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Abstract. Burning and mowing are two of the most common grassland disturbances across millions of hectares worldwide, but uncertainty remains about when and why these disturbances increase plant production. One of the main hypotheses for increased plant production is that disturbances increase soil temperature in the early growing season and thereby increase plant growth. I tested this hypothesis using a multi-decade study of the frequency (annual or quadrennial) and season (spring, summer, or autumn) of reconstructed tallgrass prairie burning and mowing. To determine plant production, I measured above-ground biomass during three periods of the 2015 growing season: (1) prior to mid-May; (2) mid-May to early July; and (3) early July to the end of the growing season in late September. I also measured soil temperatures from May 2014 to January 2016. This unique dataset allows a detailed picture of when burning and mowing are increasing plant production and whether these increases are likely caused by soil temperatures. I found that, compared to other treatments, autumn burning and mowing similarly increased plant production from the beginning of the growing season to mid-May (autumn disturbances increased production from 37 to 77 g/m^2) and, compared to other treatments, both autumn and spring burning and mowing similarly increased plant production from mid-May to early July (autumn and spring disturbances increased production from 363 to 439 g/m^2). Mowing had little effect on soil temperature but burning increased average daily maximum soil temperature at 2.5 cm depth by 6.4°C in the month after burning. Overall, these results suggest that burning did not increase early growing season plant production due to increased soil temperature, given that mowing similarly affected plant production but did not similarly affect soil temperature. I explore alternate explanations for changes in plant production, including increased light and nutrient availability, and decreased detritus.

Key words: burning; detritus; disturbance frequency; disturbance season; mowing; plant production; prescribed fire; reconstructed tallgrass prairie; soil temperature.

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Introduction

Grasslands require disturbance to prevent woody plant encroachment (Bragg and Hulbert 1976), and burning and mowing are two of the most common grassland management techniques. For example, millions of hectares of prairie are burned every year in central North America, primarily to prevent woody plant encroachment and improve cattle forage (Mohler and Goodin 2012). As another example, approximately 7 million hectares of federally managed roadsides in the USA are mowed to prevent woody plant encroachment, improve visibility, and reduce the likelihood of fires from discarded cigarettes and other ignition sources (Ament et al. 2014). Both burning and mowing can increase plant production, depending on the season and frequency of disturbance. Annual burning in the spring has been shown to increase prairie plant production relative to unburnt prairie (Anderson et al. 1970, Launchbaugh and Owensby 1978), and a more recent study suggests that annual autumn and winter burning increase prairie plant production the same amount as spring burning (Towne and Craine 2014, but see Towne and Owensby 1984). Spring mowing tends to increase plant production the first time it occurs (Rice and Parenti 1978, Hover and Bragg 1981), but may increase or decrease plant production in subsequent years, depending on the frequency of mowing and the defoliation history of the land (Ehrenreich and Aikman 1963, Seastedt et al. 1993). The increased plant production that occurs after spring and autumn burning and mowing has been hypothesized to be caused by the increased soil temperatures in the early growing season (Rice and Parenti 1978).

The effect of burning and mowing on soil temperature varies by soil depth, time of the day, and time since disturbance. Soil temperatures can increase to a depth of 7.5 cm in the weeks after burning or vegetation removal via clipping (Sharrow and Wright 1977, Rice and Parenti 1978). Burning appears to increase afternoon (maximum) soil temperature in the spring and summer months after a burn but has little effect on sunrise (minimum) soil temperature (Kucera and Ehrenreich 1962). However, in the winter burning may reduce sunrise (minimum) soil temperature because there is evidence that removal of the detritus layer can decrease soil temperature (Kohnke and Werkhoven 1963) and thereby lead to increased mortality of fine roots (Tierney et al. 2001, Cleavitt et al. 2008). Finally, the effect of burning and mowing on soil temperature decreases as vegetation regrows (Ehrenreich and Aikman 1963).

Burning and mowing in the dormant season has been hypothesized to increase early growing season plant production at least partly because of warmer soil temperatures (Rice and Parenti 1978). The effect of burning on plant production has received much more attention than the effects of mowing, and most researchers suggest that multiple factors likely increase plant production after burning. For example, Knapp (1984) found that spring burning increases the percentage of light availability the same amount as the percentage of plant production, and that spring burning decreased June leaf temperatures and water stress. Hulbert (1988) completed experiments to attempt to isolate the effects of increased soil temperature, available nitrogen, and light levels on increased plant production after burning and found that each could potentially increase plant production. As another example, Knapp and Seastedt (1986) reviewed evidence for effects of soil temperature, available nitrogen, light levels, and microclimate due to detritus and found that changes in each could potentially increase plant production after a burn. Other studies have also suggested that at least part of the effects of burning and mowing on plant production are due to increased soil temperatures (Abrams et al. 1986, Svejcar 1990, Fuhlendorf and Engle 2001). Although most of these studies suggest increased soil temperatures are increasing early growing season production, none of them focus on early growing season production. Rather, they examine cumulative plant production across the entire growing season. Therefore, these studies cannot definitively show that burning is primarily increasing plant production in the early growing season due to warmer soil temperatures. Also, these studies do not continuously measure soil temperature, which further complicates efforts to determine whether changes in soil temperature cause changes in plant production. In the current study, I separately examine plant production in the early spring, late spring, and summer, and I continuously measure soil temperature. Therefore, I can focus on measuring the effects of disturbance and soil temperature on plant production during different periods of the growing season.

Hypotheses

In order to examine the effects of burning and mowing on plant production during different seasons, I harvested biomass before spring, summer, and autumn disturbances in 2015. In order to examine soil temperature, I installed temperature probes into every replicate of the experiment and measured soil temperature every 155 min from May 2014 to January 2016, and I installed separate temperature probes to measure soil temperature every minute during burns. I hypothesize that earlier increases in soil temperature will cause earlier photosynthetic activity (green-up) and greater plant production early in the growing season. Therefore, I predict that burning will increase early growing season plant production by removing detritus and thereby increasing soil temperature, but I predict that mowing will have minimal effects on early growing season plant production because mowing does not remove detritus and so soil temperature should be minimally affected. Finally, I hypothesize that soil temperature during burns will not become hot enough to cause root mortality.

