no data available from a two-year fire frequency site). Unlike soil $CO_2$ flux, the magnitude of this response did not vary between annual and four-year fire frequencies ($p = 1.00$). Historic fire frequency did alter plant community composition, with forb ANPP higher in grassland burned every four years and in unburned grassland than in annually burned grassland, and fire treatment significantly affected grass ANPP (df = 5, F = 60.3, p < 0.0001, online resource Table S4). Thus, although grass ANPP in the year of a fire was higher under an annual fire regime than a four-year fire regime ($p = 0.0002$), consistent with the soil $CO_2$ flux response, total herbaceous ANPP was not. The long-term average annual total herbaceous ANPP in the year of a fire was 593 ± 23.2 g m$^{-2}$ (grass ANPP: 576 ± 11.3 g m$^{-2}$) under an annual fire regime and 559 ± 29.7 g m$^{-2}$ (grass ANPP: 410 ± 9.0 g m$^{-2}$) under a four-year fire regime. Average annual total herbaceous ANPP in long-term unburned grassland was 383 ± 19.7 g m$^{-2}$ (grass ANPP: 251 ± 5.7 g m$^{-2}$). Unlike soil $CO_2$ flux, the stimulation of ANPP in the year of a fire did not persist into the following years. Under a four-year fire frequency, ANPP only differed significantly from long-term unburned grassland in the year of the fire ($p = 1.00$ for 1, 2, and 3 years since fire vs. long-term unburned grassland). This was true for both grass and total herbaceous ANPP.

## Discussion

We have long known that ecosystem responses to key biotic and abiotic drivers can be mediated by ecosystem history, particularly in grasslands (e.g., Knapp et al. 1998a; Lauenroth and Sala 1992; Sala et al. 2012; Seastedt et al. 1991). In this study, we attempted to distinguish the effects of two aspects of fire history, long-term fire frequency and the number of years since the most recent fire, on mesic grassland soil $CO_2$ flux and its response to a fire. We found that, while fire increased soil $CO_2$ flux in all burned plots (compared to long-term unburned plots), soil $CO_2$ flux responded more strongly to fire with long-term annual burning than with less frequent burning (once every two or four years). The stimulatory effect of fire persisted through the growing season and into subsequent years (i.e., soil $CO_2$ flux was still elevated in plots burned in previous years). In contrast, stimulation of ANPP by fire did not differ between grassland historically burned annually and burned once every four years (compared to long-term unburned grassland) and ANPP stimulation did not persist into subsequent years. The difference in ANPP vs. soil $CO_2$ flux responses emphasizes the importance of directly quantifying multiple ecosystem processes

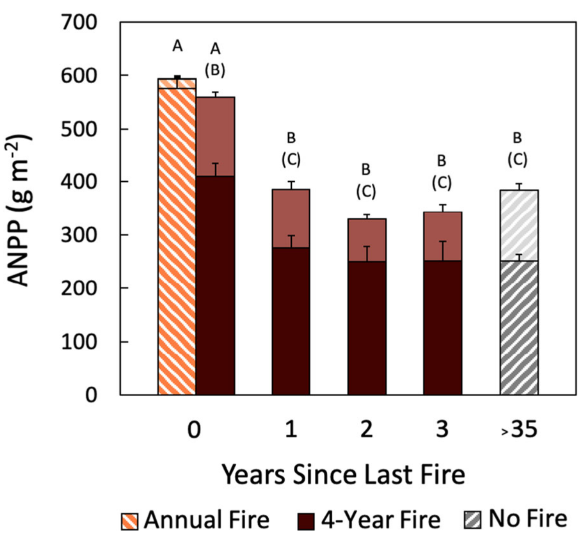


**Fig. 4** Annual herbaceous ANPP, by fire frequency and the number of years since the last fire. The bottom darker-colored segments show average (+ one standard error) grass ANPP. The top lighter-colored segments show average (+ one standard error) forb ANPP. Different letters signify a significant difference ($p < 0.05$) among treatments in total herbaceous ANPP, letters in parenthesis indicate where and how significance changed when we analyzed only grass ANPP

rather than assuming that different fluxes respond similarly to a disturbance. The strong impact of past fire frequency on soil $CO_2$ flux shows that history can affect responses to future fires and is important to consider when predicting fire impacts.

