

Tallgrass prairie plant responses to seasonal timing of prescribed fire

by

Alec Glidden

B.S., University of Northern Iowa, 2019

M.S., University of Northern Iowa, 2021

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2026

Abstract

Tallgrass prairie is among the most endangered ecosystems in North America, and the remaining prairie landscapes are increasingly threatened by woody encroachment, often as a result of altered disturbance regimes. Prescribed fire is widely used to maintain an open grassland state and limit woody encroachment; however, contemporary management practices concentrate prescribed burning in a narrow spring window. This not only contrasts with historical fire regimes but also homogenizes grassland communities and exacerbates air quality issues both locally and regionally. Burning outside the traditional spring window may provide unique opportunities for conservation and restoration. The overarching goal of my research was to examine how the timing of prescribed fire influences the tallgrass prairie ecosystem at multiple spatial and temporal scales using a combination of short- and long-term experiments conducted at Konza Prairie Biological Station.

I first evaluated the long-term effects of prescribed fire applied in different seasons (annual burning in spring, fall, and winter, and biennial burning in summer) on tallgrass prairie plant communities using data from a 31-year experiment. I found that repeated burning in different seasons significantly altered plant community composition, native species richness and diversity, and functional group dynamics over time. Annual spring burning promoted high cover of the dominant warm-season grasses and reduced native species richness and diversity, while summer burning supported greater native species richness and diversity and increased cool-season graminoid cover. Plant community responses to fall or winter fires were generally intermediate relative to spring and summer, but with greater legume cover. Many responses varied with topographic position (uplands vs. lowlands) and exhibited delayed or non-linear dynamics that emerged only after years of repeated fire treatments.

The second objective of my research was to determine how these same fire treatments affected aboveground net primary productivity (ANPP), precipitation-productivity relationships, and the cumulative effects of repeated burning on soil properties. Despite pronounced differences in plant community composition, annual burning in spring, fall, and winter dormant seasons yielded similar levels of graminoid and total ANPP over three decades. Biennial summer burning reduced mean ANPP in lowlands relative to dormant-season fire, although responses varied depending on whether comparisons with dormant-season treatments were made in burned versus non-burned years. Across all burn seasons, ANPP was strongly positively associated with growing-season precipitation, and fire timing did not alter the sensitivity of productivity to interannual climate variability. Soil properties differed primarily between topographic positions rather than among fire treatments. Collectively, these results suggest that environmental factors such as interannual climate variability and topographic gradients exerted stronger controls on ecosystem functioning than the seasonal timing of prescribed fire.

Last, I established a new field experiment to investigate the effects of reintroducing annual fire in contrasting seasons (spring vs. late-summer) in a bison-grazed, shrub-encroached grassland previously managed under a 4-year fire return interval. I established vegetation transects in lowland and upland positions to evaluate the short-term effects of an increase in fire frequency in different seasons and established baseline data for longer-term measurements. In addition to these watershed-scale measurements, I implemented plot-scale treatments that included mowing prior to burning and grazing exclosures to restrict access by bison. I found that herbaceous communities responded in broadly similar ways to reintroducing annual fire, regardless of the seasonal timing of fires. Annual fires increased warm-season grass cover, but also slightly reduced cover of cool-season graminoids and forbs. Across the watershed, clonal

shrub responses to season of fire diverged after the second fire application. Specifically, a repeated summer burn was less effective than a repeated spring burn at reducing the size of clonal shrub patches. When assessing combined treatments at the plot level, we did not detect any additive or synergistic effects of burn season, grazing, or mowing on *Cornus drummondii* shrub islands. Despite complete removal of aboveground tissue at the time of mowing, the effects of mowing were limited to a transient increase in stem recruitment. The presence of grazers reduced herbaceous cover in and around shrub islands, which could alter the effectiveness of subsequent fires; however, stem density of *C. drummondii* increased regardless of bison presence. The effects of two years of annual burning were offset by rapid stem regrowth despite reductions in aboveground biomass, with most responses occurring at the grass-shrub boundary.

Collectively, my results highlight that the seasonal timing of fire is an important but underutilized driver of tallgrass prairie ecosystem structure and function. Prescribed burning in different seasons altered plant community composition, diversity, productivity, and woody plant dynamics, while interactions with topography, climate variability, and grazing strongly mediated these responses. Expanding prescribed fire beyond spring may provide opportunities to increase landscape heterogeneity, diversify management outcomes, and improve grassland conservation and restoration from woody encroachment, while maintaining key ecosystem functions of the tallgrass prairie.

Tallgrass prairie plant responses to seasonal timing of prescribed fire

by

Alec Glidden

B.S., University of Northern Iowa, 2019

M.S., University of Northern Iowa, 2021

A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2026

Approved by:

Major Professor
Dr. John Blair

Copyright

© Alec Glidden 2026.

Abstract

Tallgrass prairie is among the most endangered ecosystems in North America, and the remaining prairie landscapes are increasingly threatened by woody encroachment, often as a result of altered disturbance regimes. Prescribed fire is widely used to maintain an open grassland state and limit woody encroachment; however, contemporary management practices concentrate prescribed burning in a narrow spring window. This not only contrasts with historical fire regimes but also homogenizes grassland communities and exacerbates air quality issues both locally and regionally. Burning outside the traditional spring window may provide unique opportunities for conservation and restoration. The overarching goal of my research was to examine how the timing of prescribed fire influences the tallgrass prairie ecosystem at multiple spatial and temporal scales using a combination of short- and long-term experiments conducted at Konza Prairie Biological Station.

I first evaluated the long-term effects of prescribed fire applied in different seasons (annual burning in spring, fall, and winter, and biennial burning in summer) on tallgrass prairie plant communities using data from a 31-year experiment. I found that repeated burning in different seasons significantly altered plant community composition, native species richness and diversity, and functional group dynamics over time. Annual spring burning promoted high cover of the dominant warm-season grasses and reduced native species richness and diversity, while summer burning supported greater native species richness and diversity and increased cool-season graminoid cover. Plant community responses to fall or winter fires were generally intermediate relative to spring and summer, but with greater legume cover. Many responses varied with topographic position (uplands vs. lowlands) and exhibited delayed or non-linear dynamics that emerged only after years of repeated fire treatments.

The second objective of my research was to determine how these same fire treatments affected aboveground net primary productivity (ANPP), precipitation-productivity relationships, and the cumulative effects of repeated burning on soil properties. Despite pronounced differences in plant community composition, annual burning in spring, fall, and winter dormant seasons yielded similar levels of graminoid and total ANPP over three decades. Biennial summer burning reduced mean ANPP in lowlands relative to dormant-season fire, although responses varied depending on whether comparisons with dormant-season treatments were made in burned versus non-burned years. Across all burn seasons, ANPP was strongly positively associated with growing-season precipitation, and fire timing did not alter the sensitivity of productivity to interannual climate variability. Soil properties differed primarily between topographic positions rather than among fire treatments. Collectively, these results suggest that environmental factors such as interannual climate variability and topographic gradients exerted stronger controls on ecosystem functioning than the seasonal timing of prescribed fire.

Last, I established a new field experiment to investigate the effects of reintroducing annual fire in contrasting seasons (spring vs. late-summer) in a bison-grazed, shrub-encroached grassland previously managed under a 4-year fire return interval. I established vegetation transects in lowland and upland positions to evaluate the short-term effects of an increase in fire frequency in different seasons and established baseline data for longer-term measurements. In addition to these watershed-scale measurements, I implemented plot-scale treatments that included mowing prior to burning and grazing exclosures to restrict access by bison. I found that herbaceous communities responded in broadly similar ways to reintroducing annual fire, regardless of the seasonal timing of fires. Annual fires increased warm-season grass cover, but also slightly reduced cover of cool-season graminoids and forbs. Across the watershed, clonal

shrub responses to season of fire diverged after the second fire application. Specifically, a repeated summer burn was less effective than a repeated spring burn at reducing the size of clonal shrub patches. When assessing combined treatments at the plot level, we did not detect any additive or synergistic effects of burn season, grazing, or mowing on *Cornus drummondii* shrub islands. Despite complete removal of aboveground tissue at the time of mowing, the effects of mowing were limited to a transient increase in stem recruitment. The presence of grazers reduced herbaceous cover in and around shrub islands, which could alter the effectiveness of subsequent fires; however, stem density of *C. drummondii* increased regardless of bison presence. The effects of two years of annual burning were offset by rapid stem regrowth despite reductions in aboveground biomass, with most responses occurring at the grass-shrub boundary.

Collectively, my results highlight that the seasonal timing of fire is an important but underutilized driver of tallgrass prairie ecosystem structure and function. Prescribed burning in different seasons altered plant community composition, diversity, productivity, and woody plant dynamics, while interactions with topography, climate variability, and grazing strongly mediated these responses. Expanding prescribed fire beyond spring may provide opportunities to increase landscape heterogeneity, diversify management outcomes, and improve grassland conservation and restoration from woody encroachment, while maintaining key ecosystem functions of the tallgrass prairie.

Table of Contents

List of Figures	xii
List of Tables	xv
Acknowledgements	xvi
Dedication	xviii
Chapter 1 - Introduction.....	1
References	9
Chapter 2 - Long-term Plant Community Dynamics Vary with Season of Fire in Tallgrass Prairie	12
Abstract	12
Introduction.....	13
Methods	17
Results.....	21
Discussion	32
Acknowledgements	41
Author Contributions	42
References	43
Chapter 3 - Long-term Aboveground Productivity Responses to Fire Timing in Tallgrass Prairie	57
Abstract	57
Introduction.....	58
Methods	63
Results.....	68
Discussion	73
References	79
Chapter 4 - Reintroducing Frequent Seasonal Fire to Shrub-Encroached Bison-Grazed Grasslands	92
Abstract	92
Introduction.....	93
Methods	98

Results.....	105
Discussion.....	111
References.....	119
Chapter 5 - Conclusion	133
Appendix A - Chapter 2 supplementary material	137
Appendix B - Chapter 3 supplementary material	158
Appendix C - Chapter 4 supplementary material	173

List of Figures

Figure 2-1: Relative cover of native warm-season graminoids (A), non-legume forbs (B), cool-season graminoids (C), and legumes (D) in lowlands and uplands under contrasting season-of-burn treatments. Note differences in scale for cover of different plant functional groups.	52
Figure 2-2: Native species richness at the plot (spp. 10 m ⁻²) (A) and catchment (spp. 200 m ⁻²) (B) scale, and changes in the exponent of Shannon's index at the plot (10 m ⁻²) (C) and catchment (200 m ⁻²) (D) scale in lowlands (left) and uplands (right) under contrasting burn seasons. Note differences in scale for richness and diversity metrics.	53
Figure 2-3: Native annual and perennial forb species richness over time at the catchment scale among burn seasons: spring (A), summer (B), fall (C), and winter (D), and between topographic positions. Solid lines indicate a significant ($p < 0.05$) regression slope, while dashed lines are non-significant trends.	54
Figure 2-4: Relative cover of species in lowlands and uplands under contrasting burn regimes: <i>Andropogon gerardii</i> (A), <i>Schizachyrium scoparium</i> (B), <i>Sorghastrum nutans</i> (C), <i>Panicum virgatum</i> (D), <i>Sporobolus compositus</i> (E), <i>Carex inops</i> (F), <i>Carex meadii</i> (G), <i>Koeleria macrantha</i> (H), <i>Symphyotrichum ericoides</i> (I), <i>Solidago altissima</i> (J), <i>Symphyotrichum oblongifolium</i> (K), <i>Lespedeza violacea</i> (L), <i>Amorpha canescens</i> (M), <i>Poa pratensis</i> (N), <i>Rhus glabra</i> (O). Note differences in scale for cover of different plant species.....	55
Figure 2-5: Non-metric multidimensional scaling (NMDS) of community composition from 1994 to 2024, based on Bray-Curtis dissimilarity of relative cover among burn regime and topographic position. Stress value = 0.14.	56
Figure 3-1: Annual net primary productivity for graminoids (ANPP _G) (A, B), forbs (ANPP _F) (C, D), and combined herbaceous groups (ANPP _H) (E, F) in lowlands and uplands from 1994 to 2023. Solid lines represent significant linear mixed model trends, with dashed lines for non-significant trends. Growing season (April – September) precipitation is shown as shaded background.....	88
Figure 3-2: Mean ($\pm$ SE) annual productivity for graminoids (A), forbs (B), and total productivity (C). Values represent means averaged across 30 years for each burn season and topographic position combination. Different letters indicate significant differences ($p < 0.05$) among	

burn seasons within each topographic position, derived from linear mixed models using the transect-level dataset (Table 3.1).	89
Figure 3-3: Linear regressions of ANPP and growing season precipitation for each burn season and topographic position combination for graminoids (A, B), forbs (C, D), and total herbaceous (E, F). Solid lines represent significant relationships ($p < 0.05$), while dashed lines represent non-significant relationships.	90
Figure 3-4: Mean ($\pm$ SE) annual aboveground net primary productivity for graminoids (A), forbs (B), and total productivity (C) by burn classifications (burned and non-burned) for each burn season and topographic combination. Different letters indicate significant differences ($p < 0.05$) among burn season within each burn category, derived from linear mixed models (Table B.6).	91
Figure 4-1: Site map of watershed N4C at KPBS (A) and GPS mapping conducted on N4C (B) of <i>C. drummondii</i> (white), <i>R. aromatica</i> (yellow), and the species composition transects (black circles). Upland transects are on the south side of the map. Annual spring burning occurred on the west side of the fire break, and late-summer burning occurred on the east side of the fire break.	126
Figure 4-2: Relative percent cover of warm-season grasses (A), cool-season graminoids (B), forbs (C) and woody (D) from vegetation surveys under spring and summer burns in both the lowland (left) and upland (right) topographic positions.	127
Figure 4-3: Native species richness (A) and Shannon diversity (B) at the plot scale (10 m^2) from vegetation surveys under contrasting spring and summer burns in both the lowland (left) and upland (right) topographic positions.	128
Figure 4-4: Percent change in shrub area relative to 2023 and changes in shrub irregularity from 2023 to 2025 under prescribed spring and summer burning for <i>C. drummondii</i> (A, C) and <i>R. aromatica</i> (B, D). Points represent means $\pm$ SE for each species within each year and burn season.	129
Figure 4-5: Stem density (A) and aboveground biomass (B) of <i>C. drummondii</i> from 2023 to 2025 across outside, edge, and interior of shrub islands. Points represent means $\pm$ SE for spring (square) and summer (circle) burn treatments, with bison present (dashed, open symbols) or excluded (filled symbols).	130

Figure 4-6: Percent cover of graminoids (A), forbs (B), woody vegetation (C) and bare ground (D) from 2023 to 2025 across outside, edge, and interior of shrub islands. Points represent means $\pm$ SE for spring (square) and summer (circle) burn treatments, with bison present (dashed, open symbols) or excluded (filled symbols)..... 131

Figure 4-7: Stem density of *C. drummondii* recruits (< 0.15 cm in height) from 2023 to 2025. Points represent means $\pm$ SE averaged across of shrub island positions (outside, edge, and interior) for spring (square) and summer (circle) burn treatments, with (dashed, open symbols) and without (filled symbols) mowing. 132

List of Tables

Table 3.1: Summary ANOVA statistics from linear mixed-effects models evaluating graminoids, forbs, and total herbaceous productivity over time among burn seasons and between topographic positions. Forbs were square-root transformed prior to analysis.	85
Table 3.2: Coefficient of determination (r^2) depicting the relationship between ANPP and growing season precipitation for each burn season within lowlands and uplands. Values represent the proportion of interannual variation in productivity explained by precipitation and are shown for graminoid, forb, and total productivity.	86
Table 3.3: Mean and standard error for each soil property in the different seasonal burn treatments. Means were calculated across all replicate samples for each burn season $\times$ topographic position combination. Global Mean represents the mean across all burn seasons within a topographic position. Different letters indicate significant differences based on Tukey-adjusted pairwise comparison ($\alpha = 0.05$) from mixed-effects models using Kenward-Roger degrees of freedom. Upper-case letters indicate significant topographic differences within a burn season or for the global mean.	87

Acknowledgements

Thank you to all the individuals and organizations who have supported me over the past few years. I am especially grateful to my advisor, John Blair, for his support and mentorship throughout graduate school. John's ability to think across broad ecological scales has continuously been an inspiration and helped me grow as a scientist. I am also very thankful to my committee members – Jesse Nippert, Zak Ratajczak, and Sara Baer, whose feedback has been immensely valuable and thought-provoking. I appreciate the time and effort each of you has invested in helping me on my journey.

I would also like to thank all the individuals who contribute to maintaining a functional LTER program at Konza, including Patrick O'Neal and Peyton Thorell, for their reliability and assistance, particularly with getting my woody encroachment project off the ground. I would also like to thank Amanda Kuhl and her arsenal of undergraduate students who collected and sorted much of the biomass for this dissertation. Big thanks to Jeff Taylor who collected the species composition data I used and always took the time to chat and answer questions. Thank you to Nathan King for always being willing to talk about fire and Konza-related things. Thank you to all those I got to spend time with while prescribing fire and rounding up bison, it was a real treat to experience. I am also grateful to Micke Ramirez and Patrick Hartsock for helping me collect soil samples and field data, and to Jessica Schmeidler for your time spent grinding and sieving through so many soil cores.