Methods

Experimental site

This study was completed at the University of Nebraska at Omaha (UNO) Glacier Creek Preserve near Omaha (96°8′29.4″W, 41°20′23.8″N). From 1978 to 2016, yearly precipitation averaged 78.8 cm with 74% of precipitation falling between April and September (Eppley Airport Weather Station, Omaha, Nebraska, USA). Average monthly low and high air temperatures ranged from −10°C to 0°C in January and from 19°C to 31°C in July. Air temperatures during the study were similar to historic averages (Appendix S1: Fig. S1). The Preserve had been in cultivation for many decades prior to restoration, alternating between corn (*Zea mays*) and soybeans (*Glycine max*). In the spring of 1970, 52 ha of the Preserve was taken out of cultivation and planted to tallgrass prairie grasses (planted with seed mix of *Andropogon gerardii, Bouteloua curtipendula, Panicum virgatum, Schizachyrium scoparium,* and *Sorghastrum nutans*). In 1978, 2.7 ha of the Preserve was set aside to establish the long-term study reported here. In 1979, *Amorpha canescens, Aster ericoides, Baptisia lactea, Dalea candida, Desmodium illinoense, Gentiana puberulenta, Potentilla arguta,* and *Rudbeckia hirta* were seeded into the plots and three transplants of *Hesperostipa spartea* were added to each plot (further seeding details in Dickson et al. 2019). No other vegetation management occurred in the plots, other than the burning and mowing treatments, except for yearly tree sapling stump herbicide application to prevent woody encroachment, primarily in the control plots. There are no large mammal grazers (e.g., cattle) at the Preserve other than a few deer (*Odocoileus virginianus*), and plant biomass removal due to animals should mostly occur from insect or rodent herbivores.

The study area is situated on a north- and east-facing aspect with slopes varying from 6–16%. All plots have a 2 m wide walkway of mown vegetation surrounding them, and plots are not all the same size but are generally rectangular, with a median size of 400 m^2 (31.5 × 12.7 m) and with 82% of the plots being within 100 m^2 of this size (Appendix S1: Fig. S2). Soils of the study area are primarily loess-based, silty clay loams and clay loams of either the Burchard-Contrary-Steinauer complex or the Contrary-Marshall silty clay loam complex (NRCS and USDA 2016). In 1982, a fire study was begun on the site with burns occurring at different seasons (spring, summer, or autumn) and at different frequencies (every year to every 10 yr). There were also unburned control treatments, even though I acknowledge that lack of disturbance does not represent the historical condition of prairie. In 2002, the treatments of some of the plots were changed to incorporate a mowing aspect to the study, and to create a fully factorial combination of burning and mowing seasons and frequencies. The current configuration of the study is a factorial combination of disturbance type (burning or mowing) × frequency (every year or every 4 yr) × season (spring, summer, or autumn). There is also a control treatment in which no burning or mowing occurs. The factorial treatments and control treatment combine to 13 treatments, and each treatment is replicated in 3 plots for 39 total plots (Appendix S2: Table S1 shows the original treatments initiated in 1982 and how they were changed in 2002). Although the treatments of some plots were changed in 2002, this should have little effect on results reported here because I collected data from 2014 to 2016 after every treatment had been in place for at least 13 yr.

Burning and mowing methods

Burning occurred by igniting the edge of the plots with a drip torch and allowing a backfire to burn through either the entire plot or a sufficient area to then ignite a headfire through the remainder of the plot. Based on the biomass collection data (methods described in *Data collection: biomass and light levels*), there was a higher fuel load (more detritus) in the quadrennially burned vs.

annually burned plots (245 g/m^2 vs. 535 g/m^2 detritus, respectively). Not surprisingly, the ratio of live biomass to dead detritus was lower in the quadrennially burned vs. annually burned plots (0.28 vs. 0.73 live:dead, respectively), and the ratio of live biomass to dead detritus was lower in the spring burns vs. summer burns (0.06 vs. 0.96 live:dead, respectively), with no live biomass present during autumn burns. Burns varied depending on weather conditions, with backfires used for spring and autumn burns to facilitate better fire control. Summer burns were headfires because green vegetation reduced the need for fire control and because backfires did not carry well through green vegetation. Burning always occurred at least 2–3 d after precipitation or snow melt and occurred on days with low wind speeds (5–20 km per hour). During burning, spring relative humidity was 25–35%, summer relative humidity was 50–60%, and autumn relative humidity was 40–50%. Mowing occurred by cutting all vegetation to approximately 10 cm height, and the vegetation was mulched and left in place by the lawnmower.

Data collection: biomass and light levels

Biomass from each plot was harvested to ground level in mid-May, mid-June, and late-September 2015. Harvests were completed with hand shears in randomly placed 0.25 × 1 m quadrats and all plants rooted within the quadrat were clipped, as well as all detritus laying within the quadrat. Biomass produced in the current year (i.e., 2015) was sorted to species, and biomass not produced in the current year was classified as detritus. Detritus was differentiated from current-year biomass by examining whether any part of each plant was green and by visually examining whether decomposition patterns were consistent with plants having been produced in the previous year(s).

To estimate the amount of aboveground plant production that occurred between seasonal burning and mowing disturbances, two calculations were necessary: (1) To estimate the amount of live aboveground biomass from the June and September harvests that had been produced since the previous harvest, the amount of live aboveground biomass from the previous harvest was subtracted from the current harvest for each plot, unless burning or mowing had occurred since the last harvest, in which case live aboveground biomass from the previous harvest was not subtracted because the disturbance had destroyed the live aboveground biomass present in the previous harvest; (2) the number of days of plant growth varied between plots for each harvest because the managers of the experiment mowed 4–8 d after each seasonal burn, meaning burned plots had more days of growth until the next harvest than did mown plots. Also, biomass harvests generally occurred over multiple days to prevent biomass from decomposing before it was sorted. For each harvest, a linear regression was used to examine the predictive ability of days since the previous harvest/disturbance on aboveground plant production. On average, aboveground plant production increased 9.5 $g \cdot m^{-2} \cdot d^{-1}$ before the May harvest, 12.0 $g \cdot m^{-2} \cdot d^{-1}$ between the May and June harvests, and 5.8 $g \cdot m^{-2} \cdot d^{-1}$ after the June harvest. I used these daily production values to add or subtract the appropriate number of days of plant production from each harvest to estimate 2015 aboveground plant production until May 11 (average date of spring disturbance), aboveground plant production from May 11 until July 2 (average date of summer disturbance), and aboveground plant production from July 2 until September 26 (date of final harvest). For example, if a plot was harvested two days before May 11 and contained 70.0 g/m^2 of live aboveground biomass, I added 19.0 g/m^2 of production to estimate how much more would be produced by May 11 (i.e., 89.0 g/m^2 total). Results are generally similar between corrected and uncorrected plant production data (Appendix S1: Fig. S3), although corrected data should more accurately depict production between disturbances. From here onwards, I only present results for aboveground plant production corrected for days between harvests/disturbances.