Our study is distinguished from previous grassland fire and soil $CO_2$ flux research by its simultaneous assessment of very fine-scale differences in fire frequencies and time since fire. Previous studies have often focused on burned vs. unburned comparisons (e.g., before vs. after wildfire or burned vs. unburned areas) or coarse categories of fire frequency (e.g., frequent vs. infrequent). Our findings show that the impacts of fire are more nuanced than simply burned or unburned, or even frequent vs. infrequent burning. Indeed, our results show that even minimal frequency differences can have significant impacts on soil $CO_2$ flux. Though this result will not apply in all cases (see our ANPP results), it suggests that future fire and disturbance studies should assess changes at very fine temporal scales.

In general, increased soil $CO_2$ flux after fire likely results at least in part from fire stimulating plant productivity. Here, we expand on earlier observations of increased grassland ANPP after burning (Hulbert 1986; Knapp and Seastedt 1986; Knapp et al. 1998b) using a > 30-year dataset. Though comparable long-term records of belowground production do not exist for our study site, several individual studies have found greater root biomass in burned than in unburned grassland (Hadley and Kieckhefer 1963; Hayes and Seastedt 1987; Johnson and Matchett 2001; Kitchen et al. 2009; Kucera and Dahlman 1968; Ojima et al. 1994). In addition, annual fire at our study site has been shown to increase the dominance of grasses (Collins et al. 1998), which have particularly high root: shoot ratios. Thus, increased allocation of NPP belowground likely contributed to elevated soil $CO_2$ flux with annual burning. A few studies have also found increased soil microbial C following fire in tallgrass prairie (Garcia and Rice 1994; Ojima et al. 1994). The higher soil C content that we found with annual burning could be due in part to higher NPP increasing substrate availability and microbial C. It is thus likely that a combination of increased belowground plant production and microbial abundance and/or activity contributed to the stimulation of soil $CO_2$ flux after fire. Some support for this is provided by recent work suggesting that fire regime influenced a grassland soil bacterial community more than any single fire (Qin et al. 2019).

Though the general increase in soil $CO_2$ flux following fire is consistent with the increase in ANPP, these two major fluxes did not mirror each other in their responses to fire. Compared to unburned grassland, the relative increase in ANPP after fire was smaller than the increase in soil $CO_2$ flux under an annual fire frequency (55% vs. 100%, respectively), but larger than the increase in soil $CO_2$ flux under a four-year fire frequency (46% vs. 41%, respectively). This demonstrates that belowground impacts cannot always be reliably predicted from aboveground impacts, likely because different factors control belowground vs. aboveground responses to fire. This may have consequences for long-term ecosystem C sequestration. The higher soil C content with annual burning indicates that increased production has offset the high soil $CO_2$ flux. Previous studies have reported a range of positive to negative impacts of fire on soil C, depending on factors including vegetation, soil type, and the frequency and total number of fires (Pellegrini et al. 2018; McCarron et al. 2003; Richards et al. 2011; Jackson et al. 2002). Indeed, previous research at our study site found no change in soil C with fire frequency (Kitchen et al. 2009), in contrast with our results, but we sampled from plots where fire treatments have been maintained for more than twice as long. However, a recent global synthesis did find a general decline in grassland soil C with elevated fire frequency vs. fire suppression (Pellegrini et al. 2018), and recent research near our study site produced similar results (Connell et al. 2020). Our findings do not follow this pattern, possibly because those studies sampled to greater soil depths than we did, but they are generally consistent with an increase in soil $CO_2$ flux and with the biological changes discussed above (NPP, soil microbes). We sampled relatively shallow soil (0–10 cm) because most root biomass and soil C occurs at this depth at our study site (Kitchen et al. 2009; Johnson and Matchett 2001; Smith and Johnson 2004), and we expect that most soil $CO_2$ is produced here (Fang and Moncrieff 2005). We thus reasoned that this shallow depth would best explain differences in soil $CO_2$ flux among treatments. Soil C from deeper depths may differ from what we report here. Soil $CO_2$ flux was the focus of this study, and additional research is required to fully understand the impacts of fire history on grassland total soil C stocks.