I would also like to thank my friends and family for their support and encouragement. First of all, thank you Grandma for always being there for me! To all my friends afar, you're the best, and even though I'm not great at keeping in touch, just know your presence was always felt. Klara Stevermer, it was a genuine treat to get to know you these last few years; thank you for

always being a happy spirit and a spark of joy in the office. Corina McTigue and Chloe Danner, though our time together was short, you two were always so fun to talk with! To Aleah Querns, Bess Bookout, and Alex Anderson, thank you all for being awesome people. I would also like to thank David Hayes and Elle Krellwitz for all the outdoor activities I got to participate in.

This work was supported by the National Science Foundation's Long-Term Ecological Research Program (LTER), the Division of Biology at Kansas State University, and the Grassland Heritage Foundation. Thank you all for your support and happy reading!

Dedication

To our Lost Landscape.

Chapter 1 - Introduction

The rise of North American tallgrass prairie took place approximately 8,000–10,000 years ago during the early Holocene. As continental glaciers retreated and warming climates exposed newly available landscapes, interactions among climate, fire, and grazing led to the expansive grasslands that came to define much of central North America. For thousands of years, these prairies supported a diverse array of plant and animal communities, extensive populations of large grazers such as bison and elk, and some of the most fertile soils on the continent (Axelrod, 1985). At its historical extent, tallgrass prairie occupied roughly 677,000 km² and formed one of the largest continuous grassland ecosystems in North America (White et al., 2000). Following European settlement, widespread conversion of prairie to cropland, urban development, and fragmentation drastically reduced the extent of tallgrass prairie across the Great Plains. At the same time, changes in historical disturbance regimes, including widespread fire suppression and the loss of large native grazers, altered many of the ecological processes that once maintained open grasslands across the region. These changes, coupled with other global environmental changes, led to the expansion of woody vegetation (i.e., trees and shrubs) and the continued decline of remaining prairie ecosystems. Today, despite its historical extent and ecological importance, less than 4% of the original tallgrass prairie remains (Samson & Knopf, 1994), making it one of the most endangered ecosystems in North America (Hoekstra et al., 2005). With so little prairie remaining, identifying and refining management approaches that conserve native plant communities, maintain grassland function, and limit woody expansion have become increasingly important. The overarching goal of my research was to examine how the timing of prescribed fire influences tallgrass prairie ecosystems at multiple spatial and

temporal scales using a combination of short-and long-term experiments conducted at Konza Prairie Biological Station in Manhattan, Kansas, USA.

To address the growing threat of woody expansion and concurrent loss of grassland habitat, contemporary management relies heavily on prescribed fire to replicate the historical processes that once maintained grassland states and kept woody encroachment at bay. In this region, high growing season precipitation provides enough moisture to support closed-canopy forest; however, that same precipitation amount falling on open grasslands produces dense herbaceous biomass, that, when senesced, provides the fine fuels needed to carry frequent fires. In the absence of fire and grazers, large amounts of surface detritus accumulate with negative impacts on plant productivity and potential undesirable shifts in plant community composition. By removing accumulated litter and stimulating herbaceous growth, fire maintains a grass-dominated community and ensures the continued production of fuels necessary for future burns (Knapp & Seastedt, 1986). However, prescribed fire regimes today are not analogous to the fires that historically maintained these grasslands. Prior to widespread wildfire suppression and implementation of human management of burn regimes, fires occurred across multiple seasons and under a broader range of environmental conditions than those typically associated with contemporary prescribed burning. During periods of drought, for instance, the increased flammability of accumulated fuels often led to massive lightning-ignited fires that swept across the region. Native Americans also purposefully applied fire to the landscape to improve forage for bison, facilitate hunting and maintaining open grassland states (Stewart, 2002). This variability in fire frequency, intensity, and timing paired with large-scale grazing by migratory native herbivores (e.g., bison and elk) created a shifting mosaic of disturbed and undisturbed patches, supporting high levels of biodiversity and maintaining heterogeneous grassland

structure at both local and regional scales. However, these complex historical interactions have largely been replaced by more uniform management practices, often designed to achieve specific outcomes (e.g., maximizing forage production for cattle). This contrast is particularly evident in the Flint Hills region of Kansas and Oklahoma, which is home to the largest remaining expanse of native tallgrass prairie. Across this region, roughly half of the grass-dominated area (840,000 ha) is burned annually within a few short weeks in early spring (KDHE, 2025), while much of the remaining half is either burned less frequently or not burned at all (Ratajczak et al., 2016), and comparatively little burning occurs during other times of the year (Towne & Craine, 2016).

The promotion of annual spring burning is largely a result of research summarized in the 1960s that concluded late spring fires are the least harmful to forage yields and soil moisture (McMurphy & Anderson, 1963; Owensby & Anderson, 1967). Since then, continued research on the effects of spring burning has supported the notion that repeated spring fire stimulates highly productive warm-season grasses (Towne & Kemp, 2003; Towne & Owensby, 1984). These grasses have extensive root systems and can form dense canopies that reduce light availability and suppress subdominant species (McCaine et al., 2010), ultimately leading to increasingly homogeneous plant communities over time (Collins & Calabrese, 2012). Beyond these ecological consequences, a temporally compressed burning season produces concentrated smoke emissions that can severely impact regional air quality and affects citizens downwind (Sablin et al., 2024). Because plant species differ in their phenology, growth strategies, and disturbance responses, altering the seasonal timing of prescribed fire may influence competitive dynamics and plant community composition. Some studies have shown that autumn and winter burning increase the cover of cool-season graminoids and forbs without detrimental effects on overall biomass (Dickeson et al., 2019; Towne & Kemp, 2003). Similarly, growing season fires are

associated with increased native species richness and diversity (Towne & Kemp, 2008), but little is known about their effects on productivity. While these studies provide strong support for the use of fire outside of spring, they are over a decade old, and a more comprehensive, in-depth analysis of the effects of prescribing fire in different seasons that incorporates all four burn seasons together may be necessary before widespread adaption can take place. Further, because many ecological responses to repeated disturbance develop over decades, extending these long-term experiments is critical for understanding plant community trajectories that may not have been apparent during earlier stages of ecosystem change. In a similar vein, because fire behavior and intensity are strongly related to herbaceous biomass and fuel loads, shifts in plant communities associated with seasonal burning may also alter the ability of fire to suppress woody species and restore encroached prairie.

The expansion of woody species into grasslands is one of the leading drivers of grassland decline and loss of ecosystem services in tallgrass prairie and many other grasslands globally (Archer et al., 2017). In many cases, the fire return intervals that have historically maintained open grassland states are no longer sufficient to suppress woody plant establishment and expansion. Increased propagule pressure, elevated CO₂, and changes in disturbance regimes all contribute to the ongoing increase in woody proliferation (Scholtz et al., 2018; Van Auken, 2009). To prevent woody species from establishing, land managers must now incorporate frequent burning with no release; otherwise, the chance of woody species establishment and spread increases, highlighting the potential importance of incorporating greater variability in fire timing to management regimes with frequent burning.

Burning outside the traditional spring window may provide unique opportunities to combat the expansion of resilient clonal shrubs, particularly in grazed settings where traditional

fire regimes have proven insufficient to reverse woody encroachment (Noble & Ratajczak, 2025). While frequent fire may have been effective in preventing the establishment of woody plants, it is often not sufficient to remove them or prevent them from spreading once established (Collins et al., 2021; Miller et al., 2017). Successful restoration of shrub encroached grasslands may depend on the timing of fire and its interaction with large grazers (e.g., bison), or may necessitate compound disturbances (e.g., mechanical removal) that alter resource and fuel availability. However, clonal shrubs can utilize deep water reserves and substantial belowground carbohydrate stores to resist even repeated and compound disturbances (Bond & Midgley, 2001; O'Connor et al., 2020; Keen et al., 2024). Furthermore, as woody cover increases, light limitation reduces understory herbaceous vegetation and fine fuel accumulation, which feeds back to constrain the effectiveness of prescribed burning for shrub reduction (Ratajczak et al., 2011). These challenges may be especially pronounced in grazed systems, where herbivory can further reduce fuel availability even under frequent fire (Briggs et al., 2002; Knapp et al., 1999). The timing of prescribed burning may also alter its impact on established woody plants. For example, growing-season fires may have a greater impact on woody species than traditional spring burning because they occur during periods of active growth and aboveground resource allocation. However, summer fire intensity can be highly variable depending on local weather conditions, fuel loads, and aboveground plant moisture. It remains unclear whether the timing of prescribed fire and its interaction with mowing and grazing will alter the effectiveness of fire in reducing the extent or cover of established woody shrubs.

In this dissertation, I asked: How does the timing of prescribed fire affect tallgrass prairie ecosystems? Does changing the season of fire influence the composition of native plant communities and their functional role in capturing carbon and maintaining soil fertility, and how

do these dynamics vary with time and topography? Further, do contrasting fire timing regimes vary in their effectiveness to restore shrub-encroached grasslands, and do these responses change in the presence of large grazers such as bison? To address these questions, I used a combination of long- and short-term experiments conducted at Konza Prairie Biological Station to assess ecosystem responses to seasonal fire.

In Chapter 2, I evaluated the long-term effects of prescribed fire applied in different seasons (spring, summer, fall, and winter) on tallgrass prairie plant communities. Using a 31-year experiment featuring permanent vegetation transects located in lowland and upland topographic positions, I assessed how burn season influenced plant community composition, native species richness and diversity, the relative abundance of major plant functional groups, and species-specific responses through time. The primary goal of this chapter was to determine how the seasonal timing of fire affects long-term plant community dynamics in tallgrass prairie.

In Chapter 3, I examined how long-term prescribed burning in different seasons influenced ecosystem function in tallgrass prairie, with a particular focus on aboveground net primary productivity (ANPP) and soil fertility. Using 30 years of annual biomass production data collected from the same experimental watersheds described in Chapter 2, I evaluated how burn season influenced graminoid, forb, and total ANPP in lowland and upland topographic positions. Because productivity in mesic grasslands is strongly influenced by precipitation variability, I also assessed whether relationships between precipitation and ANPP differed among seasonal fire treatments. In addition, I collected soil cores adjacent to long-term biomass transects in lowland and upland positions to evaluate whether long-term seasonal fire regimes altered soil properties. The primary goal of this chapter was to determine whether prescribed fire applied in

different seasons alters long-term ecosystem productivity, precipitation–productivity relationships, and soil properties in tallgrass prairie.

In Chapter 4, I investigated whether reintroducing annual fire in contrasting seasons (spring vs. late summer) could be used to restore shrub-encroached tallgrass prairie within a bison-grazed landscape. This study was conducted in a watershed previously managed under a 4-year spring fire return interval that had experienced extensive expansion of clonal shrubs. Beginning in 2023, I divided a 77.8 ha watershed into two subcatchments assigned to either annual spring or annual late-summer burning treatments. I evaluated how reintroducing annual fire influenced herbaceous plant community composition, shrub cover dynamics, and the persistence of clonal woody species across the landscape using permanent vegetation transects and annual GPS mapping of shrub islands. I also evaluated how fire timing interacted with bison grazing and mowing treatments on individual shrub islands by using grazer exclosures and experimentally mowed shrubs to assess effects on shrub stem density, biomass, recruitment, and herbaceous recovery across the grassland-shrub boundary. The primary goal of this chapter was to determine whether changing the timing of reintroduced annual prescribed fire could promote restoration toward a more open grassland state in shrub-encroached, grazed grasslands.

These chapters demonstrate that the timing of prescribed fire is an important but underutilized driver of tallgrass prairie ecosystem structure and function. Across these studies, fire timing altered plant community composition, productivity, diversity, and woody plant dynamics, while interactions with topography, climate variability, and grazing strongly mediated ecosystem responses. In doing so, this dissertation emphasizes the importance of expanding prescribed fire beyond a narrow spring burn window to promote greater heterogeneity in

tallgrass prairie ecosystems and provide managers with greater flexibility for achieving different conservation and management objectives.

References

- Archer, S. R., E. M. Andersen, K. I. Predick, S. Schwinning, R. J. Steidl, and S.R. Woods. 2017. "Woody plant encroachment: causes and consequences." In *Rangeland systems: Processes, management and challenges*, edited by Briske, D, 25–84. Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-46709-2_2
- Axelrod, D.I. 1985. "Rise of the grassland biome, central North America." *The Botanical Review*, 51(2): 163–201.
- Bond, W. J., and J. J. Midgley. 2001. "Ecology of sprouting in woody plants: the persistence niche." *Trends in Ecology & Evolution*, 16(1), 45–51. [https://doi.org/10.1016/S0169-5347\(00\)02033-4](https://doi.org/10.1016/S0169-5347(00)02033-4).
- Briggs, J. M., A. K. Knapp, and B. L. Brock. 2002. "Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing interactions." *The American Midland Naturalist*, 147(2): 287–294. [https://doi.org/10.1674/0003-0031\(2002\)147\[0287:eowpit\]2.0.co;2](https://doi.org/10.1674/0003-0031(2002)147[0287:eowpit]2.0.co;2)
- Collins, S. L., and L. B. Calabrese. 2012. "Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie." *Journal of Vegetation Science*, 23(3): 563–575. <https://doi.org/10.1111/j.1654-1103.2011.01369.x>.
- Collins, S. L., J. B. Nippert, J. M. Blair, J. M. Briggs, P. Blackmore, and Z. Ratajczak. 2021. "Fire frequency, state change and hysteresis in tallgrass prairie." *Ecology Letters*, 24(4): 636–647. <https://doi.org/10.1111/ele.13676>.
- Dickson, T. L., B. A. Hayes, and T. B. Bragg. 2019. "Effects of 34 years of experimentally manipulated burn seasons and frequencies on prairie plant composition." *Rangeland Ecology & Management*, 72(1): 82–91. <https://doi.org/10.1016/j.rama.2018.07.014>.
- Hoekstra, J. M., T. M. Boucher, T. H. Ricketts, and C. Roberts. 2005. "Confronting a biome crisis: global disparities of habitat loss and protection." *Ecology Letters*, 8(1): 23–29. <https://doi.org/10.1111/j.1461-0248.2004.00686.x>.
- KDHE. 2025. Kansas Department of Health and Environment: Flint Hills Wildland Fire Update, 2025 Summary. https://ksfire.org/media/Flint_Hills_Update_2025_Summary-77e3962.pdf.
- Keen, R. M., S. Bachle, M. Bartmess, and J. B. Nippert. 2024. "Combined effects of fire and drought are not sufficient to slow shrub encroachment in tallgrass prairie." *Oecologia*, 204(4): 727–742. <https://doi.org/10.1007/s00442-024-05526-x>.
- Knapp, A. K., and T. R. Seastedt. 1986. "Detritus accumulation limits productivity of tallgrass prairie." *BioScience*, 36(10): 662–668. <https://doi.org/10.2307/1310387>.

- Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. "The keystone role of bison in North American tallgrass prairie: Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes." *BioScience*, 49(1): 39–50. <https://doi.org/10.1525/bisi.1999.49.1.39>.
- McCain, K. N., S. G. Baer, J. M. Blair, and G. W. Wilson. 2010. "Dominant grasses suppress local diversity in restored tallgrass prairie." *Restoration Ecology*, 18: 40–49. <https://doi.org/10.1111/j.1526-100X.2010.00669.x>.
- McMurphy, W. E., and K. L. Anderson. 1963. "Burning bluestem range: forage yields." *Transactions of the Kansas Academy of Science (1903-)*, 66(1): 49–51. <https://doi.org/10.2307/3626834>.
- Miller, J. E., E. I. Damschen, Z. Ratajczak, and M. Özdoğan. 2017. "Holding the line: three decades of prescribed fires halt but do not reverse woody encroachment in grasslands." *Landscape Ecology*, 32(12): 2297–2310. <https://doi.org/10.1007/s10980-017-0569-9>.
- Noble, S., and Z. Ratajczak, Z. 2025. "Restoring frequent fire results in habitat improvement for bison but minimal early reduction of woody encroachment." *Ecological Restoration*, 43(4): 288–301. <https://doi.org/10.3368/er.43.4.288>.
- O'Connor, R. C., J. H. Taylor, and J. B. Nippert. 2020. Browsing and fire decreases dominance of a resprouting shrub in woody encroached grassland. *Ecology*, 101(2): e02935. <https://doi.org/10.1002/ecy.2935>.
- Owensby, C. E., and K. L. Anderson. 1967. "Yield response to time of burning in the Kansas Flint Hills." *Journal of Range Management*, 20(1): 12–16 <https://doi.org/10.2307/3896282>
- Ratajczak, Z., J. M. Briggs, D. G. Goodin, L. Luo, R. L. Mohler, J. B. Nippert, and B. Obermeyer. 2016. "Assessing the potential for transitions from tallgrass prairie to woodlands: are we operating beyond critical fire thresholds?" *Rangeland Ecology & Management*, 69(4): 280–287. <https://doi.org/10.1016/j.rama.2016.03.004>.
- Ratajczak, Z., J. B. Nippert, J. C. Hartman, and T. W. Ocheltree. 2011. "Positive feedbacks amplify rates of woody encroachment in mesic tallgrass prairie." *Ecosphere*, 2(11): 1–14. <https://doi.org/10.1890/ES11-00212.1>.
- Sablan, O., B. Ford, E. Gargulinski, M. S. Hammer, G. Henery, S. Kondragunta, R. V. Martin, et al. 2024. "Quantifying prescribed-fire smoke exposure using low-cost sensors and satellites: Springtime burning in Eastern Kansas." *GeoHealth*, 8(4): e2023GH000982. <https://doi.org/10.1029/2023GH000982>.
- Samson, F., and F. Knopf. 1994. "Prairie conservation in North America." *BioScience*, 44(6): 418–421. <https://doi.org/10.2307/1312365>

- Stewart, O. C. 2002. *Forgotten Fires: Native Americans and the Transient Wilderness*. Norman: University of Oklahoma Press.
- Scholtz, R., S. D. Fuhlendorf, and S. R. Archer. 2018. "Climate–fire interactions constrain potential woody plant cover and stature in North American Great Plains grasslands." *Global Ecology and Biogeography*, 27(8): 936–945. <https://doi.org/10.1111/geb.12752>.
- Towne, E. G., and J. M. Craine. 2016. "A critical examination of timing of burning in the Kansas Flint Hills." *Rangeland Ecology & Management*, 69(1): 28–34. <https://doi.org/10.1016/j.rama.2015.10.008>.
- Towne, E., and K. E. Kemp. 2003. "Vegetation dynamics from annually burning tallgrass prairie in different seasons." *Journal of Range Management*, 56: 185–192. <https://doi.org/10.2307/4003903>.
- Towne, E. G., and K. E. Kemp. 2008. "Long-term response patterns of tallgrass prairie to frequent summer burning." *Rangeland Ecology & Management*, 61(5): 509–520. <https://doi.org/10.2111/08-043.1>.
- Towne, G., and C. Owensby, C. 1984. "Long-term effects of annual burning at different dates in ungrazed Kansas tallgrass prairie." *Journal of Range Management*, 37(5): 392–397. <https://doi.org/10.2307/3899622>.
- Van Auken, O. W. 2009. "Causes and consequences of woody plant encroachment into western North American grasslands." *Journal of Environmental Management*, 90(10): 2931–2942. <https://doi.org/10.1016/j.jenvman.2009.04.023>
- White, R. P., S. Murray, M. Rohweder, S. D. Prince, and K. M. Thompson. 2000. "*Pilot Analysis of Global Ecosystems: Grassland Ecosystems*." Washington D. C. World Resources Institute.