The depth of detritus in each plot was measured 12 May 2017 by using a ruler to measure the depth at which detritus no longer prevented me from reading the ruler (Appendix S1: Fig. S4). Detritus depth was measured from nine randomly located points within each plot, and these nine points were then averaged to calculate a plot average.

The percentage of photosynthetically active radiation (PAR) reaching ground level was measured from plots in 4 October 2014, 16 June 2015, and 22 April 2018 using an AccuPAR LP-80 ceptometer (Decagon Devices, Pullman, Washington, USA). Four measurements were collected above the plant canopy of each plot and another four at ground level (below most detritus) between 11 am and 2 pm on cloudless days, and the percentage of PAR reaching ground level is presented. The ceptometer is 1 cm in height and therefore could not be pushed below the bottom 1-cm layer of detritus.

Data collection: soil temperature

All soil temperature data were collected using Maxim Integrated (San Jose, California, USA) Thermochron iButtons model DS1921G-F5. These iButtons can collect 2048 readings from −40°C to 85°C, with an accuracy of ±1°C when temperatures are between −30°C and 70°C. I used two sets of iButtons, one for long-term monitoring over many months and another for short-term monitoring of soil temperatures during burns. For long-term monitoring, I programmed iButtons to record soil temperatures every 155 min, and iButtons were buried to 2.5 cm because this depth is similar to many studies (DeBano et al. 1979, Savadogo et al. 2007, Ohrtman et al. 2015). Data collection required connecting iButtons to a Maxim Integrated DS1402D reader, which required removing the iButtons from the soil approximately every six months. The data were not recovered from long-term iButtons that could not be found or where the battery failed due to cold temperatures or moisture infiltration and on average 22% of plots did not contain usable temperature data for each long-term collection period (data shown in Data S1). When an iButton failed, it was discarded and a new iButton was reinserted for the next collection period. For short-term monitoring during burns, I programmed a separate set of iButtons to record soil temperatures every minute, buried iButtons to 1 cm and to 2.5 cm depth, and determined the minute the fire passed over the iButtons by examining when fire began to increase the 1 cm depth iButton temperature. Further iButton methods are in Appendix S3.

Data analysis

All analyses were conducted in SAS 9.4 (Cary, North Carolina, USA), and SAS code and data are shown in Data S1. For plant production analyses, the MIXED procedure was used to analyze plant production since each disturbance. I used a three-way analysis of variance (ANOVA) with burn vs. mow, season, and frequency as predictors. Although graphs show plant production from each functional group (C_4 graminoids, C_3 graminoids, and forbs), only total plant production data since the previous disturbance were analyzed statistically. Detritus depth and PAR analyses utilized the same three-way ANOVA used for plant production analyses. For long-term temperature analyses, the MIXED procedure was used to analyze daily maximum and minimum temperatures by month, and I used a repeated-measures four-way ANOVA with burn vs. mow, season, and frequency as predictors and month as a repeated-measures predictor. For short-term temperature analysis, the MIXED procedure was used to analyze the maximum temperature that occurred during the burn, and I used a split-plot three-way ANOVA with season and frequency as whole-plot predictors and soil depth as a split-plot predictor. Data for detritus depth data were $\log_{10}$ transformed to improve normality. Least squares means and standard errors were calculated in SAS using the LSMEANS statement. All analyses used the Kenward and Roger (1997) procedure to determine degrees of freedom, in part because this procedure handles missing data well.

For the plant production data, contrast statements were used in SAS to compare effects of particular treatments. However, given the difficulty of interpreting interactions across the many months of long-term temperature data, pairwise comparisons were completed to test a priori hypotheses regarding the effects of burning and mowing treatments. I completed a priori tests of the effects of each disturbance on soil temperatures in the month preceding disturbance and four growing season months following each disturbance, as well as testing the effects of autumn burning and mowing on minimum soil temperatures in the winter. Burning and mowing treatments were compared to the control treatment because I wanted to compare the presence of disturbance to the absence of disturbance, and the control treatment showed the effects of the absence of disturbance with soil temperatures that were very similar to treatments that had not been disturbed for many months. I compared to the control treatment by calculating 99.9% confidence intervals using the experiment wise standard error estimated for a particular month. To be conservative, I used 99.9% rather than the standard 95% confidence intervals because even though the analyses were a priori, a number of monthly comparisons were completed. To be conservative, I also calculated confidence intervals as if I were conducting *t*-tests across just six replicates in 2014 (three annual treatment replicates + three control replicates), and across just nine replicates in 2015 (three annual treatment replicates + three quadrennial treatment replicates + three control replicates). Overall, this meant that if the mean of a 2014 annual treatment was more than 8.610 standard errors ($t_{4,\ 0.001}$) apart from the control or if the mean of a 2015 average annual + quadrennial treatment was more than 5.408 standard errors ($t_{7,\ 0.001}$) apart from the control, then I reported the treatment as being different than the control.

Results

Seasonal plant production

Before spring disturbances, total plant production was only significantly affected by the season of disturbance (Fig. 1A; Appendix S2: Table S2). Plant production was increased by autumn disturbances but not other seasons of disturbance (contrast of autumn disturbance vs. spring/summer disturbance: $P < 0.001$). A visual examination of the data suggests that most plant