The difference in soil $CO_2$ flux among fire regimes occurred despite little difference in soil moisture and soil temperature. Soil moisture and temperature varied with the weather throughout the growing season, and soil $CO_2$ flux generally followed this variation, but growing season average soil moisture and temperature did not differ among treatments. This is consistent with previous research at this site, which found that microclimatic impacts after fire are relatively short-lived, resulting in little difference in average soil water content over the course of a growing season (Knapp 1985, 1986). Our results thus suggest that factors such as NPP amount and allocation, soil microbial abundance and/or activity, and soil C (all discussed above) play a larger role than soil microclimate in driving variation in the soil $CO_2$ flux response to fire.

The encroachment of woody vegetation into grass-dominated ecosystems is a prominent conservation concern. Frequent fires play a pivotal role in preventing woody encroachment into grasslands, including our study site (Bragg and Hulbert 1976; Briggs et al. 2005; Fuhlendorf et al. 2011; Hulbert 1986; Ratajczak et al. 2014). Though invasion by woody plants can increase aboveground production and C storage, this C is highly susceptible to rapid loss from fire or other removal methods (Fuhlendorf et al. 2011). Previous studies have measured lower soil $CO_2$ fluxes in shrub-encroached areas than in open grassland, possibly due to differences in litter quality, microclimatic alterations, or faster decay rates in grassy areas (Lett et al. 2004; McCarron et al. 2003; Norris et al. 2001; Smith and Johnson 2004). Consistent with these previous studies, we found lower soil $CO_2$ fluxes in vegetation patches dominated by woody plants vs. by herbaceous plants. However, this difference did not explain the overall higher soil $CO_2$ flux in more frequently burned grassland. That is, shrub encroachment contributed to, but was not entirely responsible for, significantly lower soil $CO_2$ fluxes with less frequent fire.

Our results suggest a different relationship between fire and soil $CO_2$ flux in grasslands than in forests. Previous research in forest and woodland ecosystems has often found that fire has little to no effect on soil $CO_2$ flux (Irvine et al. 2007; Plaza-Álvarez et al. 2017; Sun et al. 2016). Others have found that repeated infrequent fire, not frequent fire, elevate soil $CO_2$ flux above unburned levels (10-year vs. 3-year fire frequency; Fest et al. 2015), and that soil $CO_2$ flux generally tends to increase with stand age/time since fire (Gough et al. 2007; O'Connell 1987), contrary to what we found. Our results may thus be specific to fire-maintained, grass-dominated ecosystems. Removal of litter by fire has a disproportionately large positive effect on production in mesic grasslands (Knapp and Seastedt 1986; Hulbert 1969). It seems that frequent litter removal may also increase soil $CO_2$ flux more in productive grasslands than in other biomes.

In summary, we found that even subtle differences in historic fire frequency can significantly alter the response of grassland soil $CO_2$ flux to fire, and that fire history altered ANPP and soil $CO_2$ flux differently. Ongoing changes to fire regimes will have important consequences for ecosystem dynamics, including those that affect the global terrestrial C cycle. Knowing how historic fire regimes may alter responses to future fires can improve Earth system modeling, management decision making, and C accounting, which can ultimately lead to more accurate predictions of fire impacts and better management outcomes.

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**Data availability** The data generated during this study are available in the Colorado State University Libraries repository [https://doi.org/10.25675/10217/203620], and the ANPP data analyzed for this study are available from the LTER Network Data repository [https://doi.org/10.6073/pasta/38de94ec00e7d553197910b835c37b7d].

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