Chapter 2 - Long-term Plant Community Dynamics Vary with Season of Fire in Tallgrass Prairie

Authors: Alec J. Glidden, Zak Ratajczak, Jeffrey H. Taylor, John M. Blair

Abstract

Many ecosystems depend on periodic disturbances to maintain native species diversity and avoid large shifts in community composition. This is especially true for productive grasslands like tallgrass prairie, where frequent fires remove detritus, stimulate forage production, and combat woody encroachment. Historical accounts document fires throughout the year as a result of lightning and activities of Indigenous people. However, timing of contemporary prescribed burning in grasslands globally is often temporally restricted to coincide with phenology and weather conditions amenable to controlling fire (e.g., moderate winds, less green vegetation). In tallgrass prairie, most prescribed burning occurs at the end of the dormant season, resulting in extensive regional burning in a narrow spring window that impacts air quality and may homogenize grassland communities. Expanding prescribed burning beyond the spring could diversify management outcomes, reduce air quality impacts, and enhance landscape-scale heterogeneity in grassland communities, yet few long-term studies have assessed how burn season influences plant communities. We report on a 31-year experiment at the Konza Prairie Biological Station that manipulated seasonal timing of fires (i.e., spring, summer, fall, and winter burning). We contrast responses in lowland and upland landscape positions using a network of long-term plant sampling plots. Burn season and topography significantly affected plant community composition, dynamics, and species responses over time. Annual spring burning increased the cover of dominant warm-season graminoids at the expense of cool-season

graminoids and reduced native species richness and diversity. In contrast, summer burning led to lower warm-season graminoid cover, increased cool-season graminoid cover, and greater native species richness and diversity. Fall and winter burning functional group responses and native species richness and diversity were generally intermediate to spring and summer burns, but with a strong positive effect on legume cover. Our results demonstrate that the season of fire is an important, but underutilized, driver of tallgrass prairie plant community composition and diversity. Management strategies that incorporate a broader range of burn seasons can meet specific conservation objectives and promote more heterogeneous grasslands.

Introduction

Preserving natural landscapes and the ecosystem services and biodiversity they support is a major conservation goal. In many instances, maintaining or restoring disturbance regimes, such as periodic fires or herbivory, can benefit conservation outcomes (Turner, 2010). In tallgrass prairie, for example, frequent fires are essential to avoid transitioning to shrublands or woodlands (e.g., Palmquist et al., 2014; Ratajczak et al., 2014), and reintroducing native grazers can increase native plant diversity (Ratajczak et al., 2022; Bookout et al., 2025). Ecological responses to many aspects of disturbance regimes (frequency, size, intensity) have been studied extensively (Connell, 1978; Pickett & White, 1985). However, there are fewer studies of disturbance timing (i.e., seasonality), though timing of disturbances can have strong effects on communities (Engle & Bidwell, 2001; Miller et al., 2019; Vermeire et al., 2024). In this study, we evaluated the long-term effects of varying the seasonal timing of a common disturbance, prescribed fire, on plant communities in tallgrass prairie, a mesic grassland ecosystem where prescribed fire is used widely for management and conservation.

Temperate grasslands are at great conservation risk globally (Hoekstra et al., 2005), and tallgrass prairies are among the most endangered ecosystems in North America (Corner et al., 2018; Sampson & Knopf, 1994). Before European colonization, tallgrass prairies covered a large portion of the eastern North American plains, but now occupy less than four percent of their pre-colonization extent (Samson & Knopf, 1994). Understanding how to effectively manage remaining tallgrass prairie is critical for both conservation and economic objectives (i.e., as grazing lands in areas where extensive prairie remains). Tallgrass prairie occurs in areas with sufficient rainfall to support woody vegetation, and periodic fires were important in the establishment and persistence of these grasslands (Axelrod, 1985; Blair et al., 2014; Collins & Wallace, 1990). Fire reduces litter accumulation and associated light limitation, stimulates productivity of the dominant warm-season grasses, and limits woody plant encroachment (Archer et al., 2017; Bowman et al., 2009; Collins & Wallace, 1990). Variation in the frequency, intensity, and timing of fires alters plant responses and community composition, and may influence the stability and resilience of prairie ecosystems (Collins, 2000; Driscoll et al., 2010; Tilman et al., 2006). Prior to European colonization, fires in tallgrass prairies were initiated by lightning or Native Americans (Bragg, 1982; Stambaugh et al., 2013; Stewart, 2002) and occurred at different times of year (Anderson, 2006). Lightning tends to ignite fires from early spring through late fall. Indigenous groups also lit fire through the year for various reasons, including to attract game (especially bison), as signal fires, and for warfare; escaped fires were also likely (Allen & Palmer, 2011; Courtwright, 2011; Stambaugh, 2013). From an ecological standpoint, this patchwork of fires at different times of year and different return intervals across the Great Plains was likely essential for creating and maintaining landscape heterogeneity. This contrasts sharply with the current use of prescribed fire in prairie management, which is often

limited to a narrow spring window (Howe, 1994; Towne & Craine, 2016; Twidwell et al., 2016) and applied uniformly across contiguous areas of prairie, such as in the Flint Hills ecoregion of the U.S. (Mohler & Goodin, 2012), which includes the largest remaining areas of native tallgrass prairie (Sampson & Knopf, 1994). This restriction in timing of prescribed fires reflects a broader trend across contemporary fire cultures globally where, in many regions, it is now common to have a preferred burn season when the majority of prescribed fires occur (Hsu et al., 2025).

In tallgrass prairies and other highly productive grasslands globally, prescribed fire is widely used as a cost-effective, scalable approach for multiple management objectives. In the Flint Hills ecoregion of Kansas, an average of about 840,000 ha of prairie is burned each year, mainly in early- to mid-April as a management practice to support cattle grazing (KDHE, 2025). Burning in this narrow window is effective for specific predictable agricultural objectives, such as early green-up, enhanced growth of warm-season grasses, and greater cattle weight gain (Smith & Owensby, 1978). However, concentrating fire within a narrow timeframe reduces variability in disturbance regimes and community outcomes, and limits flexibility in management options. It can also exacerbate air quality impacts of regional burning, creating a period where ozone and other pollutants exceed federal limits in urban areas downwind (Aurell et al., 2023; Liu et al., 2018; Simoneit, 2002). Because weather conditions (e.g., humidity, wind speed and direction) further limit opportunities for burning, establishing management practices that spread out the fire season can provide additional opportunities for applying fire and aid in conservation efforts (Wier, 2011). Broadening the burn window would allow more opportunities to effectively apply fire to achieve targeted outcomes, and could reduce negative impacts on regional air quality by decreasing the total area burned at one time and increasing the potential to burn under conditions that increase smoke dispersal. Greater flexibility in the timing of

prescribed burning could also enhance safety margins and reduce the chances of harming desirable species.

Prescribed burning in different seasons might also promote different species or functional groups of native plants to support greater landscape heterogeneity and biodiversity (Turner, 2010). For instance, spring burning enhances the early season growth and forage quality of warm-season grasses (Engle & Bidwell, 2001; Launchbaugh & Owensby, 1978). In the absence of grazers, the increase in warm-season grasses is accompanied by a decline in cool-season graminoids and forbs (Collins & Calabrese, 2012; Towne & Kemp, 2003), which are important components of plant biodiversity and resources for insects, including pollinators (Kral-O'Brian et al., 2021; Welte et al., 2018). Some plant functional groups also respond to timing of spring burns [e.g., warm-season grasses increase with late spring burning (Towne & Owensby, 1984), while forb species richness can be higher with early spring burning (Hulbert, 1986)]. Fall and winter burning (Nov–Feb) may benefit some forb and legume species (Dickson et al., 2019; Towne & Kemp, 2003). Prescribed summer fires are less common than dormant season fires due to fuel availability and condition, weather, and safety concerns. Despite these challenges, summer fires can increase native species richness and diversity, particularly among forbs (Towne & Kemp, 2008), and suppress certain invasive species (Alexander et al., 2021), though these outcomes are not consistent across prairies (Dickson et al., 2019; Engle & Bidwell, 2001; Weir & Scasta, 2017). A better understanding of the long-term effects of prescribed burning in different seasons on native plant species and functional groups is necessary to provide land managers and practitioners with effective strategies to influence grassland plant communities (Penman et al., 2011).

In this study, we evaluated the long-term effects of recurring prescribed fires applied in contrasting seasons (spring, summer, fall, and winter) on plant species and functional group composition in a native tallgrass prairie. We assessed plant community responses using 31 years of annual plant cover data collected in permanent sampling plots, replicated across two different topographic positions (lowland and upland) on two watersheds per fire treatment. We partitioned sampling by topographic position because variation in soil depth and water availability associated with topography in the Flint Hills and many other grasslands has a strong influence on plant community composition and responses to management (Collins & Calabrese, 2012; Milchunas et al., 1989). Our specific objectives were to (1) evaluate the effects of season-of-fire on plant community composition, including relative cover of major functional groups, native species richness, and native species diversity, (2) identify species-specific responses among burn treatments, and (3) assess how those responses vary by topographic position.

Methods

Study Site

The study was conducted at the Konza Prairie Biological Station, a 3,487-ha area of native tallgrass prairie located in the Flint Hills of Kansas (96.61° W, 39.11° N). The site is topographically complex and divided into a series of small watersheds, each assigned to a specific prescribed fire and/or grazing regime. Soils in lowlands feature deeper colluvial and alluvial deposits (typified by Pachic Argiustolls, Tully series), whereas the uplands are characterized as relatively shallow, silty clay loams overlaying layers of limestone and shale (typified by the Udic Argiustolls, Florence series) (Jantz et al., 1975). Plant communities vary with topography and fire/grazing treatments but are primarily composed of perennial warm-

season grasses (i.e., *Andropogon gerardii*, *Sorghastrum nutans*, *Schizachyrium scoparium*) and a mix of subdominant cool-season grasses, sedges, and forbs. Average annual precipitation is 817 mm with high interannual variability. During this study (1994–2024) the site experienced excessive heat and drought in 2011 and 2012 (Figure A.1). The 2012 drought, in particular, affected much of the Central Great Plains.

Experimental Design

We used data from eight watersheds assigned to one of four seasonal prescribed fire treatments (annual spring, fall, winter, or biennial summer burning) with two replicate watersheds per burning season treatment (Figure A.2). Watershed size varied from ~11 to 36 ha. Large grazers are excluded from these watersheds, which were last grazed by cattle in the mid-1960s (>25 years prior to the start of this study). Prior to 1994, fire return intervals on these watersheds varied but averaged about every 3 years. Beginning in 1994, watersheds assigned to winter, spring, and fall fire treatments were burned annually in February, April, and November, respectively, while watersheds assigned to the summer treatment were burned biannually typically in late July to mid-August, with timing depending on conditions suitable for prescribed burning. Summer burning was biannual because late summer burning in this region does not allow sufficient fuel accumulation to support another summer fire the following year (Table A.1).

Data Collection

Eight permanent transects for assessing plant species composition responses were established in 1994 in lowland (n=4 replicate transects) and upland (n=4 replicate transects)

topographic positions on each watershed. Each 50-m transect includes five 10-m² circular sampling plots spaced every 10 meters (n=20 sample plots per topographic position per watershed). This resulted in 40 plots for each combination of fire season and topographic position (two watersheds per fire season × four transects per watershed × five plots per transect). In each plot, canopy cover of all vascular plant species was recorded using a modified Daubenmire scale with 7 cover class categories (1 < 0–1%, 2 = 1–5%, 3 = 5–25%, 4 = 25–50%, 5 = 50–75%, 6 = 75–95%, 7 = 95–100%) (Bailey & Poulton, 1968; Hartnett et al., 2025). Species cover was assessed twice annually (late-May and August) over a 31-year period (1994–2024). Late-season sampling in the summer burn treatment always occurred before burning. Data from late-May and August surveys was combined by year and if the same species occurred in the same plot in both late-May and August, only the highest value was used. For all analyses, we used the midpoint value of a species' cover class and converted that to a relative cover value based on total plant cover in each plot by year. In 2011, prior to the late-season survey, watershed FB (a fall burn) experienced a wildfire and was removed from all analyses for that year.

Data Analysis

To evaluate treatment effects on community composition, we aggregated native species into functional groups: warm-season graminoids, cool-season graminoids, non-legume forbs, and legumes. Relative cover values were summed by functional group for each plot, averaged within transects, and then averaged across burn treatments and topographic positions. We calculated native species richness and effective number of equivalent species (e^H) from Shannon's index (H) (Jost, 2006) at two spatial scales: plots (10 m²) and catchments (200 m²), with catchment-level values representing the combined response across all plots within each topographic

position. Separately, we calculated native annual and perennial forb richness at the catchment scale. Catchment-scale averages of functional group cover are very similar at both scales, whereas species richness and Shannon's diversity vary by scale. We also conducted multivariate community composition analysis by topographic position and burn treatment.

To characterize temporal changes in functional group and species cover, we fit generalized additive models (GAMs) (Wood, 2017) for each combination of burn treatment and topographic position (Tables S2 and S3) using the formula $y \sim s(x, bs = 'cs') + \text{burn season} \times \text{topographic position}$, with Gaussian distribution and knots 'k' set to 15 (i.e., half the number of years per treatment). We used model predictions with 95 percent confidence intervals of the mean to visualize community dynamics. We interpreted non-overlapping intervals as significant differences among burn treatments (similar to Collins et al., 2021).

We also assessed potential directional changes in functional group cover over the entire study period using linear mixed-effects models (LMMs). For each response variable, we created an LMM with burn season, topographic position, and year as fixed effects, and watershed as a random intercept. Slopes for each burn season $\times$ topographic position combination were estimated using the Kenward-Rogers method in the *emmeans* package (Lenth et al., 2024). To meet assumptions of normality and homoscedasticity, response variables were transformed as follows: 1) cool-season graminoid cover and catchment-level Shannon diversity were log-transformed; 2) non-legume forb cover and plot-level richness were square-root transformed; 3) legume cover and plot-level Shannon diversity were cube-root transformed; and 4) catchment-level richness was reciprocal-transformed.

To examine changes in annual and perennial forb richness, we fit linear regressions to each burn season $\times$ topographic position $\times$ life history (annual or perennial) combination.

Richness was calculated as the number of unique native forb species at the catchment scale and averaged by year. Model predictions with 95% confidence intervals were used to compare and visualize temporal trends.

Representative species within functional groups were selected for further analysis based on relative abundance using average species cover in the first (1994–1998) and last five (2020–2024) years. Species were chosen separately for lowlands and uplands to reflect differences in dominant species. Because cover deviated from normality, changes over time were tested using Kruskal-Wallis, followed by Dunn’s post hoc test with Hochberg correction. Post hoc contrasts were used to evaluate 1) differences among burn seasons within each period (first and last five years) and topographic position, and 2) differences between initial and final cover within each burn season and topographic position.

Effects of burn season and topographic position on multivariate community composition were evaluated using non-metric multidimensional scaling (NMDS) based on a Bray-Curtis dissimilarity. Rare species (occurring in < 5% of plots) were excluded, and cover values were square-root transformed to reduce mean-variance correlation (Warton & Hui, 2017). NMDS was performed using the metaMDS function in the *vegan* package (Oksanen et al., 2024). Significance of burn season, topographic position, year, and their interactions was tested using permutational multivariate ANOVA (PERMANOVA; *adonis2* in *vegan*). All analyses were performed in R (v. 4.2.2; R Core Team, 2022).

Results

Overview: Over 31 years, we recorded 208 unique species across all burn treatments and topographic positions. Total species observed per year ranged from 115–149. Native plant

species comprised >97% of the total plant cover. Relative cover of some functional groups (e.g., warm-season graminoids and non-legume forbs) exhibited pronounced fluctuations, driven largely by interannual variation in total plant cover. However, some general patterns in functional group responses emerged; both annual and biennial fires promoted or maintained high graminoid cover and reduced or maintained low cover of non-legume forbs regardless of fire season. Warm-season grasses were the dominant functional group across all treatments and topographic positions. Cool-season graminoids decreased under spring burning but maintained moderate cover under all other season-of-burn treatments, with large increases in uplands. Native species richness and diversity varied more with burn season than topography, while species-specific responses varied with both burn season and topographic position.