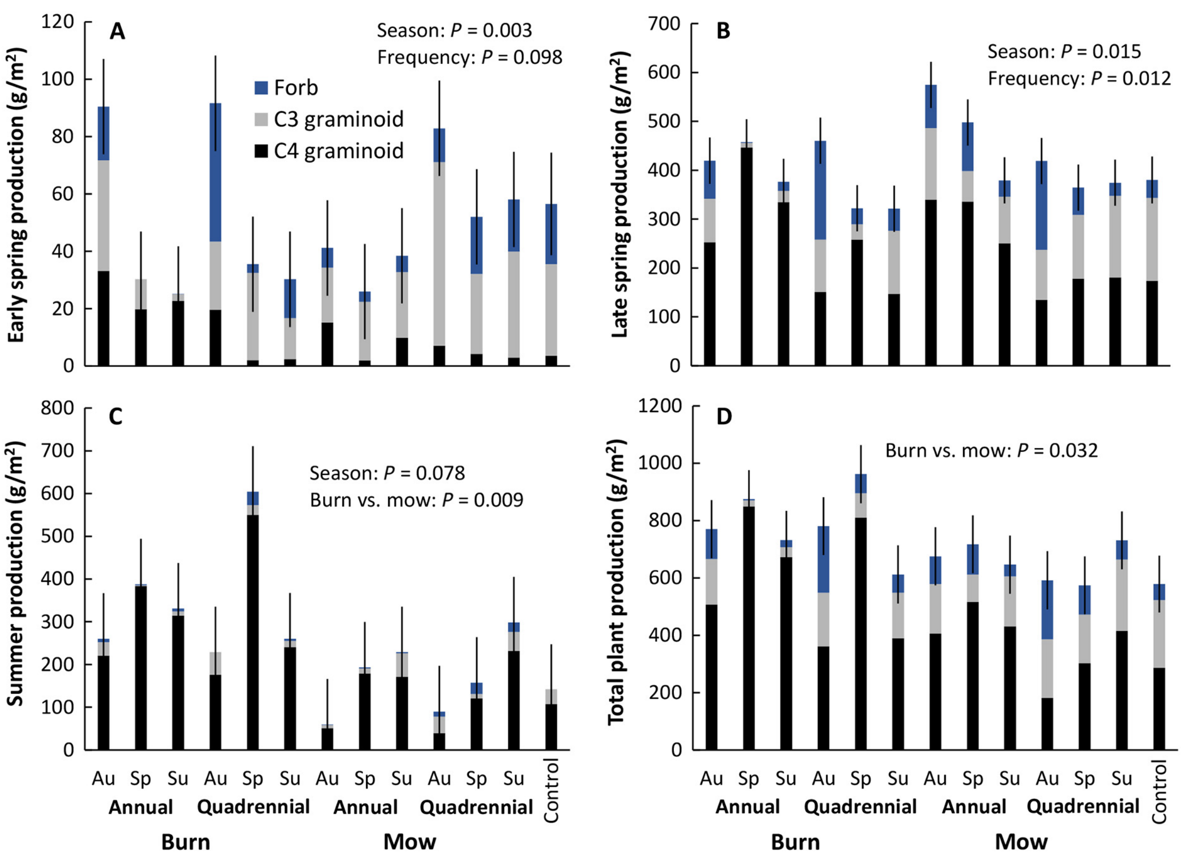

Fig. 1. Corrected 2015 plant production during three periods of the growing season (A–C) and across the entire 2015 growing season (D). Error bars are ±1 SE and only *P*-values <0.10 are shown. Although plant production from forb, C_3 graminoid, and C_4 graminoid functional groups are shown individually, error bars and statistics all refer to the sum of these three groups. Note the *y*-axis scale differs between panels.

production was from forbs and C_3 graminoids, with less production from C_4 graminoids (Fig. 1A).

Between the spring and summer disturbances, total plant production was only significantly affected by the season of disturbance and frequency of disturbance (Fig. 1B; Appendix S2: Table S2). Plant production was higher after autumn than summer disturbances (contrast of autumn disturbance vs. summer disturbance: $P = 0.004$) but was not much different between autumn and spring disturbances (contrast of autumn disturbance vs. spring disturbance: $P = 0.096$) or between spring and summer disturbances (contrast of spring disturbance vs. summer disturbance: $P = 0.167$). The significant frequency effect shows that plant production was higher after annual than quadrennial disturbances. A visual examination of the data suggests that most plant production was from C_4 graminoids, although this varied somewhat by treatment (Fig. 1B).

After the summer disturbance, total plant production was significantly higher in the burned than mown treatment (Fig. 1C; Appendix S2: Table S2). The season of disturbance also had some effect on plant production, with higher plant production after spring than autumn disturbances (contrast of autumn disturbance vs. spring disturbance: $P = 0.028$) and with plant production after summer disturbances not being significantly different than spring or autumn disturbances (contrast of summer disturbance vs. other seasons: $P > 0.100$). A visual examination of the data suggests that most plant production was from C_4 graminoids (Fig. 1C).

Across the entire 2015 growing season, total plant production was only significantly affected by the burn vs. mow treatment (Fig. 1D; Appendix S2: Table S2), with higher plant production in the burned than mown treatment. A visual examination of the data suggests that most plant production across the entire 2015 growing season was from C_4 graminoids, although this varied by treatment, with burned treatments on average having more C_4 graminoid production than mown treatments (Fig. 1D).

Although the control treatment was not part of the analyses, a visual examination of the data suggests that plant production in the control treatment was generally similar to production in mown plots that had been disturbed the longest time ago (Fig. 1A–D).

Long-term maximum temperature

Average daily maximum soil temperature at 2.5 cm depth always increased after burning and sometimes increased after summer mowing (Fig. 2A). Every treatment interaction with month was highly significant ($P < 0.001$) because treatment effects were largest in the month following disturbance and treatment effects then lessened through time as vegetation regrew (Table 1). Akaike information criterion (AIC) scores indicate that the treatment interactions with month were most important for improving model fit (Appendix S2: Table S3), suggesting that any explanation of treatment effects should focus on the months during which treatments had large effects. Therefore, the following is an examination of the effects of individual treatments by month, remembering that only annual disturbances occurred in 2014, whereas both annual and quadrennial disturbances occurred in 2015. Relative to the 99.9% confidence intervals around the control treatment, annual autumn burning increased post-burn daily maximum soil temperature in May 2014, annual spring burning increased post-burn daily maximum soil temperature from May to July 2014, and annual summer burning increased post-burn daily maximum soil temperature from July to August 2014. When examining the combined effects of annual and quadrennial burns relative to the 99.9% confidence intervals around the control treatment, autumn burning increased post-burn daily maximum soil temperature from March to April 2015 and in June 2015, spring burning increased post-burn daily maximum soil temperature in June 2015, and summer burning increased post-burn daily maximum soil temperature in July 2015. Relative to the 99.9% confidence intervals around the control treatment, neither annual autumn nor annual spring mowing increased 2014 daily maximum soil temperature, but annual summer mowing increased post-mowing daily maximum soil temperature from July to August 2014. When examining the combined effects of annual and