Functional group responses: Spring burning is the most common regional burn practice. For each response variable, we begin with spring burning as a baseline to which we contrast the alternative seasonal burn treatments. We present cover responses in lowlands first and then uplands. Warm-season graminoids, consisting mainly of perennial C₄ grasses, were the dominant functional group across all burn treatments, though relative cover varied among treatments (Figure 2.1A). In spring-burned lowlands, warm-season graminoid cover increased for the first five years, then decreased before settling around a relatively stable cover of 65%. Lowland warm-season graminoid cover in all other seasonal fire treatments was substantially lower than under spring burns for most of the first ~20 years and ended between 50–55%. Warm-season graminoid cover in upland spring burns increased significantly ($p < 0.001$, Table A.4) to ~75%. Warm-season graminoid cover was more variable in non-spring burned uplands, but still increased with time ($p < 0.001$), despite notable oscillations in summer burns, and a sharp

decrease across summer, fall, and winter burns in 2011 and 2012, coinciding with an extreme drought. By the end of the study, all non-spring burned uplands had lower warm-season graminoid cover than spring burns, averaging ~50% in summer burns and ~57% in fall and winter burns (Figure 2.1A).

Cool-season graminoids were mainly sedges but included some C₃ grasses. Spring burning significantly reduced cool-season graminoid cover in both uplands and lowlands over the first ~10 years to near 0% ($p < 0.001$, Table A.4, Figure 2.1B). In lowlands under non-spring burning, cool-season graminoid cover initially decreased for ~8 years, then increased for ~10 years before settling at a final cover of ~9% in summer burns and ~7% in fall and winter burns. Upland responses to non-spring burns were similar, except that the increases in cool-season graminoid cover under summer, fall, and winter burning were larger. By the final year, upland cool-season graminoid cover in summer burns was ~17% and potentially increasing. In the fall and winter burns, cool-season graminoid cover appears to have plateaued at ~14% (Figure 2.1B).

Non-legume forb cover initially ranged from 15–28%, exhibited large interannual fluctuations, and ended significantly lower across all burn treatments in both lowlands and uplands (Figure 2.1C, Table A.4). In lowland spring burns, non-legume forb cover decreased by ~50% in the first five years before rebounding and fluctuating between 13% and 24% cover through the remainder of the study. In lowland non-spring burns, non-legume forb cover initially increased, with summer burns peaking around 42% cover and fall and winter burns around 31% cover. This was followed by sharp declines in all non-spring burns. Non-legume forb cover in lowlands oscillated widely under summer burns, while fall burning maintained cover similar to spring burns after 2008 and cover in winter burns declined throughout the study. Final non-legume forb cover was ~13% for spring, summer and fall burns and ~7% for winter burns. Non-

legume forb cover responses in uplands were similar to lowlands, except that cover among burn seasons converged during the last ten years to 11–15%.

Legume cover was much higher in lowlands than uplands for all burn treatments (Figure 2.1D). In lowlands, initial cover ranged from 8–9% and increased under all burn treatments ($p < 0.001$; Table A.4). In lowland spring burns, legume cover increased linearly to 22%. Legume cover in summer burns remained below 10% until ~2011 and then gradually rose to ~18%. Legume cover increased most in fall and winter burns to ~26% by 2016. Cover in fall burns experienced a transient decline to 17% around 2020 before recovering to 24% while cover in winter burns continued to rise to 34%. In uplands, legume cover remained below 8% across all burn treatments. Spring burning maintained 5–6% cover, while upland legume cover exhibited small but significant increases in all non-spring burns (Figure 2.1D, Table A.4).

Native species richness and diversity: Native species richness at the plot level (10 m^{-2}) responded similarly to season-of-burn treatments across topographic positions (Figure 2.2A). Initial richness was 18–20 species in lowlands and 17–20 in uplands and generally increased in all treatments during the first decade (Table A.4) before diverging. Plot-level richness then decreased under spring burning ($p < 0.001$), falling sharply from ~24 to 16 species (33% decrease) in the lowlands and from ~23 to 18 species (22% decrease) in the uplands after 2007. In contrast, summer burning increased plot-level richness from 19 to 24 species (26% increase) in lowlands ($p < 0.001$) and from 18 to 28 species (56% increase) in uplands ($p < 0.001$). After 2002, summer burning maintained higher richness than any of the dormant-season burn treatments. Fall and winter burning produced comparable plot-level richness, which was intermediate to spring and summer. However, richness in fall burned lowlands had a decreasing

trend ($p < 0.001$), while winter burned uplands increased slightly with time ($p = 0.03$). By the end of the study, fall and winter burns supported between 19–21 species per plot in lowlands and 22–23 in uplands.

Native species richness responses to season-of-burn treatments at the catchment scale (200 m², Figure 2.2B) were similar to plot-scale responses. Initial richness across treatments ranged from 52–62 species in lowlands and 46–55 in uplands. Spring burning led to decreasing richness at both topographic positions ($p < 0.001$, Table A.4). Although richness under spring burning was relatively stable or marginally increasing for the first 14 years, it then declined to ~46 species by year 31. In contrast, summer burning resulted in consistently higher catchment-scale richness compared to any dormant-season treatment. In lowlands, richness ranged from 61 to 69 species, while in uplands, richness increased by 70%, from 46 to 78 species ($p < 0.001$). Catchment-scale richness under both fall and winter burning generally declined over time in lowlands. Richness under fall burning declined steadily from 59 to 52 species ($p < 0.001$) and diverged from spring burns after 2012. In contrast, richness under winter burns initially rose to 62 species before declining to 53 species by year 31 ($p < 0.01$). Catchment-scale richness in uplands under fall and winter burns followed trajectories similar to spring burns, remaining relatively stable at 52–53 species and becoming intermediate to spring and summer burns after 2018 (Figure 2.2B).

Native species diversity responses were generally similar to species richness, although diversity declined during the first five years in all treatments (Figure 2.2C). At the plot level, initial diversity across treatments was 7–10 effective species. Species diversity in all dormant-burning treatments decreased over time, with spring burning producing the strongest declines ($p < 0.001$, Table A.4) and maintaining the lowest diversity (5–6 effective species) for most of the

study. In contrast, plot-level diversity under summer burning recovered following initial declines and remained the highest after 2008 (7–9 effective species), with a significant increasing trend in uplands ($p < 0.01$). Fall and winter burning yielded plot-level diversity that was intermediate to spring and summer treatments after 2006 (Figure 2.2C).

Catchment-level diversity exhibited prominent declines in the first five years (Figure 2.2D) with the steepest declines under spring burning, with 8–10 effective species after 1998 and diversity in uplands briefly dropping to 6 effective species during the 2012 drought. Summer burning supported the highest catchment level diversity (13–16 effective species in lowlands and 11–15 in uplands) which was greater than all dormant season treatments after 2008. Catchment-level diversity in both fall and winter burns was more variable, but generally declined over time. In lowlands, diversity under fall burns had high variability and was generally intermediate to spring and summer burning. Winter-burned lowlands began with the lowest diversity and, after 2000, remained similar to spring burns. In uplands, fall and winter burning maintained diversity comparable to summer burns from 1996 to 2007, before declining to levels comparable with spring burns while catchment-scale diversity under summer burns increased. By the end of the study, diversity in all dormant-season burn treatments averaged 8–9 effective species in both lowlands and uplands, while summer burns averaged 13–14 species.

Native perennial and annual forb richness: Forbs contribute disproportionately to diversity in tallgrass prairie, and both native annual and perennial forb richness varied with burn season and topographic position (Figure 2.3). Perennial forb richness at the catchment-scale ranged from 25–43 species, while annual forb richness ranged from 1–19 species. Dormant season fires supported ten or fewer annual forb species in any given year and spring burning

significantly reduced both groups ($p < 0.02$, Table A.5). In lowlands, perennial richness under spring burning declined from 31 to 25 species, and annual richness declined from 8 to 3 species (Figure 2.3A). In uplands, perennial richness decreased from 34 to 30 species, while annual richness decreased from 4 to 2 species. Summer burning produced no directional change in forb richness in lowlands, while in uplands, perennial richness increased from 34 to 40 species ($p < 0.001$) (Figure 2.3B). Both fall and winter burned reduced perennial richness in lowlands ($p < 0.01$) (Figure 2.3C, Figure 2.3D). Fall burning also reduced annual forb richness from 4 to 1 species in both topographic positions ($p < 0.001$). In uplands, winter burning decreased annual forb richness from 4 to 2 species ($p < 0.01$) but increased perennial forb richness from 32 to 34 species ($p < 0.01$).

Species-specific responses: Next we present responses of species that were most representative of their respective plant functional groups (Figure 2.4, Figure A.3) based on relative cover in each topographic position during the first and last five years of the study (Table A.6, A.7). In the first five years, these species accounted for 78% of total cover in the lowlands and 73% in the uplands; in the last five years, their contribution rose to 86% and 83%, respectively.

Warm-season grass species: *Andropogon gerardii* was dominant in all burn treatments. Initial cover ranged from 22–42% in lowlands and 22–31% in uplands. In lowlands, there was little difference in initial and final cover under spring burns, but cover increased under summer burns ($p = 0.024$) and decreased under winter burns ($p < 0.001$). After the first 14 years, treatment differences diminished and cover in lowlands stabilized between 28–32% in all

treatments. In uplands, spring burning nearly doubled *A. gerardii* cover from 22% to 39% ($p < 0.001$), whereas non-spring burns maintained around 26–31% cover. Cover of *A. gerardii* exhibited high interannual variability, particularly in the summer burns (Figure 2.4A, Figure A.2A). *Schizachyrium scoparium* was most abundant in uplands and responded more strongly to treatments in uplands than in lowlands. In lowlands, *S. scoparium* cover remained below 10% in all burn treatments, with small decreases under spring burning ($p < 0.01$) and small increases under summer burns ($p < 0.01$). In uplands, *S. scoparium* cover remained around 14% under spring burning but increased from 1% to 10% in summer burns ($p < 0.001$), from 10% to 28% in fall burns ($p = 0.014$), and from 11% to 30% in winter burns ($p < 0.01$) (Figure 2.4B, Figure A.2B). *Sorghastrum nutans* responded most strongly to spring burning. In spring-burned lowlands, cover rose from 8% to 25% before declining to 17% ($p < 0.01$). In spring-burned uplands, *S. nutans* cover increased from 13% to 20% before declining to 15%. Across both topographic positions, all non-spring burns resulted in low cover (5–9%) of *S. nutans*, with winter burned uplands declining from initially higher cover into this range ($p < 0.001$) (Figure 2.4C, Figure A.2C). *Panicum virgatum* was initially 1–3% cover in all treatments and increased under all dormant-season burns in both uplands and lowlands, but remained below 1% under summer burns. In lowlands, *P. virgatum* cover increased to 9–11% under spring ($p = 0.021$), fall ($p < 0.001$), and winter burns ($p < 0.01$). In uplands, increases in *P. virgatum* cover were smaller, with spring burning producing the highest cover (6%) (Figure 2.4D, Figure A.2D). *Sporobolus compositus* cover in lowlands declined under all dormant season burns, dropping from 3–5% to ~1% (spring & fall: $p < 0.001$; winter: $p = 0.024$). In contrast, summer burning increased *S. compositus* cover in lowlands from 5% to 8% with high interannual variability throughout. In

uplands, spring burns reduced cover of *S. compositus* ($p < 0.001$), while summer, fall, and winter burns had little effect (Figure 2.4E, Figure A.2E).

Cool-season species: *Carex inops*, a sedge, was the most abundant cool-season graminoid, particularly in the uplands. While initially absent in the sample plots, its cover increased across all treatments ($p < 0.01$) except spring-burned lowlands. In lowlands, summer burns supported higher cover of *C. inops* relative to dormant season burns, where cover was $< 1\%$. In uplands, non-spring burns resulted in a sharp increase between 1998 and 2008 to 10–14% cover (Figure 2.4F, Figure A.2F). *Carex meadii* was more abundant in lowlands than uplands. In lowlands, non-spring burning increased cover of *C. meadii* from $\sim 1\%$ to 2–4% ($p < 0.001$), with winter burns generally yielding the highest cover. There was also a notable transient decrease in *C. meadii* in the summer burn treatment during the 2011–12 drought. In uplands, *C. meadii* cover averaged $< 2\%$ across all burn seasons, but increased with summer burns ($p < 0.01$) (Figure 2.4G, Figure A.2G). *Koeleria macrantha* was the most abundant C_3 grass, but a minor species overall, with nearly zero cover in lowlands. In uplands, it had some transient increases but ended near zero under spring burns, and $\sim 2\%$ cover in all other treatments. One surprising response was a sharp peak of *K. macrantha* in the summer burn during the 2012 drought (Figure 2.4H, Figure A.2H).

Forb and legume species: *Symphytotrichum ericoides* had the highest cover of non-legume forbs early in the study, but generally declined in all burn treatments. Spring burns had low cover ($< 2\%$) of *S. ericoides* throughout the study in both topographic positions. In non-spring burned lowlands, cover increased to over 20% in the first decade, then declined by

approximately 75–90% by the end of the study ($p < 0.001$). In uplands, *S. ericoides* cover also declined following transient initial increases, dropping to ~3–4% under summer ($p < 0.01$), fall ($p < 0.01$), and winter burns (Figure 2.4I, Figure A.2I). *Solidago altissima* occurred primarily in lowlands, where initial cover ranged from 4–7% under spring, summer, and fall burns. Spring and fall burns generally maintained this level, while *S. altissima* cover declined to $< 1\%$ under summer burns. Winter burning increased *S. altissima* cover to ~6% over the first 15 years before declining to $< 1\%$ in both winter and summer burns (Figure 2.4J, Figure A2J). *Symphytotrichum oblongifolium* was largely absent in lowlands but relatively abundant in uplands. Under spring burning, cover initially declined before increasing to 4%. In non-spring burns, *S. oblongifolium* cover initially increased to 6–12%, potentially representing a transient peak, before declining and stabilizing at ~2–4%. Despite these different dynamics, cover of *S. oblongifolium* was similar in all treatments during the last five years (Figure 2.4K, Figure A.2K). *Lespedeza violacea* was the most abundant legume and occurred primarily in lowlands where the initial cover of *L. violacea* ($< 4\%$) increased substantially under all burn treatments. Under spring burns, cover increased linearly to ~15% ($p < 0.01$), while cover in summer burns increased from $< 1\%$ to ~7% ($p < 0.001$). Fall burning also increased *L. violacea* cover, which peaked at 23% and ended at ~19% ($p < 0.001$). Winter burning produced the strongest increase in *L. violacea*, with cover reaching 29% by the end of the study ($p < 0.001$). Cover of *L. violacea* appeared to be continuing to increase in all treatments at the end of the study (Figure 2.4L, Figure A.2L). *Amorpha canescens*, another legume, either declined or maintained relatively low cover in both lowlands and uplands. In lowlands, cover declined from 3–4% initially to 1–2% in all burn treatments during the first 15 years. *A. canescens* cover remained near 2% under spring burns, increased to ~5% under summer burns and 3% under winter burns, and declined to 2% under fall burns ($p = 0.013$). In

uplands, *A. canescens* cover declined under spring burning. Cover under summer and fall burns also declined slightly during the initial 15 years, but later regained lost cover, while *A. canescens* cover in winter-burned uplands remained < 1% throughout the study (Figure 2.4M, Figure A.2M).

Exotic and woody species: *Poa pratensis* was the most abundant non-native species in the study. In most burn treatments, *P. pratensis* cover dropped quickly and remained ~1% in both lowland and uplands. Cover of *P. pratensis* was initially higher in the summer burn treatment (6% in lowlands and 15% in uplands), but declined to ~2% except for a brief transient increase to ~6–7% between 2012 and 2014 following a 2011 drought (Figure 2.4N, Figure A.2N). *Rhus glabra*, a clonal woody species, had low initial cover in all treatments, except for summer burned uplands where cover was 10–15% as a legacy of pre-treatment conditions. In lowlands, *R. glabra* cover was low and declined to near zero under all burn treatments, with no detection in the last five years under summer and fall burns. In uplands, *R. glabra* cover also declined to near 0% in all treatments, except for spring burns, where cover increased slightly to ~2%. In summer-burned uplands, *R. glabra* cover started high but declined steadily after the first six years to < 1 % by 2012 (Figure 2.4O, Figure A.2O).

Multivariate community composition: Community composition differed significantly with burn season, topographic position, year, and their interactions (PERMANOVA $p < 0.001$; Table A.8). Differences between upland and lowland topographic positions explained the greatest variation (32%) in composition, followed by burn season (21%) and year (5%). Treatments clustered distinctly by topographic position, with a secondary clustering among burn seasons

within each position (Figure 2.5). Spring and summer burned communities were consistently furthest apart in ordination space, with fall and winter burned communities intermediate. Although fall and winter burned communities appear to overlap in many years, pairwise comparisons confirmed that all burn regime treatments were significantly different from one another ($p < 0.001$).

Discussion

Prescribed fire is used widely for managing many grasslands, including tallgrass prairie (Courtwright, 2011; Rowe, 2010; Pyne, 2017), but the frequency, intensity, and environmental conditions under which fire is applied play a major role in driving plant responses and community outcomes (Collins & Calabrese, 2012; Engle & Bidwell, 2011). In the Flint Hills and many other grasslands, late spring shortly before green-up is the most common time for prescribed burning (KDHE, 2025; Hsu et al. 2025; Mohler & Goodin, 2012). However, fires historically occurred at other times of year (Courtwright, 2011; Pyne, 2017). We found that three decades of burning outside of the typical spring-window resulted in distinct plant communities, and that both functional group and species-specific responses to different season-of-burn treatments were often highly dependent on topographic position and associated soil differences. Many plant responses to season-of-burn were neither linear nor unidirectional, and they often differed substantially between early and late stages of the study, with some responses still changing even after 31 years. These topoedaphic differences and temporal dynamics complicate prediction and inference based on short-term or topographically-constrained studies, and highlight the need for long-term studies that incorporate key features of landscape-scale variation. Below, we first discuss the temporal dynamics of plant community changes and the

importance of topography as a driver of spatial variability in plant community responses to season-of-fire, then summarize our major findings regarding responses to prescribed fire in different seasons.

Temporal Variability and Transient Dynamics. The season-of-burn treatments produced a surprisingly rich range of dynamics, including non-linear, delayed, and cyclical responses that only emerged over decadal scales. As a result, the plant cover values or dynamic behavior of species early in the experiment often differed substantially from the end of the experiment, when many community responses appeared to have leveled out for at least the last eight years of data. Non-linear responses were common. For instance, in lowlands, cool-season graminoid cover decreased more than 50% across all burn seasons over the first seven years. Based on this trajectory, we might have expected near extirpation of cool-season graminoids from all treatments in 10–12 years, yet this occurred in none of the treatments. Under spring burning, cool-season graminoid cover did eventually decline to nearly zero, but not until around year 20. Under fall and winter burns, cover rebounded over a 15-year period, followed by a slight decrease and then a plateau. Under summer burning, cover recovered almost entirely. Delayed and cyclical dynamics were also evident, including responses that appeared to overshoot initial or long-term average cover values (e.g., upland cool-season graminoid cover under summer, fall, and winter burns; lowland legume cover under fall burns), as well as 4–5 year cyclical patterns, most pronounced in biennial summer burns. Some responses exhibited an initial period of non-response followed by an eventual decline, including native species richness in many burn seasons and non-legume forbs in fall and winter burns. Other studies in tallgrass prairie and other productive grasslands have also reported delayed and transient responses to novel or altered

experimental treatments (Blair, 1997; Knapp et al., 2012; Komatsu et al., 2025) and noted differences between short- and long-term responses to a change in disturbance regimes or chronic resource alterations (Ratajczak et al., 2017; Smith et al., 2009).

Topographic Position. We expected some divergent effects of burn season in uplands versus lowlands since plant community composition varies with topographic position across these landscapes. Lowlands, at this site and regionally, have deeper soils (>1 m), fewer rock fragments, and much higher water-holding capacity than upland soils (Briggs & Knapp, 1995; Ransom et al., 1998). Upland soils are generally much shallower (~0.25 m) and overlay fractured limestone layers, limiting both water-holding capacity and plant rooting depth. Not surprisingly, we found plant community composition was strongly influenced by topographic position, resulting in a pronounced separation in ordination space (e.g., Figure 2.5). These environmental differences are reflected in both community composition and ecosystem processes (e.g., plant productivity, Nippert et al., 2007). Although frequent burning can homogenize aspects of prairie plant communities under comparable soil and environmental conditions (Collins & Calabrese, 2012; Gibson & Hulbert, 1987), we found that many species-specific and plant functional responses to burn season varied with topographic position (e.g., Figs. 2.4 and 2.5). For example, cover of some dominant tallgrass species, *P. virgatum* and *S. altissima*, was greatest in lowlands, whereas the short bunchgrass *S. scoparium* and forb *S. oblongifolium* favored uplands. These differences occurred even though native species richness and diversity values were broadly similar. This suggests that management strategies using fire should account for species-specific responses among topographic positions in topographically complex landscapes.

Responses to Burning in Different Seasons:

Spring Burning: Prescribed burning during the dormant season is common in grasslands, especially in parts of South America, Eurasia, and certain regions of Europe (Hsu et al. 2025). In the Flint Hills, prescribed spring burning typically occurs in or around April when warm-season grasses and most other native plants are dormant, though some early-season graminoids and forbs may be active. This favors warm-season grasses, as spring fires create conditions favorable for early emergence, rapid growth, and enhanced acquisition of resources (Blair et al., 2014; Knapp & Medina, 1999). Spring burning amplifies the competitive advantages of C₄ grasses, which typically grow taller, develop more tillers and fibrous roots, and exhibit faster growth rates and higher nutrient-use efficiencies than many other herbaceous species (Benson & Hartnett, 2006; Knapp & Medina, 1999; Nippert & Helliker, 2026). In our study, spring burning increased warm-season graminoid cover more than burning in any other season, primarily by increasing cover of three tall productive species: *A. gerardii*, *S. nutans*, and *P. virginica*. This increase in warm-season graminoid cover coincided with a pronounced decline in cool-season graminoids, consistent with previous studies (Henderson, 1990; Towne & Kemp, 2003, 2008), and likely reflects enhanced competition for resources (Smith & Knapp, 2003). Dominance of warm-season grasses is generally correlated with reduced plant richness and diversity in these grasslands at local scales (Collins & Calabrese, 2012). When extensive areas of grasslands in a region are all managed with frequent prescribed spring burning, the enhanced dominance of warm-season grasses also diminishes landscape-level heterogeneity by limiting the recruitment of native forbs and other subdominant species (Collins & Calabrese, 2012; Zimmermann et al., 2008). These effects may be further compounded if fire occurs during the early phenological stages of some forb species (Lovell et al., 1982; Pavlovic et al., 2011).

We found that spring burning reduced both annual and perennial forb richness in both lowlands and uplands, relative to burning in other seasons. However, spring burning also had the largest impact on reducing cover of *P. pratensis*, a non-native species (e.g., Tables S6 and S7), consistent with prior findings of reduced invasibility of tallgrass prairie managed with annual spring burning (Smith & Knapp, 1999). Our results mirror previous studies showing that frequent spring burning favors a few highly productive warm-season grasses at the expense of other functional groups, resulting in lower diversity communities and a likely reduction of ecosystem services associated with greater diversity (Hooper et al., 2005; Tilman et al., 2014). Although these plant community responses may align with management goals that emphasize warm-season grass dominance (e.g., maximizing forage for domestic grazers), suppression of other functional groups conflicts with goals focused on conserving and maintaining biodiversity. These ecological trade-offs, coupled with rising concerns associated with degraded air quality from temporally compressed fire highlight the need to diversify the seasonal timing of prescribed burning.

Summer Burning. Prescribed summer fires are less common in tallgrass prairies, although there is historical precedent and growing interest in their application (Howe, 1994). Because summer fires occur while dominant warm-season grasses are active, they may alter competitive dynamics and resource availability in ways distinct from dormant season burns. Growing season fires are typically less intense than dormant season fires (Aurell et al. 2023; Engle & Bidwell, 2001; Knapp et al., 2009), but still remove accumulated litter, open the canopy, and alter the resource environment (i.e., light, nutrients, and soil warming) at a time that may benefit less competitive species (Bakker et al., 2003; Howe, 2011; Knapp et al., 2009). The

timing of summer fires is critical, as summer burning overlaps with a period of high photosynthetic rates and growth, especially for dominant warm-season grasses and mid-to-late flowering forbs (e.g., goldenrods), potentially impacting flowering or seed production of these species (Pavlovic et al., 2010). Despite this, we observed a trend for increasing cover of warm-season grasses at a similar rate as dormant-season burns, although total cover remained lower in uplands. This trend for increasing cover was driven in part by subdominant species such as *S. compositus* and *Sporobolus heterolepis* (Table A.6, A.7), whereas dominant grass species like *P. virgatum* and *S. scoparium* either maintained low cover or increased slowly. Suppressing the dominant warm-season grasses may enable the late-season recruitment of cool-season graminoids without negatively affecting existing warm-season cover (Copeland et al., 2002). Cool-season graminoids, which benefited most under summer burns in our study, may improve forage quality and provide important resources for livestock and wildlife during cooler, wetter periods.

Despite declines in cover of non-legume forbs and only gradual increases in legume cover, we found that summer-burned communities had higher native species richness and diversity compared to dormant-season burns, driven by both native annual and perennial species across multiple functional groups, particularly perennial forbs. The increase in forb diversity may increase resources for pollinators and a diverse array of insect herbivores and associated trophic interactions (Kral-O'Brian et al., 2021; Robertson & Rebar, 2022), thereby reinforcing ecosystem stability; as higher diversity may also contribute to greater ecosystem resilience (Isbell et al., 2015; Loreau et al. 2021; Tilman et al., 2014). While our summer burns were conducted biennially, we believe that the differences we observed compared to dormant season fires were driven by seasonal timing of burning, rather than annual versus biennial fire frequency.

Comparable data from our study site (Hartnett et al., 2025) suggests that plant communities burned biennially in the spring are more similar to those burned annually in spring than those under biennial summer burns. Overall, our results indicate that growing season burning supports additional subdominant and uncommon species, especially in upland sites, suggesting that incorporating summer burns into management plans may promote more heterogeneous and resilient plant communities compared to spring burns.

Fall and Winter Burning. Dormant season burning in fall or winter has some similarities with spring burning (i.e., removal of detritus at a time most plants are dormant) and can provide increased flexibility for conducting prescribed burning under suitable weather conditions. A broader window for dormant season burning may also lessen the negative air quality impacts associated with limiting extensive regional burning to a narrow spring window (Aurell et al., 2023; Liu et al., 2018). Both fall and winter burns were consistent in their effects on functional groups and native species richness and diversity after the initial five years. This trend was also apparent in ordination space where fall- and winter-burned communities either converged or followed similar directional changes depending on topographic position. The similarities in fall and winter burning are likely due to similar fuel conditions, fire intensity, and reduced above and belowground biological activity during this period (Nov–Feb). During this time, most vegetation is dormant and soil microbial activity is low, limiting physiological and biogeochemical responses to fire.

Both fall and winter burns generally resulted in warm and cool-season graminoid cover and native species richness and diversity that was intermediate to spring and summer fires. There was also a substantial shift from non-legume forb cover to greater legume cover, particularly in

the lowlands, where legume cover more than doubled. Though this was driven largely by one species, violet bushclover (*L. violacea*). Similar responses have been documented in other late-season burn studies, although the separation between non-legume forb cover and legume cover is less clear (Dickeson et al., 2019). Increased legume cover may enhance nitrogen fixation, an important ecosystem service in frequently burned grasslands where nitrogen is a limiting resource (Blair, 1997; Ojima et al., 1994; Seastedt et al., 1991), thereby helping sustain long-term productivity. While fall and winter burning did not promote plant species diversity to the same extent as summer burns, they may be a viable management alternative for increasing legume cover and balancing plant functional groups, particularly when spring burning is constrained by weather, safety, or environmental concerns. Overall, fall or winter burns represent a management option that balances the dominance of highly productive warm-season grass species in spring burns with the biodiversity benefits associated with summer burns.

Summary and Management Implications

Our findings highlight that the timing of fire, and its interaction with topography, can drive community change, with important implications for prairie management at broader spatial and temporal scales. Long-term data were essential for understanding these dynamics, as high interannual variability among treatment responses demonstrated that conclusions could differ depending on study duration.

The most striking differences in plant community outcomes were between spring and summer burns. For almost all metrics and scales, native plant richness and diversity were lowest under spring burning and highest under summer burning. Spring burning consistently produced the highest cover of the perennial C₄ grasses that typically dominate these communities (e.g.,

Figure 2.1A). Burning at other times of year also maintained or enhanced warm-season graminoid cover, but generally at a lower level than spring burning. This is noteworthy because competition from the dominant warm-season grasses is generally thought to reduce the abundance and cover of subdominant species (i.e., cool-season graminoids and most forbs) and reduce biodiversity in these grassland communities (Collins et al., 1998; Howe, 1995). In our study, cool-season graminoids were nearly absent from spring burns, but relatively abundant in all non-spring burns (e.g., Figure 2.1B), consistent with a lower warm-season grass cover in non-spring burn treatments that was most evident in the uplands. Burning in any season tended to reduce non-legume forb cover, though burning outside of the spring produced transient periods of high forb cover that did not occur under spring burning (e.g., Figure 2.1C). Burning also increased legume cover in the lowlands, particularly under fall and winter burns (e.g., Figure 2.1D). The observed differences in functional group cover can be largely attributed to a few abundant species in each group and their specific response to burn season $\times$ topographic interaction.

Our results suggest that diversifying burn timing can produce communities that vary in functional group composition and aid in creating more heterogeneous and diverse landscapes. This could offset some of the trade-offs currently associated with widespread prescribed spring burning in areas like the Flint Hills, where frequent burning is necessary to limit woody expansion and maintain a grassland state. Prescribed burning at the same time each year creates consistent environmental constraints that favor a few species and reduce recruitment opportunities, whereas introducing variation in burn timing across the landscape can provide a flexible and cost-effective means to counteract these pressures and maintain more diverse tallgrass prairie. Importantly, this does not imply burning entire properties out-of-season, which

is impractical for most managers, but rather incorporating variation in burn season to enhance heterogeneity, creating a mosaic of patches that differ in species composition, structure, and functional group dominance (McGranahan et al., 2018). Heterogeneity in timing and spatial application of fire can help maintain a balance between highly productive dominant species and the diverse suite of subdominant and uncommon species that contribute to ecosystem resilience and functioning while distributing smoke emissions more evenly throughout the year (Aurell et al., 2023; Dickeson et al., 2019; McGranahan et al., 2018). While many factors influence temperate grasslands, the interaction between burn season, variable burn timing, and grazing remains understudied (Towne & Craine, 2016). Relatively few studies have examined how fire timing affects primary productivity (Dickson et al., 2019; Towne & Craine, 2014), soil properties, and erosion potential, or how the effects of fire season may be modified by large herbivores such as cattle or bison. Addressing these gaps will improve our understanding of how fire timing can be used to maintain diverse and functional temperate grasslands.

Acknowledgements

This research was supported by DEB-2025849 and multiple grants from the National Science Foundation's Long-Term Ecological Research Program (LTER) to support the Konza Prairie LTER program. JMB and ZR were supported by the Agricultural Experimental Station at Kansas State University. We thank Gene Towne for collecting species composition data from 1994–2014, Patrick O'Neal and Jim Larkins for overseeing the management of these watersheds and Konza Prairie as a whole, and the numerous people who have voluntarily helped with prescribed burning over the years. This is contribution number 26-XXX-J from the Kansas Agricultural Experiment Station.

Author Contributions

JMB and AJG conceptualized the study. JHT conducted field sampling and collected much of the data. ZR assisted with statistical analysis. All authors contributed to writing and editing the manuscript.

References

- Allen, M. S., and M. W. Palmer. 2011. "Fire history of a prairie/forest boundary: more than 250 years of frequent fire in a North American tallgrass prairie." *Journal of Vegetation Science*, 22(3): 436–444. <https://doi.org/10.1111/j.1654-1103.2011.01278.x>.
- Alexander, J. A., W. H. Fick, S. B. Ogden, D. A. Haukos, J. Lemmon, G. A. Gatson, and K. C. Olson. 2021. "Effects of prescribed fire timing on vigor of the invasive forb sericea lespedeza (*Lespedeza cuneata*), total forage biomass accumulation, plant-community composition, and native fauna on tallgrass prairie in the Kansas Flint Hills." *Translational Animal Science* 5(2): txab079. <https://doi.org/10.1093/tas/txab079>.
- Anderson, R. C. 2006. "Evolution and origin of the Central Grassland of North America: climate, fire, and mammalian grazers." *The Journal of the Torrey Botanical Society* 133(4): 626–647. [https://doi.org/10.3159/1095-5674\(2006\)133\[626:eaootc\]2.0.co;2](https://doi.org/10.3159/1095-5674(2006)133[626:eaootc]2.0.co;2).
- Archer, S. R., E. M. Andersen, K. I. Predick, S. Schwinning, R. J. Steidl, and S.R. Woods. 2017. "Woody plant encroachment: causes and consequences." In *Rangeland systems: Processes, management and challenges*, edited by Briske, D, 25–84. Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-46709-2_2
- Aurell, J., B. Gullett, G. Grier, A. Holder, and I. George. 2023. "Seasonal emission factors from rangeland prescribed burns in the Kansas Flint Hills grasslands." *Atmospheric Environment* 304: 119769. <https://doi.org/10.1016/j.atmosenv.2023.119769>.
- Axelrod, D.I. 1985. "Rise of the grassland biome, central North America." *The Botanical Review*, 51(2): 163–201. <https://doi.org/10.1007/BF02861083>.
- Bailey, A. W., and C. E. Poulton. 1968. "Plant communities and environmental interrelationship in a portion of the Tillamook burn, northwestern Oregon." *Ecology* 49(1): 1–13. <https://doi.org/10.2307/1933554>.
- Bakker, C., J. M. Blair, and A. K. Knapp. 2003. "Does resource availability, resource heterogeneity or species turnover mediate changes in plant species richness in grazed grasslands?" *Oecologia* 137(3): 385–391. <https://doi.org/10.1007/s00442-003-1360-y>.
- Blair, J. M. 1997. "Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis." *Ecology* 78(8): 2359–2368. [https://doi.org/10.1890/0012-9658\(1997\)078\[2359:fnaapr\]2.0.co;2](https://doi.org/10.1890/0012-9658(1997)078[2359:fnaapr]2.0.co;2)
- Blair, J. M., J. B. Nippert, J. M. Briggs. 2014. "Grassland Ecology." In *Ecology and the Environment*, edited by Russell K. Monson, 398–423. New York, NY: Springer. https://doi-org.er.lib.k-state.edu/10.1007/978-1-4614-7612-2_14-1.
- Benson, E.J., and D. C. Hartnett. 2006. "The role of seed and vegetative reproduction in plant recruitment and demography in tallgrass prairie." *Plant Ecology* 187(2): 163–178.