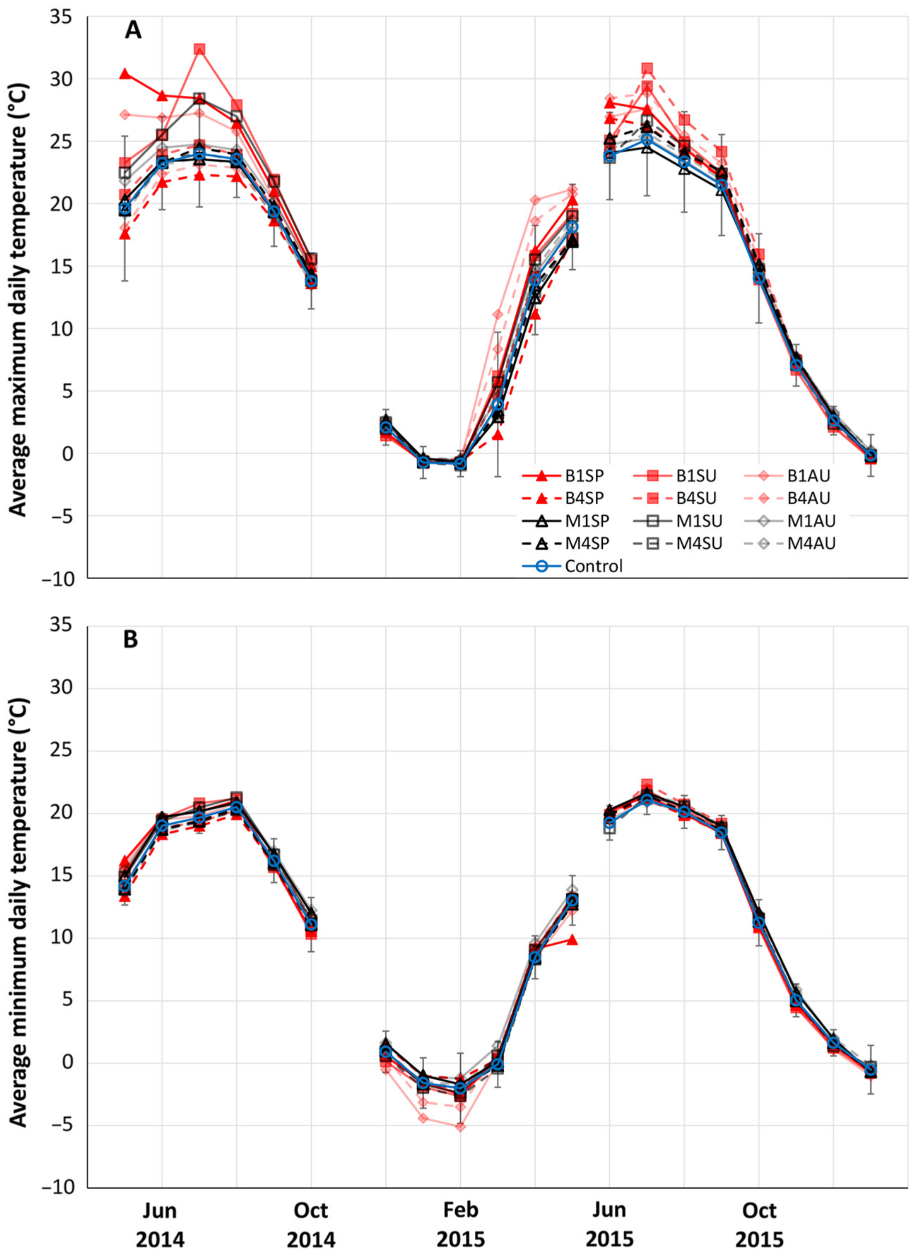

Fig. 2. The average daily maximum (A) and minimum (B) temperature at 2.5 cm soil depth, averaged across different months from May 2014 to January 2016. Error bars are 99.9% confidence intervals (see description in Methods) and are only shown around control treatments to reduce clutter. Lines just connect points and are for visual purposes only. The two breaks in lines connecting months represent the two periods during which iButtons were temporarily removed from the soil to collect data. The first letter in the treatment codes indicates burning or mowing, the number indicates annual or quadrennial disturbances, and the final letters indicate spring, summer, or autumn disturbance. Given the large number of significant interactions with months, statistical output is shown in Table 1.

Table 1. The effects of treatments and the month of measurements on long-term soil temperatures.

Predictor variables	Maximum soil temperature			Minimum soil temperature		
	F	df	*P*	*F*	df	*P*
Burn vs. Mow	**24.5**	**1, 43.3**	**<0.001**	**10.1**	**1, 48.3**	**0.003**
Frequency	**33.8**	**1, 44.1**	**0.001**	**5.1**	**1, 49.2**	**0.029**
Season	**6.3**	**2, 42.8**	**0.004**	0.5	2, 47.8	0.624
BvM × Freq	**8.1**	**1, 44.1**	**0.007**	**7.4**	**1, 48.2**	**0.009**
BvM × Seas	2.3	2, 43.5	0.116	**7.3**	**2, 47.4**	**0.002**
Freq × Seas	1.4	2, 43.2	0.265	0.5	2, 47.1	0.584
BvM × Freq × Seas	**11.6**	**2, 44.3**	**0.001**	1.6	2, 45.5	0.213
Month	**10173.6**	**19, 90.7**	**<0.001**	**11706.6**	**19, 88.8**	**<0.001**
Month × BvM	**9.3**	**19, 91.9**	**<0.001**	**9.1**	**19, 89.6**	**<0.001**
Month × Freq	**29.6**	**19, 91.5**	**<0.001**	**19.5**	**19, 89.2**	**<0.001**
Month × Seas	**8.7**	**38, 117**	**<0.001**	**6.3**	**38, 115**	**<0.001**
Month × BvM × Freq	**13.0**	**19, 92.8**	**<0.001**	**8.9**	**19, 90.4**	**<0.001**
Month × BvM × Seas	**3.5**	**38, 119**	**<0.001**	**3.5**	**38, 116**	**<0.001**
Month × Freq × Seas	**5.4**	**38, 118**	**<0.001**	**3.1**	**38, 115**	**<0.001**
Month × BvM × Freq × Seas	**4.9**	**30, 122**	**<0.001**	**3.0**	**30, 120**	**<0.001**

Note: Bold terms indicate effects where $P < 0.050$. The degrees of freedom include decimals because SAS used some degrees of freedom to model ARH(1) covariance structure between months and treatments.

quadrennial mowing relative to the 99.9% confidence intervals around the control treatment, autumn, spring, and summer mowing did not affect 2015 daily maximum soil temperature.