<https://doi.org/10.1007/s11258-005-0975-y>.

- Bookout, B., S. Herzog, and Z. Ratajczak. 2025. "Resilience and multi-faceted diversity of grazed and ungrazed great plains grassland plant communities to severe drought." *Biological Conservation* 305: 111088. <https://doi.org/10.1016/j.biocon.2025.111088>.
- Bowman, D.M., J. K. Balch, P. Artaxo, W. J. Bond, J. M. Carlson, M. A. Cochrane, C. M. d'Antonio, et al. 2009. "Fire in the Earth system." *Science* 324(5926): 481–484. <https://doi.org/10.1126/science.1163886>.
- Bragg, T. B. 1982. "Seasonal variations in fuel and fuel consumption by fires in a bluestem prairie." *Ecology* 63(1): 7–11. <https://doi.org/10.2307/1937024>.
- Briggs, J. M., and A. K. Knapp. 1995. "Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass." *American Journal of Botany* 82(8): 1024–1030. <https://doi.org/10.1002/j.1537-2197.1995.tb11567.x>.
- Collins, S.L. 2000. "Disturbance frequency and community stability in native tallgrass prairie." *The American Naturalist* 155(3): 311–325. <https://doi.org/10.1086/303326>.
- Collins, S. L., and L. B. Calabrese. 2012. "Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie." *Journal of Vegetation Science* 23(3): 563–575. <https://doi.org/10.1111/j.1654-1103.2011.01369.x>.
- Collins, S.L., A. K. Knapp, J. M. Briggs, J. M. Blair, and E. M. Steinauer. 1998. "Modulation of diversity by grazing and mowing in native tallgrass prairie." *Science* 280(5364): 745–747. <https://doi.org/10.1126/science.280.5364.745>.
- Collins, S. L., J. B. Nippert, J. M. Blair, J. M. Briggs, P. Blackmore, and Z. Ratajczak. 2021. "Fire frequency, state change and hysteresis in tallgrass prairie." *Ecology Letters* 24(4): 636–647. <https://doi.org/10.1111/ele.13676>.
- Collins, S. L., and L. L. Wallace, eds. 1990. *Fire in North American Tallgrass Prairies*. Norman: University of Oklahoma Press.
- Connell, J.H., 1978. "Diversity in tropical rain forests and coral reefs: high diversity of trees and corals is maintained only in a nonequilibrium state." *Science* 199(4335): 1302–1310. <https://doi.org/10.1126/science.199.4335.1302>.
- Copeland, T.E., W. Sluis, and H. F. Howe. 2002. "Fire season and dominance in an Illinois tallgrass prairie restoration." *Restoration Ecology* 10(2): 315–323. <https://doi.org/10.1046/j.1526-100x.2002.02023.x>.
- Comer, P. J., J. C. Hak, K. Kindscher, E. Muldavin, and J. Singhurst. 2018. "Continent-scale landscape conservation design for temperate grasslands of the Great Plains and Chihuahuan

- Desert." *Natural areas journal* 38(2): 196–211. <https://doi.org/10.3375/043.038.0209>.
- Courtwright J. 2011. *Prairie Fire: A Great Plains History*. Lawrence: University Press of Kansas.
- Dickson, T. L., B. A. Hayes, and T. B. Bragg. 2019. "Effects of 34 years of experimentally manipulated burn seasons and frequencies on prairie plant composition." *Rangeland Ecology & Management* 72(1): 82–91. <https://doi.org/10.1016/j.rama.2018.07.014>.
- Driscoll, D.A., D. B. Lindenmayer, A. F. Bennett, M. Bode, R. A. Bradstock, G. J. Cary, M. F. Clarke, N. Dexter, R. Fensham, G. Friend, and M. Gill. 2010. "Fire management for biodiversity conservation: key research questions and our capacity to answer them." *Biological Conservation* 143(9): 1928–1939. <https://doi.org/10.1016/j.biocon.2010.05.026>.
- Engle, D. M., and T. G. Bidwell. 2001. "Viewpoint: The response of central North American prairies to seasonal fire." *Journal of Range Management* 54(1): 2–10. <https://doi.org/10.2307/4003519>.
- Gibson, D.J. and L. C. Hulbert. 1987. "Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie." *Vegetatio* 72: 175–185. <https://doi.org/10.1007/BF00039839>.
- Hartnett, D., S. Collins, and Z. Ratajczak. 2025. *PVC02 Plant Species Composition on Selected Watersheds at Konza Prairie*, ver. 24. Environmental Data Initiative. <https://doi.org/10.6073/pasta/c2dde97352fb0e25ab749765967997b9>. (accessed 22 October 2025).
- Henderson, R. A. 1992. "Ten-year response of a Wisconsin prairie remnant to seasonal timing of fire." In *Proceedings of the Twelfth North American Prairie Conference: Recapturing a Vanishing Heritage*, ed. Daryl D. Smith, and Carol A. Jacobs, 121–125. Cedar Falls, IA: History of Education Book Gallery.
- Hoekstra, J. M., T. M. Boucher, T. H. Ricketts, and C. Roberts. 2005. "Confronting a biome crisis: global disparities of habitat loss and protection." *Ecology Letters* 8(1): 23–29. <https://doi.org/10.1111/j.1461-0248.2004.00686.x>.
- Hooper, D.U., F. S. Chapin III, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, and B. Schmid. 2005. "Effects of biodiversity on ecosystem functioning: a consensus of current knowledge." *Ecological monographs* 75(1): 3–35. <https://doi.org/10.1890/04-0922>.
- Howe, H. F. 1994. "Managing species diversity in tallgrass prairie: assumptions and implications." *Conservation Biology* 8(3): 691–704. <https://doi.org/10.1046/j.1523-1739.1994.08030691.x>.

- Howe, H. F. 1995. "Succession and fire season in experimental prairie plantings." *Ecology* 76(6): 1917–1925. <https://doi.org/10.2307/1940723>.
- Howe, H. F. 2011. "Fire season and prairie forb richness in a 21- y experiment." *Ecoscience* 18(4): 317–328. <https://doi.org/10.2980/18-4-3421>.
- Hsu, A., M.W. Jones, J. R. Thurgood, A. J. Smith, R. Carmenta, J. T. Abatzoglou, L. O. Anderson, et al. 2025. "A global assemblage of regional prescribed burn records—GlobalRx." *Scientific Data* 12(1): 1083. <https://doi.org/10.1038/s41597-025-04941-w>.
- Hulbert, L. C. 1986. "Fire effects on tallgrass prairie." In *Proceedings of the Ninth North American Prairie Conference*, ed. Gary K. Clambey, and Richard H. Pemble, 138–142. Fargo, ND: Tri-College University Center for Environmental Studies.
- Isbell, F., D. Craven, J. Connolly, M. Loreau, B. Schmid, C. Beierkuhnlein, T. M. Bezemer et al. 2015. "Biodiversity increases the resistance of ecosystem productivity to climate extremes." *Nature* 526(7574): 574–577. <https://doi.org/10.1038/nature15374>.
- Jantz, D.R., 1975. *Soil survey of Riley county and part of Geary county, Kansas* (Vol. 16). US Department of Agriculture, Soil Conservation Service.
- Jost, L. 2006. "Entropy and diversity." *Oikos* 113(2): 363–375. <https://doi.org/10.1111/j.2006.0030-1299.14714.x>.
- KDHE. 2025. Kansas Department of Health and Environment: Flint Hills Wildland Fire Update, 2025 Summary. https://ksfire.org/media/Flint_Hills_Update_2025_Summary-77e3962.pdf. (accessed 11 January 2025).
- Knapp, A.K., J. M. Briggs, and M. D. Smith. 2012. "Community stability does not preclude ecosystem sensitivity to chronic resource alteration." *Functional Ecology* 26(6): 1231–1233. <https://doi.org/10.1111/j.1365-2435.2012.02053.x>.
- Knapp, E. E., B. L. Estes, and C. N. Skinner. 2009. "Ecological effects of prescribed fire season: a literature review and synthesis for managers." Gen. Tech. Rep. PSW-GTR-224. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. <https://doi.org/10.2737/PSW-GTR-224>
- Knapp, A.K., and E. Medina. 1999. "Success of C4 photosynthesis in the field: lessons from communities dominated by C4 plants". In *C4 Plant Biology*, edited by, Rowan F. Sage, and Russell K. Monson, 251–283. Academic Press
- Komatsu, K.J., M. L. Avolio, J. Blair, S. E. Koerner, Z. Ratajczak, M. D. Smith, E. Welti, K. R. Wilcox, and L. H. Zeglin. 2025. "Consistent timelines, divergent end points: plant community change in multiple tallgrass nitrogen addition experiments." *Oecologia* 207(11): 1–13. <https://doi.org/10.1007/s00442-025-05819-9>.

- Kral-O'Brien, K. C., P. L. O'Brien, T. J. Hovick, and J. P. Harmon. 2021. "Meta-analysis: Higher plant richness supports higher pollinator richness across many land use types." *Annals of the Entomological Society of America* 114(2): 267–275. <https://doi.org/10.1093/aesa/saaa061>.
- Launchbaugh, J. L., and C. E. Owensby. 1978. "Kansas Rangelands: their management, based on half a century of research." Manhattan, KS. Kansas Agricultural Experiment Station.
- Lenth, R.V., B. Banfai, B. Bolker, P. Buerkner, I. Giné-Vázquez, M. Herve, M. Jung, J. Love, F. Miguez, J. Piaskowski, et al. 2024. *Emmeans: estimated marginal means, aka least-squares means*. <https://doi.org/10.32614/cran.package.emmeans>. (accessed 15 July 2025).
- Liu, Z., Y. Liu, J. P. Murphy, and R. Maghirang. 2018. "Contributions of Kansas rangeland burning to ambient O₃: Analysis of data from 2001 to 2016." *Science of The Total Environment* 618: 1024–1031. <https://doi.org/10.1016/j.scitotenv.2017.09.075>.
- Loreau, M., M. Barbier, E. Filotas, D. Gravel, F. Isbell, S. J. Miller, J. M. Montoya, et al. 2021. "Biodiversity as insurance: from concept to measurement and application." *Biological Reviews* 96(5): 2333–2354. <https://doi.org/10.1111/brv.12756>.
- Lovell, D.L., R. A. Henderson, and E. A. Howell. 1982. "The response of forb species to seasonal timing of prescribed burns in remnant Wisconsin prairies." In *Proceedings of the Eighth North American Prairie Conference*, ed. Richard Brewer, 11–15. Kalamazoo, MI: Western Michigan University Press.
- McGranahan, D. A., T. J. H., R. D. Elmore, D. M. Engle, and S. D. Fuhlendorf. 2018. "Moderate patchiness optimizes heterogeneity, stability, and beta diversity in mesic grassland." *Ecology and Evolution* 8(10): 5008–5015. <https://doi.org/10.1002/ece3.4081>.
- Milchunas, D.G., W. K. Lauenroth, P. L. Chapman, and M. K. Kazempour. 1989. "Effects of grazing, topography, and precipitation on the structure of a semiarid grassland." *Vegetatio*, 80(1): 11–23. <https://doi.org/10.1007/BF00049137>.
- Miller, R. G., R. Tangney, N. J. Enright, J. B. Fontaine, D. J. Merritt, M. KJ Ooi, K. X. Ruthrof, and B. P. Miller. 2019. "Mechanisms of fire seasonality effects on plant populations." *Trends in Ecology & Evolution* 34(12): 1104–1117.
- Mohler, R.L., and D. G. Goodin. 2012. "Mapping burned areas in the Flint Hills of Kansas and Oklahoma, 2000—2010." In *Great Plains Research*, 15–25. University of Nebraska Press.
- Nippert, J. B., and B. R. Helliker. 2026. "Physiological and Anatomical Traits of Grass Species: Diversification facilitates persistence in grassy ecosystems." In *Routledge Handbook of Grasslands*, edited by Heather A. Hagar, David J. Gibson, and Jonathan A. Newman, 80–97. Routledge.
- Nippert, J. B., and A. K. Knapp. 2007. "Soil water partitioning contributes to species coexistence

- in tallgrass prairie." *Oikos* 116: 1017–29. <https://doi.org/10.1111/j.2007.0030-1299.15630.x>.
- Ojima, D. S., D. S. Schimel, W. J. Parton, and C. E. Owensby. 1994. "Long-and short-term effects of fire on nitrogen cycling in tallgrass prairie." *Biogeochemistry* 24(2): 67–84. <https://doi.org/10.1007/bf02390180>.
- Oksanen, J., G. L. Simpson, F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, P. Solymos, M. H. H. Stevens, Szoecs, E., et al. 2024. *Vegan: community ecology package*. <https://cran.r-project.org/web/packages/vegan/index.html>. (accessed 22 June 2025).
- Palmquist, K. A., R. K. Peet, and A. S. Weakley. 2014. "Changes in plant species richness following reduced fire frequency and drought in one of the most species-rich savannas in North. America." *Journal of Vegetation Science* 25(6): 1426–1437. <https://doi.org/10.1111/jvs.12186>.
- Pavlovic, N. B., S. A. Leicht-Young, and R. Grundel. 2011. "Short-term effects of burn season on flowering phenology of savanna plants." *Plant Ecology* 212(4): 611–625. <https://doi.org/10.1007/s11258-010-9851-5>.
- Penman, T. D., . J. Christie, A. N. Andersen, R. A. Bradstock, G. J. Cary, M. K. Henderson, O. Price, et al. 2011. "Prescribed burning: how can it work to conserve the things we value?." *International Journal of Wildland Fire* 20(6): 721–733. <https://doi.org/10.1071/wf09131>.
- Pickett, Steward T., and Peter S. White, eds. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. New York: Academic Press.
- Ransom, Michel D., Charles W. Rice, Timothy C. Todd, and William A. Wehmueller. 1998. "Soils and soil biota." In *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie*, edited by Alan K. Knapp, John M. Briggs, David C. Hartnett, and Scott L. Collins, 48–66. New York, NY: Oxford University Press.
- R Core Team. 2022. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Ratajczak, Z., S. L. Collins, J. M. Blair, S. E. Koerner, A. M. Louthan, M. D. Smith, J. H. Taylor, and J. B. Nippert. 2022. "Reintroducing bison results in long-running and resilient increases in grassland diversity." *Proceedings of the National Academy of Sciences* 119(36): e2210433119. <https://doi.org/10.1073/pnas.2210433119>.
- Pyne, S.J. 2017. *Fire in America: a cultural history of wildland and rural fire*. Seattle. University of Washington Press.
- Ratajczak, Z., P. D'Odorico, J. B. Nippert, S. L. Collins, N. A. Brunsell, and S. Ravi. 2017. "Changes in spatial variance during a grassland to shrubland state transition." *Journal of Ecology*, 105(3): 750–760. <https://doi.org/10.1111/1365-2745.12696>.

- Ratajczak, Z., J. B. Nippert, J. M. Briggs, and J. M. Blair. 2014. "Fire dynamics distinguish grasslands, shrublands and woodlands as alternative attractors in the Central Great Plains of North America." *Journal of Ecology* 102: 1374–1385. <https://doi.org/10.1111/1365-2745.12311>.
- Robertson, B., and D. Rebar. 2022. "Timing of prescribed burns impacts plant diversity but not investment in pollinator recruitment in a tallgrass prairie." *Ecosphere* 13(1): e3914. <https://doi.org/10.1002/ecs2.3914>.
- Rowe, H. I. 2010. "Tricks of the trade: techniques and opinions from 38 experts in tallgrass prairie restoration." *Restoration Ecology* 18: 253–262. <https://doi.org/10.1111/j.1526-100X.2010.00663.x>.
- Samson, F., and F. Knopf. 1994. "Prairie Conservation in North America." *BioScience* 44(6): 418–421. <https://doi.org/10.2307/1312365>.
- Seastedt, T. R., J. M. Briggs, and D. J. Gibson. 1991. "Controls of nitrogen limitation in tallgrass prairie." *Oecologia* 87(1): 72–79. <https://doi.org/10.1007/bf00323782>.
- Simoneit, B. R. T. 2002. "Biomass burning—a review of organic tracers for smoke from incomplete combustion." *Applied Geochemistry* 17(3): 129–162. [https://doi.org/10.1016/S0883-2927\(01\)00061-0](https://doi.org/10.1016/S0883-2927(01)00061-0).
- Stambaugh, M. C., R. P. Guyette, and J. Marschall. 2013. "Fire history in the Cherokee Nation of Oklahoma." *Human Ecology* 41(5): 749–758. <https://doi.org/10.1007/s10745-013-9571-2>.
- Stewart, O. C. 2002. *Forgotten Fires: Native Americans and the Transient Wilderness*. Norman: University of Oklahoma Press.
- Smith, M. D., and A. K. Knapp. 1999. "Exotic plant species in a C4-dominated grassland: invasibility, disturbance, and community structure." *Oecologia* 120(4): 605–612. <https://doi.org/10.1007/s004420050896>.
- Smith, M. D., and A. K. Knapp. 2003. "Dominant species maintain ecosystem function with non-random species loss." *Ecology Letters* 6(6): 509–517. <https://doi.org/10.1046/j.1461-0248.2003.00454.x>.
- Smith, E. F., and C. E. Owensby. 1978. "Intensive early stocking and season long stocking of Kansas Flint Hills range." *Journal of Range Management* 31(1): 14–17. <https://doi.org/10.2307/3897624>.
- Smith, M. D., A. K. Knapp, and S. L. Collins. 2009. "A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change." *Ecology* 90(12): 3279–3289. <https://doi.org/10.1890/08-1815.1>.