Long-term minimum temperature

Average daily minimum soil temperature at 2.5 cm depth generally increased after burning and never increased after summer mowing (Fig. 2B). Every treatment interaction with month was highly significant ($P < 0.001$) because treatment effects were largest in the month following disturbance and treatment effects then lessened through time as vegetation regrew (Table 1). Akaike information criterion (AIC) scores indicate that the treatment interactions with month were most important for improving model fit (Appendix S2: Table S3), suggesting that any explanation of treatment effects should focus on the months during which treatments had large effects. Therefore, the following is an examination of the effects of individual treatments by month. Relative to the 99.9% confidence intervals around the control treatment, annual autumn burning increased post-burn daily minimum soil temperature in May 2014, annual spring burning increased post-burn daily minimum soil temperature in May 2014, and annual summer burning increased post-burn daily minimum soil temperature in July 2014. When examining the combined effects of annual and quadrennial burns relative to the 99.9% confidence intervals around the control treatment, neither autumn nor spring burning increased 2015 post-burn daily minimum soil temperature, but summer burning increased post-burn daily minimum soil temperature in July 2015. However, autumn burning did decrease post-burn daily minimum soil temperature in January 2015. Although post-burn daily minimum temperature did appear to decrease in May 2015 due to annual spring burns, the difference between the combined annual and quadrennial spring burn temperatures and the control was minimal. Relative to the 99.9% confidence intervals around the control treatment, mowing did not affect daily minimum soil temperatures during the study.

Short-term effects of burns

The highest soil temperature recorded from any temperature probe during a burn was 47.5°C for 2 min at 1 cm depth during a quadrennial summer burn. On average, maximum soil temperatures during burns were significantly higher when burns occurred during seasons where soil temperatures were already high before the start of the burn (Fig. 3, Table 2). The maximum soil temperatures during burns were also significantly higher during quadrennial than annual burns, but only at 1 cm depth (contrast of annual vs. quadrennial disturbance at 1 cm depth: $P < 0.001$; contrast of annual vs. quadrennial

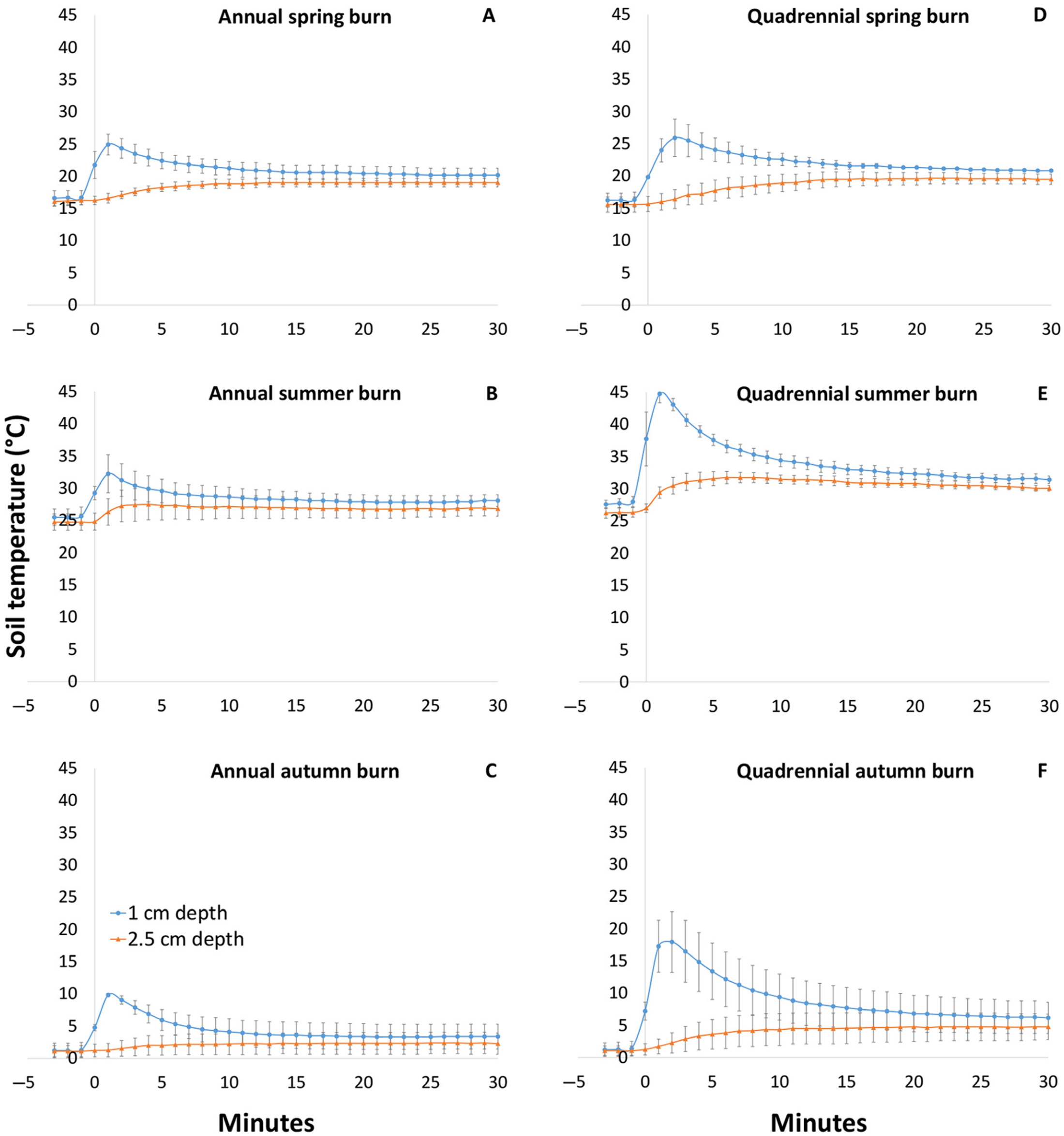

Fig. 3. Temperatures measured at 1-min intervals, with 0 min marking the first reading where temperature increased at 1 cm due to fire. Temperatures are also shown from 3 min before to 30 min after this reading. Temperatures are shown from three seasons of annual burns (A–C) and three seasons of quadrennial burns (D–F). Lines just connect points and are for visual purposes only. Error bars are ±1 SE.

disturbance at 2.5 cm depth: $P = 0.193$; significant frequency × soil depth interaction; Fig. 3, Table 2).