- Tilman, D., F. Isbell, and J. M. and Cowles. 2014. "Biodiversity and ecosystem functioning." *Annual Review of Ecology, Evolution, and Systematics* 45(1): 471–493. <https://doi.org/10.1146/annurev-ecolsys-120213-091917>.
- Tilman, D., P. B. Reich, and J. M. Knops. 2006. "Biodiversity and ecosystem stability in a decade-long grassland experiment." *Nature* 441(7093):629–4632. <https://doi.org/10.1038/nature04742>.
- Towne, E. G., and J. M. Craine. 2014. "Ecological consequences of shifting the timing of burning tallgrass prairie." *PLoS One* 9(7): e103423. <https://doi.org/10.1371/journal.pone.0103423>.
- Towne, E. G., and J. M. Craine. 2016. "A critical examination of timing of burning in the Kansas Flint Hills." *Rangeland Ecology & Management* 69(1): 28–34. <https://doi.org/10.1016/j.rama.2015.10.008>.
- Towne, E. G., and K. E. Kemp. 2003. "Vegetation dynamics from annually burning tallgrass prairie in different seasons." *Journal of Range Management* 56(2): 185–192. <https://doi.org/10.2307/4003903>.
- Towne, E. G., and K. E. Kemp. 2008. "Long-term response patterns of tallgrass prairie to frequent summer burning." *Rangeland Ecology & Management* 61(5): 509–520. <https://doi.org/10.2111/08-043.1>.
- Towne, E. G., and C. Owensby. 1984. "Long-term effects of annual burning at different dates in ungrazed Kansas tallgrass prairie." *Journal of Range Management* 37(5): 392–397. <https://doi.org/10.2307/3899622>.
- Turner, M.G., 2010. "Disturbance and landscape dynamics in a changing world." *Ecology* 91(10): 2833–2849. <https://doi.org/10.1890/10-0097.1>.
- Twidwell, D., A. S. West, W. B. Hiatt, A L. Ramirez, J. T. Winter, D. M. Engle, S. D. Fuhlendorf, and J. D. Carlson. 2016. "Plant invasions or fire policy: which has altered fire behavior more in tallgrass prairie?." *Ecosystems* 19(2): 356–368. <https://doi.org/10.1007/s10021-015-9937-y>.
- Vermeire, L. T., K. O. Reinhart, and J. Ott. 2024. "Do plants respond to multi-year disturbance rhythms and are we missing the beat?." *Oikos* 2024(11): e10791. <https://doi.org/10.1111/oik.10791>.
- Warton, D. I., and F. K. C Hui. 2017. "The central role of mean-variance relationships in the analysis of multivariate abundance data: A response to Roberts (2017)." *Methods in Ecology and Evolution* 8(11): 1408–1414. <https://doi.org/10.1111/2041-210X.12843>.
- Welti, E.A., A. Joern. 2018. Fire and grazing modulate the structure and resistance of plant–floral visitor networks in a tallgrass prairie. *Oecologia*, 186(2): 517–528.

<https://doi.org/10.1007/s00442-017-4019-9>.

Weir, J.R., 2011. Are weather and tradition reducing our ability to conduct prescribed burns?. *Rangelands* 33(1): 25–30. <https://doi.org/10.2111/rangelands-d-10-00050.1>.

Weir, J. R., and J. D. Scasta. 2017. "Vegetation responses to season of fire in tallgrass prairie: a 13-year case study." *Fire Ecology* 13(2): 137–142.
<https://doi.org/10.4996/fireecology.130290241>.

Wood, Simon N. 2017. *Generalized additive models: An introduction with R*, 2nd edition. New York: Chapman and Hall/CRC. <https://doi.org/10.1201/9781315370279>.

Zimmermann, J., S. I. Higgins, V. Grimm, J. Hoffmann, T. Münkemüller, and A. Linstädter. 2008. "Recruitment filters in a perennial grassland: the interactive roles of fire, competitors, moisture and seed availability." *Journal of Ecology* 96(5): 1033–044.
<https://doi.org/10.1111/j.1365-2745.2008.01409.x>.

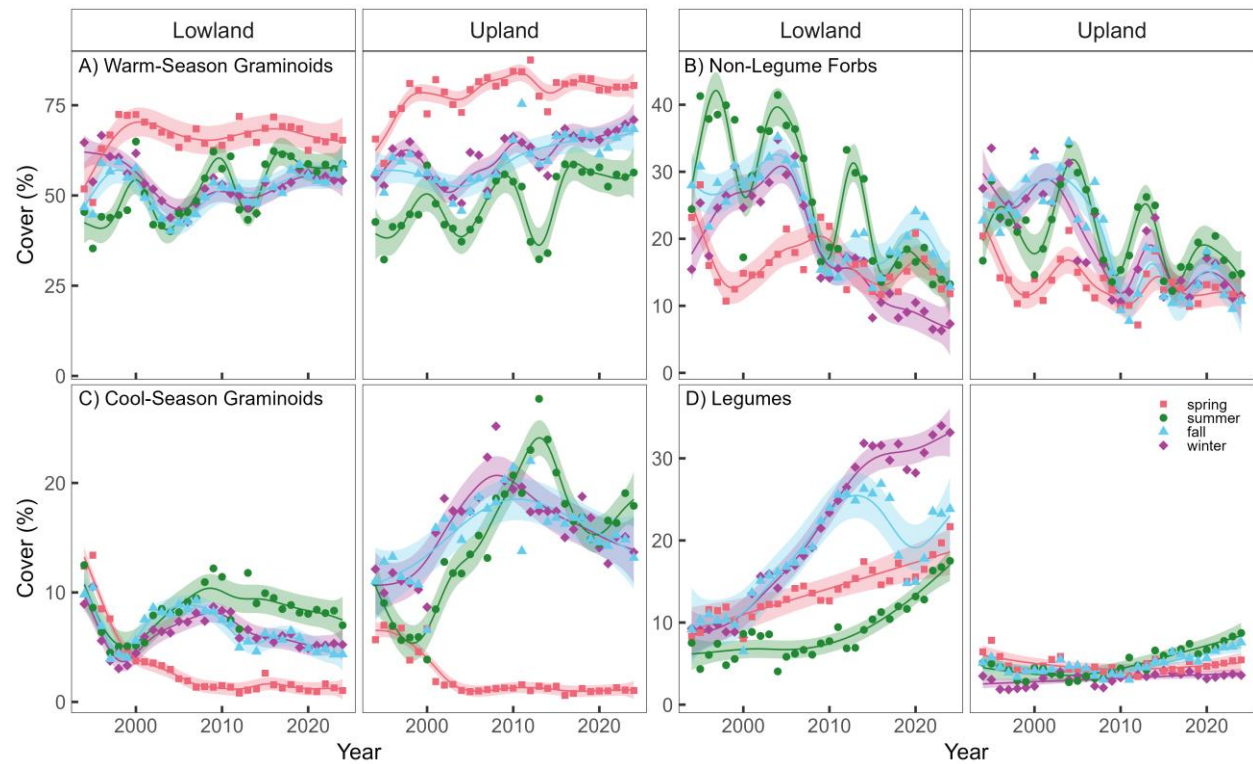


Figure 2-1: Relative cover of native warm-season graminoids (A), non-legume forbs (B), cool-season graminoids (C), and legumes (D) in lowlands and uplands under contrasting season-of-burn treatments. Note differences in scale for cover of different plant functional groups.

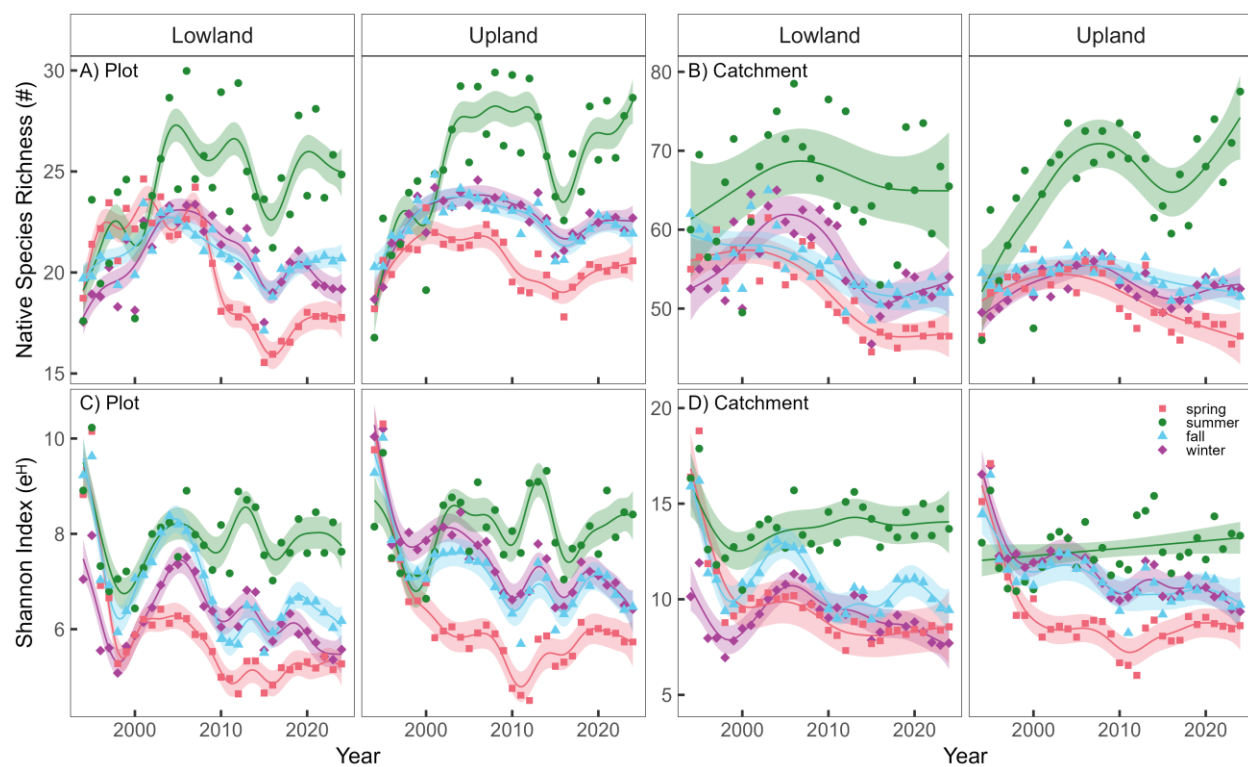


Figure 2-2: Native species richness at the plot (spp. 10 m^{-2}) (A) and catchment (spp. 200 m^{-2}) (B) scale, and changes in the exponent of Shannon's index at the plot (10 m^{-2}) (C) and catchment (200 m^{-2}) (D) scale in lowlands (left) and uplands (right) under contrasting burn seasons. Note differences in scale for richness and diversity metrics.

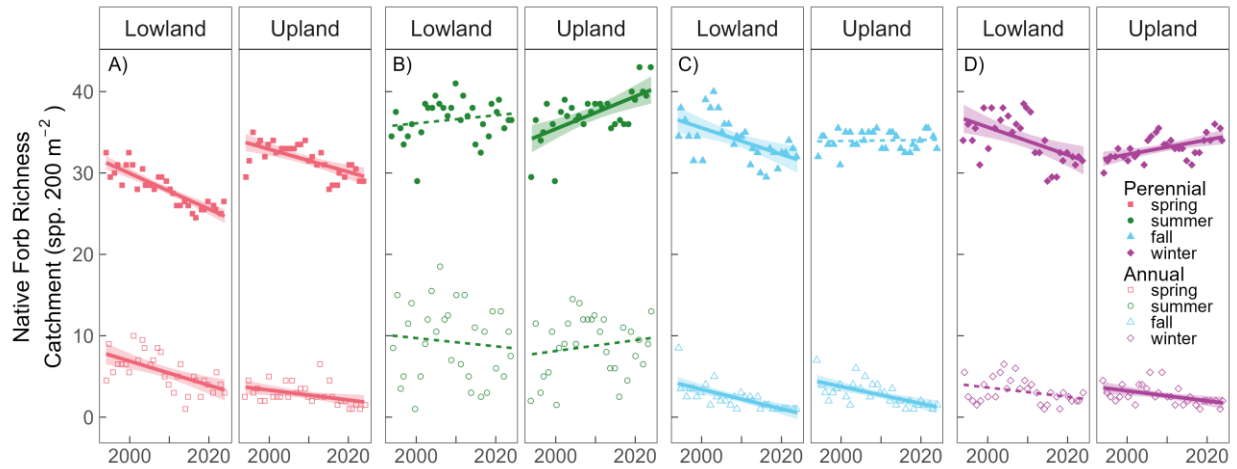


Figure 2-3: Native annual and perennial forb species richness over time at the catchment scale among burn seasons: spring (A), summer (B), fall (C), and winter (D), and between topographic positions. Solid lines indicate a significant ($p < 0.05$) regression slope, while dashed lines are non-significant trends.

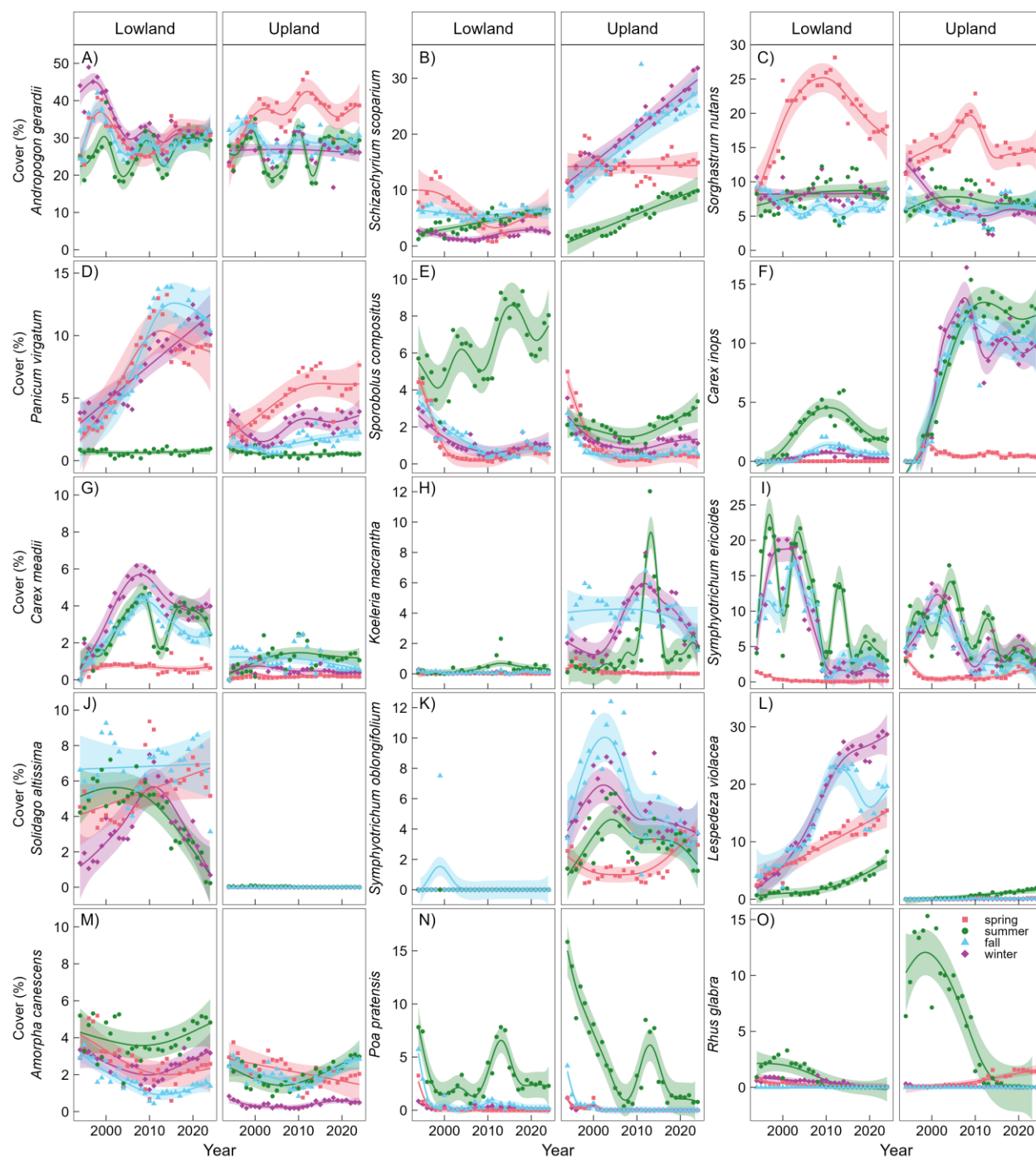


Figure 2-4: Relative cover of species in lowlands and uplands under contrasting burn regimes: *Andropogon gerardii* (A), *Schizachyrium scoparium* (B), *Sorghastrum nutans* (C), *Panicum virgatum* (D), *Sporobolus compositus* (E), *Carex inops* (F), *Carex meadii* (G), *Koeleria macrantha* (H), *Symphyotrichum ericoides* (I), *Solidago altissima* (J), *Symphyotrichum oblongifolium* (K), *Lespedeza violacea* (L), *Amorpha canescens* (M), *Poa pratensis* (N), *Rhus glabra* (O). Note differences in scale for cover of different plant species.