PAR and detritus depth

Burning increased photosynthetically active radiation (PAR) the same amount as mowing in June 2015 and October 2014 (Fig. 4B–C; Appendix S2: Table S4). In April 2018, annual autumn burning increased PAR more than annual autumn mowing (contrast of annual autumn burn vs. mow: $P < 0.001$), annual summer burning increased PAR slightly more than annual summer mowing (contrast of annual

Table 2. The effects of treatments and soil depth on the maximum soil temperature per plot during burns.

Predictor variables	Maximum soil temperature during burn F	df	P
Frequency	**9.5**	**1, 12**	**0.010**
Season	**88.3**	**2, 12**	**<0.001**
Depth	**94.2**	**1, 12**	**<0.001**
Freq × Seas	1.9	2, 12	0.198
Freq × Depth	**8.0**	**1, 12**	**0.015**
Seas × Depth	2.1	2, 12	0.165
Freq × Seas × Depth	2.1	2, 12	0.172

Note: Bold terms indicate effects where $P < 0.050$.

summer burn vs. mow: $P = 0.019$), and there were no significant PAR differences between annual spring burning and mowing (contrast of annual spring burn vs. mow: $P > 0.050$)—there were also no significant PAR differences between quadrennial burning and mowing in any season (contrasts of burn vs. mow in all quadrennial disturbances: $P > 0.050$; significant burn vs. mow × frequency × season interaction; Fig. 4A; Appendix S2: Table S4). By October, below-canopy PAR was low enough that differences between treatments were minimal, whereas differences in PAR between treatments were larger in April and June (Fig. 4A–C). Finally, although I attempted to measure PAR at ground level, the ceptometer was 1 cm in height and so the ceptometer was unable to go below the bottom 1 cm of detritus. Burning removes almost all detritus, whereas approximately 1 cm of detritus remains after mowing (Appendix S1: Fig. S4). Therefore, PAR results presented in Fig. 4 show the PAR that would reach a 1 cm tall plant after mowing, but detritus depth and soil temperature data indicate that the 1 cm of detritus remaining after mowing largely prevents increases in soil temperature.

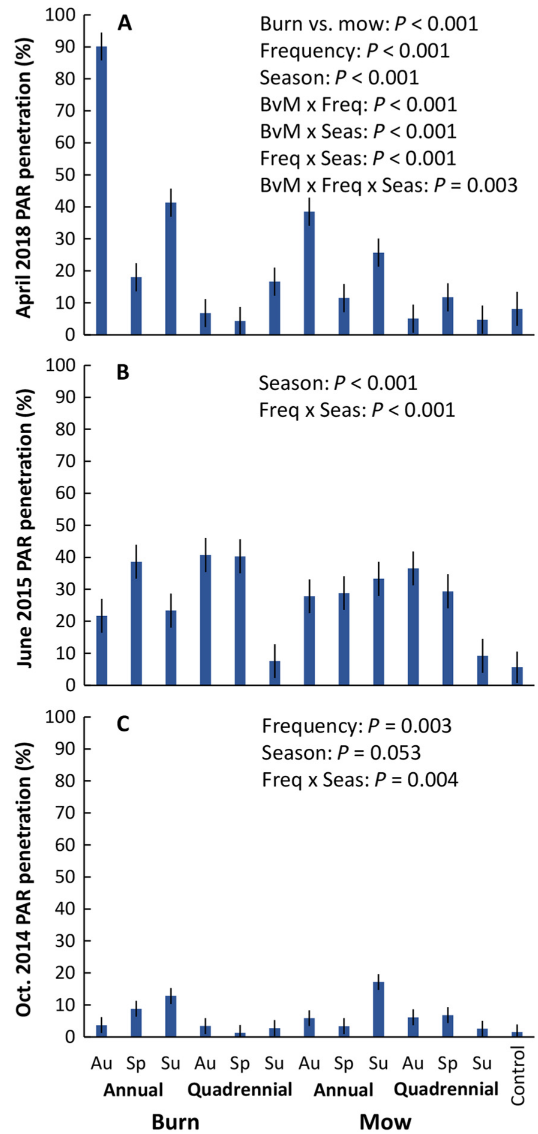

Fig. 4. The percentage of photosynthetically active radiation (PAR) reaching ground level after annual autumn disturbances (but before annual spring disturbances) in April 2018 (A), after annual and quadrennial spring disturbances in June 2015 (B), and after annual summer disturbances (but before autumn disturbances) in October 2014 (C). Error bars are ±1 SE and only P-values <0.10 are shown. Note that PAR values are from three different years, and quadrennial disturbances only occurred in 2015.

Discussion

Overall, the results of this study do not support the hypothesis that earlier increases in soil temperature cause greater plant production early in the growing season (hereafter "early growing season" will refer to the time prior to the summer disturbances). I predicted that only burning would increase early growing season plant production but burning and mowing equally increased early growing season plant production after autumn and spring disturbances, even though only burning strongly increased early growing season soil temperatures.

The results of this study supported the hypothesis that soil temperatures during burns were not hot enough to cause root mortality because the highest soil temperature recorded at 1 cm depth during a burn was 47.5°C for 2 min.

Effects of soil temperature on plant production

Increased soil temperatures in the months after burning or mowing have been hypothesized to increase plant production, especially in the spring when soil is cold in the absence of a disturbance (Rice and Parenti 1978). To test the effects of spring disturbance on spring plant production, studies should ideally measure plant production in the spring, but most studies that directly measure biomass have only quantified biomass at the end of the growing season. Studies that use eddy covariance towers to continuously measure CO_2 exchange after prairie burns can estimate plant production during different seasons, but do not separate the effects of higher soil temperatures after burning from the other effects of burning that may alter plant production (Suyker and Verma 2001, Fischer et al. 2012). I found that mowing in the autumn or spring had little effect on soil temperature but had the same effect on early growing season plant production as did burning in the autumn or spring. This suggests that changes in maximum soil temperature had little effect on early growing season production. While this is surprising, it is possible that minimum soil temperatures were more important for early growing season plant growth than maximum soil temperatures. For example, autumn burning increased maximum soil temperatures in March and April, but minimum soil temperatures were at least as cold as other treatments, suggesting that cold nighttime temperatures may still limit growth even as daytime temperatures increase after the autumn burns. Although Hulbert (1988) found that heating the soil to the same average temperatures as spring burned plots led to some increase in plant growth, it should be noted that heating in this study was continuous and so it unnaturally increased nighttime minimum soil temperatures.

It should also be noted that soil temperatures during burns did not appear to reach high enough levels to affect belowground plant structures. The highest soil temperature recorded at 1 cm soil depth from any iButton in this study was 47.5°C for 2 min during a quadrennial summer burn, and most soil temperatures during burns were considerably lower. Previous studies have shown that roots of trees in the *Pinus* genus do not show any mortality due to hot water until 52.5°C (Zeleznik and Dickmann 2004), or 5 min of exposure to 48°C water (Ursic 1961). Seeds and most other organisms are even more resistant to high temperatures than roots (Neary et al. 1999). Therefore, it appears the soil was not hot enough during burns to cause damage to belowground plant structures in this study. The maximum temperatures recorded during burns are normal for worldwide grasslands since most other researchers have found slightly lower 1 cm depth soil temperatures than the current study (Heyward 1938, Norton and McGarity 1965, Morgan 1999, Ohrtman et al. 2015, but see Bentley and Fenner 1958). However, decreases in soil temperatures due to burns, rather than increases, could potentially cause fine root mortality. The current study and Kohnke and Werkhoven (1963) show that bare soil has colder temperatures in the winter than soil covered with detritus, and colder winter soil temperatures have been shown to increase fine root mortality (Tierney et al. 2001, Cleavitt et al. 2008). Although fine roots likely grow back quickly in the spring, colder winter soil temperatures after autumn burns should be a common occurrence in the central USA because the soil is not consistently insulated by snow (Ferraro et al. 1996).

Other potential mechanisms affecting plant production

It appears that factors other than increased soil temperatures primarily drive the effects of burning and mowing on plant production. Some of the main other hypotheses for why burning and mowing increase plant production are as follows: (1) increased light availability; (2) increased convective cooling; and (3) increased nutrient availability (hypotheses further detailed in Knapp and Seastedt 1986, Hulbert 1988).

The light availability hypothesis states that burning and mowing increase light availability for growing plants and therefore increase plant production. Several studies have examined this hypothesis. Hulbert (1988) set up a study that experimentally examined hypothesized reasons for the effect of burning on plant production and showed that shading after spring burning generally reduced plant production. Other studies have found that burning increases the percentage of light availability the same amount as the percentage of plant production (Knapp 1984) and that shade decreases plant growth in non-drought years (Dickson and Foster 2011). In the current study, both burning and mowing dramatically reduced detritus depth and increased the amount of light reaching plants near the ground. Overall, it seems likely that burning and mowing increase early growing season plant production at least partly by increasing light levels.

The convective cooling hypothesis states that removal of detritus due to burning can increase convective cooling of plant leaves and prevent altered leaf morphology caused by shade or the physical impediment of detritus, thereby increasing plant production. Several studies have examined this hypothesis. Plant detritus has been shown to increase leaf temperatures by decreasing convective cooling via air movement across leaves (Knapp and Seastedt 1986). Also, leaves growing through detritus have different morphology that may decrease their productivity (Knapp 1985). However, two lines of evidence in the current study suggest the effect of detritus on convective leaf cooling or plant morphology is not the primary cause of early growing season production increases after disturbances. First, autumn burning and mowing increased plant production during April and early May (Fig. 1A), a cooler period when convective cooling is not as necessary to prevent leaf stress. Given that average daily high air temperatures were 17°C and 20°C in April and May 2015, respectively, it seems unlikely that leaf temperatures were high enough to stress the plants during these months, especially since no drought conditions occurred during the 2015 growing season (NDMC, USDA, and NOAA 2018). Second, effects of detritus on convective cooling and leaf morphology should differ between burned and mowed plots, yet there was no difference in early growing season production between burned and mowed plots. In the current study and most instances of mowing, the mulch from the mowed vegetation remains on the plots. Therefore, no detritus is removed from the plots by mowing, and although the height of plant detritus is dramatically reduced by mowing, plants still need to grow through this detritus and convective cooling and morphology should still be somewhat affected by detritus. Overall, the convective cooling hypothesis receives little support from the current study.

The nutrient availability hypothesis states that burning and mowing can lead to a short-term increase in nutrient availability as the nutrients in plants killed by disturbance enter the soil. Several studies have examined this hypothesis. Ash contains nutrients but does not appear to have large effects on soil nutrient availability (Niering and Dreyer 1989) and inorganic nitrogen is taken out of rainwater as it passes through plant detritus, suggesting that the detritus left by mowing could decrease nutrient availability (Knapp and Seastedt 1986). The ash left by spring burning could potentially increase nutrient availability enough to increase plant production in the spring. However, if nutrient availability explained the increases in plant production in the months immediately following autumn and spring mowing, then large increases in nutrient availability would need to occur shortly after mowing, which seems unlikely. Given that burning and mowing caused the same increases in early growing season production, this suggests the effects of burning were not primarily due to changes in soil nutrient levels. Overall, the nutrient availability hypothesis received little support from the current study.

While increased light availability may help to explain the effects of disturbance on early growing season production, plant production later in the growing season cannot be explained by changes in soil temperature or light availability (hereafter "late growing season" will refer to the time after the summer disturbances). If soil temperature or light availability drives late growing season plant production, then I would have expected increased production after both summer burning and mowing. However, late growing season plant production was higher in burned than mown plots, irrespective of disturbance season. It seems likely that the unique response of C_4 graminoids causes late growing season production to differ between burned and mown plots. In the current study, 86% of late growing season production was from C_4 graminoids (Fig. 1C), and the current study was similar to others in that burning appears to increase C_4 graminoid abundance (Dalgleish and Hartnett 2009) while mowing appears to decrease C_4 graminoid abundance (Van Dyke et al. 2004). Therefore, it appears late growing season plant production in mown plots was lower not because of the immediate effects of mowing, but likely because the cumulative effect of multiple mowings caused a decrease in the abundance of C_4 graminoids, thereby decreasing late growing season production. A single year study adjacent to the current study offers support for this explanation because a single spring mowing had similar effects to a single spring burn (Hover and Bragg 1981). As further support for the importance of the cumulative effects of treatments on C_4 graminoid abundance, late growing season plant production was highest after spring disturbances (Fig. 1C) and repeated spring burning has been shown to increase C_4 graminoid abundance (Collins et al. 1998, Towne and Craine 2014).

Conclusions

Burning and mowing have dramatic effects on aboveground plant production, but these effects do not appear to be mediated by increased soil temperature. I discussed hypotheses not related to soil temperature, and although the current study did not directly test the light availability hypothesis, it appears likely that burning and mowing increased early growing season production at least partly by increasing light availability. Future studies should further examine how plant production may be affected by factors not related to soil temperature, especially focusing on light availability.

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Supporting Information

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