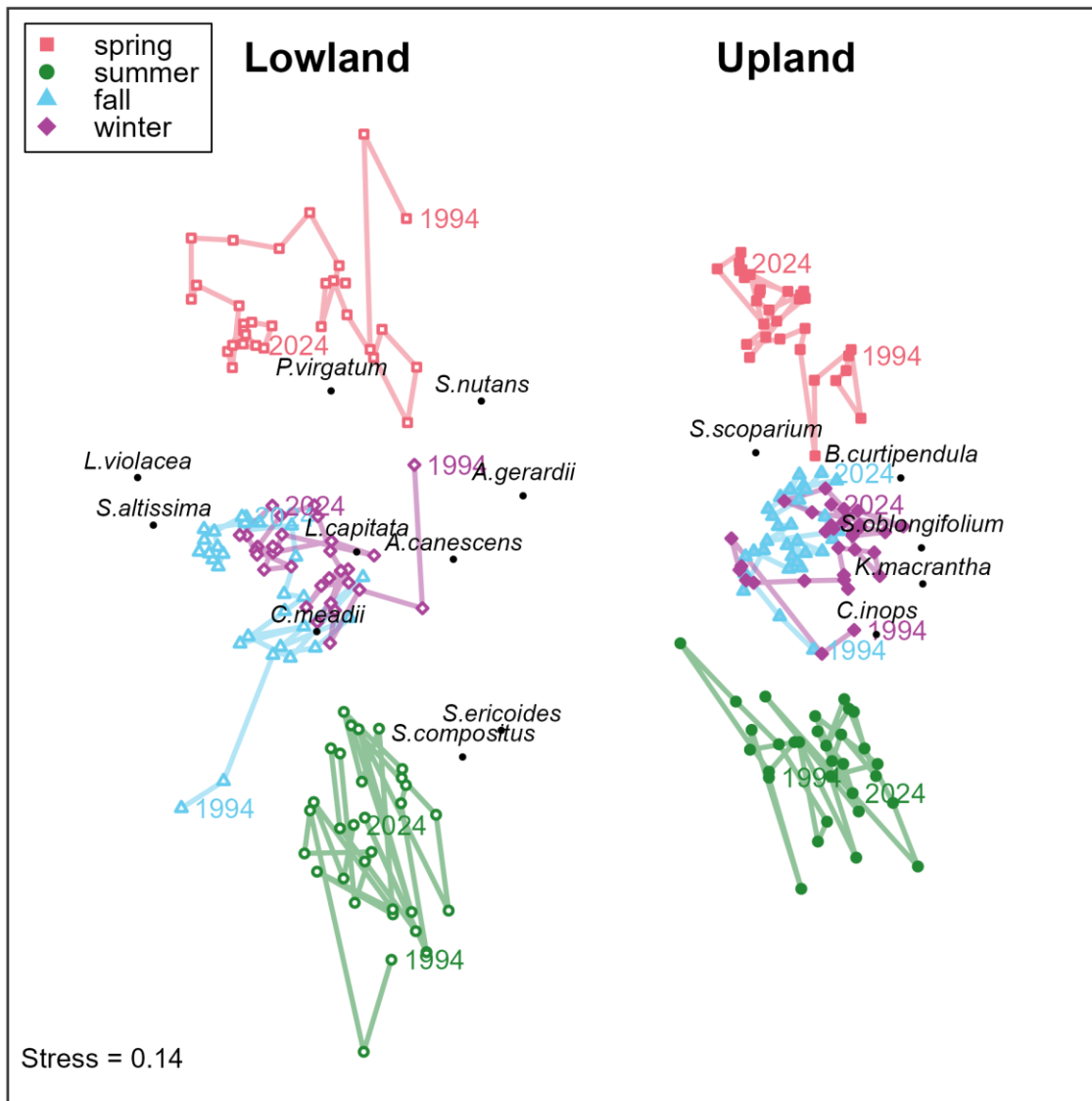


Figure 2-5: Non-metric multidimensional scaling (NMDS) of community composition from 1994 to 2024, based on Bray-Curtis dissimilarity of relative cover among burn regime and topographic position. Stress value = 0.14.

Chapter 3 - Long-term Aboveground Productivity Responses to Fire

Timing in Tallgrass Prairie

Abstract

The season in which prescribed fire is applied can alter plant community composition in tallgrass prairie, but the extent to which these changes influence ecosystem functioning is less understood. We evaluated the long-term effects of annual spring, fall, and winter burning, and biennial summer burning on aboveground net primary productivity (ANPP) using a 30-year dataset from Konza Prairie Biological Station. We also examined whether productivity responses varied with topographic position (lowland vs. upland), differed between burned and non-burned years under the summer fire regime, or altered relationships between productivity and precipitation. In addition, we assessed soil properties after more than three decades of contrasting fire treatments. Interannual productivity varied substantially over time and was consistently greater in lowlands than uplands. Graminoids accounted for most productivity across all fire treatments. Productivity under spring, fall, and winter burning was generally similar, whereas summer burning reduced graminoid and total ANPP in lowlands. However, these reductions were associated with lower productivity in years following a burn (i.e., non-burned years). Growing-season precipitation was a strong predictor of graminoid and total ANPP, and the strength of this relationship did not differ among fire treatments. Despite three decades of contrasting fire regimes, soil properties remained similar among burn treatments, and differences only existed between topographic position. Overall, variation in productivity was more strongly associated with topographic position and year-to-year climatic variability than with the seasonal timing of fire. These results suggest that broadening the seasonal application of prescribed fire is a viable management option that preserves core ecosystem functioning.

Introduction

Highly productive grasslands require recurrent disturbances to remove accumulated detritus and maintain ecosystem structure and function (Knapp and Seastedt 1986; Clark et al. 2026). In these ecosystems, prescribed fire is the primary management tool for modulating vegetation dynamics and maintaining a desirable grassland state (Bowman et al. 2009; Ratajczak et al. 2014; Uys et al. 2004; Weir et al. 2015). In tallgrass prairie, fire limits woody expansion and stimulates herbaceous productivity by removing accumulated litter and altering the energy environment and resource availability to plants (Archer et al. 2017; Bowman et al. 2009). Plant responses to fire are highly dependent on the frequency, intensity, and timing of fire, with interannual variability in precipitation further mediating these responses (Gibson and Hulbert 1987; Towne and Craine 2016; Knapp et al. 1998). Many aspects of grassland responses to fire have been studied extensively, especially fire frequency and intensity/severity. Much less attention has focused on how the seasonal timing of fire affects plant productivity.

Historical evidence suggests that fires occurred throughout the year in many grasslands, yet contemporary prescribed burning is often limited to a relatively narrow seasonal window (Hsu et al. 2025; Twidwell et al. 2016). For example, most prescribed burning in the Flint Hills of Kansas takes place in the late spring, when an average of approximately 2.1 million acres is burned over the span of a few weeks (KDHE 2025). Not only is this logistically challenging for land managers who need to identify enough days with appropriate weather conditions to conduct prescribed burns across the region, but it also produces large and concentrated emissions of smoke over an extensive area. These periods of high smoke emissions impact regional air quality in both rural and urban areas contributing to human health concerns and potential regulatory

actions (Rappold et al. 2017; Sablan et al. 2024). Expanding the timing of prescribed burning beyond a narrow spring window has been proposed as a strategy for distributing smoke more over time and reducing the concentration of harmful emissions. Burning at other times of year may also favor different species and provide opportunities for increasing landscape heterogeneity and biodiversity (Fuhlendorf and Engle 2004; Glidden et al. in review; McGranahan et al. 2017). However, few studies have assessed the ecological consequences of incorporating prescribed fire at different times of the year. Some impediments to burning in other seasons are concerns about the negative effects on plant productivity, especially of the perennial grasses that serve as forage for livestock. There are also concerns about leaving soil surfaces exposed in non-growing seasons (e.g., increased surface evaporation), as well as the potential long-term impacts on soil quality and fertility. In this study, we evaluated the long-term effects of annual or biennial prescribed burning in different seasons (spring, summer, fall, and winter) on aboveground net primary productivity (ANPP) and soil health in tallgrass prairie.

The timing of prescribed fire can have long lasting and dynamic effects on plant communities, with accompanying changes in ecosystem function, including ANPP. For instance, spring burning is used widely in tallgrass prairie and other mesic grasslands to promote the growth and cover of highly productive warm-season grasses (Buis et al. 2009; Engle and Bidwell 2001; Howe 2000; Launchbaugh and Owensby 1978) often leading to communities structured around a few tall, rhizomatous species (Kirkman et al. 2014). Increased cover of tall grasses reduces light penetration and increases competitive suppression of shorter species, reinforcing tallgrass dominance but limiting diversity (Knapp and Seastedt 1986; McCain et al. 2010). Following senescence, surface detritus and standing dead material can persist through winter until the next season, further limiting light availability for early spring species (i.e., spring

ephemerals and cool-season graminoids) (Knapp and Seastedt 1986). Although frequent burning near the end of the dormant season is the most common burn regime in many grasslands (Hsu et al. 2025; KDHE, 2025), fire can also be effectively applied during other parts of the dormant season. Fall and winter prescribed burns occur after senescence when plant growth and microbial activity are low. Unlike late spring burning, dormant season fires generally remove accumulated litter several months before spring growth. By shifting the timing of litter removal, soil warming, and nutrient availability relative to plant phenology, these burns can influence plant communities differently than spring burns (Dickeson et al. 2019; Glidden et al. in review, Towne and Kemp 2003). Despite the asynchrony between litter removal and emergence of the dominant grasses, fall and winter burning can maintain levels of graminoid productivity comparable to spring burning while supporting a more diverse and balanced species and functional plant composition, including greater C₃ graminoid and forb abundance (Towne and Craine 2014), although results are not consistent among tallgrass prairie locations (Dickson et al. 2019).

Prescribed burning during the growing season, often done in later summer, is less common than burning during the fall, winter, and spring dormant seasons. Burning in later summer occurs after a large portion of the plant community's aboveground biomass has accumulated and when many species are still green, though there must be sufficient dried biomass to carry fire. Because fire occurs during a time of active growth, it immediately reduces both litter and live biomass, providing transient increases in light and nutrient availability that can support regrowth. The timing of these changes may allow shorter, subdominant, and emerging species to capitalize on available resources during a period typically dominated by tall warm-season grasses and/or late-season forbs. Summer fires also tend to be more variable in intensity and spatial patchiness than dormant season burns (Howe 2000), which may contribute

to greater variability in productivity responses and, in some cases, higher species richness and diversity (Glidden et al. in review). Although dominant C₄ grasses are directly impacted by growing season fire, they are fire-adapted and generally recover rapidly (Ewing & Engle, 1988), with aerial cover of those species often increasing over time under frequent (e.g., annual) fire (Collins and Calabrese, 2012; Dickson et al. 2017; Glidden et al. in review; Towne and Kemp 2008). However, repeated summer fires may still result in lower relative cover of C₄ grasses and greater relative cover of C₃ graminoids compared to spring burns (Coppedge et al. 1998; Ewing and Engle 1988; Glidden et al. in review). Because C₄ grasses contribute disproportionately to production in tallgrass prairie, these compositional differences may influence overall productivity.

Although prescribed burning generally increases ANPP, productivity in tallgrass prairie and other mesic grasslands is strongly dependent on water availability, as reflected in relationships between ANPP and annual or growing season precipitation (Blair et al. 2014, Fay et al. 2011; Sala et al. 1988). The relationships between precipitation and productivity often vary with prescribed fire treatment and with landscape position and soil properties (Briggs and Knapp 1995; Knapp et al. 1998; Nippert et al., 2006, 2011), reflecting strong spatial variability in plant productivity across grassland landscapes. This is particularly evident in the Flint Hills, where rolling topography and relatively large topoedaphic gradients create strong contrasts between lowlands and uplands. Lowlands are characterized by deeper and more finely textured soils and greater water holding capacity, while uplands are shallower, rockier soils that limit rooting depth and moisture retention (Ransom et al. 1998). As a result, production is typically greater in lowlands than uplands, even when dominant grass species occur across both positions (Abrams et al. 1986; Briggs and Knapp 1995). These differences arise largely from variation in soil water

availability across topographic gradients (Nippert et al. 2011). Given that water availability regulates productivity (Tooley et al. 2025) and fire season alters plant community composition across topographic positions (Glidden et al. in review), understanding how these interactive drivers influence productivity across heterogeneous landscapes is important for effective management.

In addition to affecting plant productivity, prescribed burning alters a variety of soil properties (Connell et al. 2020; Fynn et al. 2003) that in turn, affect soil fertility and plant productivity. Frequent burning volatilizes a significant amount of nitrogen (N) from biomass and litter, and repeated burning generally reduces plant-available inorganic N and increases the C:N ratio of plant inputs and soil organic matter (Blair 1997; Fynn et al. 2003; Ojima et al. 1994). A concern with shifting the seasonal timing of burning is that growing season fires or removal of surface litter earlier in the dormant season could result in additional nutrient losses or less incorporation of surface litter into soil organic pools, relative to traditional late spring burning. For example, Fynn et al. (2003) found that 50 years of burning in the fall or winter in a South African grassland resulted in lower soil organic matter in the surface soil relative to burning in the spring. However, reductions in surface litter inputs may be offset by greater root production in response to prescribed burning (Fynn et al. 2003; Kitchen et al. 2009). While there are studies of how different fire return intervals affect soil properties in North American tallgrass prairie, we are not aware of any assessment of how the seasonal timing of burning might affect soil properties related to soil fertility.

In this study, we assessed the long-term effects of frequent (annual or biennial) prescribed fire regimes applied in different seasons (spring, summer, fall, and winter) on ANPP using 30 years of annual biomass data collected at the Konza Prairie Biological Station and

Long-Term Ecological Research site. We also compared soil properties following three decades of different seasonal fire treatments. Our specific objectives were to (1) evaluate the effects of prescribed burning in different seasons on graminoid and forb ANPP in tallgrass prairie, (2) determine whether ANPP responses to fire season vary in their sensitivity to interannual variability in precipitation, (3) assess whether long-term seasonal fire regimes have altered soil properties, and (4) determine how these responses vary with topography.

Methods

Study Site

This study took place at the Konza Prairie Biological Station (KPBS). KPBS is located in the northern Flint Hills of Kansas (96.61° W, 39.11° N) and encompasses 3,487 ha of mainly unplowed native tallgrass prairie. The site is characterized by complex topography typical of the region, and is divided into a series of small watersheds, each assigned to a specific prescribed fire and grazing regime. The dominant plants are rhizomatous perennial C₄ warm-season grasses (*Andropogon gerardii*, *Sorghastrum nutans*, and *Schizachyrium scoparium*), that co-occur with a diverse assemblage of C₃ forbs (Freeman 1998). Soil properties vary substantially with topographic position. Lowland soils are generally deep and fine-textured Pachic Argiustolls whereas upland soils are relatively shallow, silty clay loams (Udic Argiustolls) overlaying layers of limestone and shale. Differences in soil depth and soil texture affect plant rooting depth and soil water holding capacity. Mean annual temperature at KPBS is ~12.5°C and mean annual precipitation (MAP) is 835 mm yr⁻¹ with the majority occurring during the growing season. During this study (1994–2023), MAP was approximately 811 mm, with 70–75% occurring from April through September (Figure B.1). Precipitation exhibited high interannual variability, and

the site experienced extreme heat and drought in 2011-2012, below-average growing season precipitation in 2017-2018, and above average precipitation in 2004-2005 and 2008-2010.

Experimental Design

We used data collected from eight watersheds assigned in 1994 to one of four prescribed fire treatments (annual spring, fall, and winter burning, or biennial summer burning). Spring burns were generally conducted in mid- to late April, fall burns in mid-November, winter burns in mid-February, and summer burns in late July to early August. Each fire treatment was replicated on two spatially separated watersheds. Watershed size ranged from ~11 to 36 ha. Prior to 1994, all watersheds were burned in the spring with an average fire return interval of ~3 years. Large grazers were absent during the study period and had not been present for more than 25 years prior to the treatment initiation.

Data Collection

Daily precipitation data were obtained from the main KPBS climatological station (Nippert, 2026), located approximately 4 km from our study sites, and summed to get monthly totals for each year. Annual precipitation was based on a calendar year, and growing-season precipitation was calculated as the sum of precipitation from April 1 through September 30.

Aboveground biomass was collected along eight 50 m transects in each watershed (Blair and Nippert 2025). Sampling was conducted in both lowland and upland topographic positions, with four replicate transects per position: for a total of 8 transects per combination of fire treatment and topographic position. Biomass sampling transects were located parallel to permanent plant species composition transects established in 1994 (Hartnett et al. 2025). Five

evenly spaced 0.1 m² quadrats were used to sample aboveground biomass from each transect. Quadrats were clipped to ground level at the end of each growing season, typically between late August and October. In summer-burned watersheds, biomass was harvested twice during burned years: once immediately prior to burning in mid- to late July and again in late October. All harvested material was dried at 60°C for 2–3 days. Samples were subsequently separated into graminoids, forbs, and woody material and re-dried at 60°C for 24 hours prior to weighing. Woody biomass constituted a minor component and were excluded from this analysis. In 2011, prior to clipping, watershed FB (a fall burn) experienced a partial wildfire on two upland transects, these transects were excluded from all analysis for that year.

Soil samples were collected at the end of the 2025 growing season (September) year 31 of the experiment. Along each transect, five soil cores (2 cm diameter) were collected to a depth of 5 cm and pooled by transect. In the laboratory, soil from each transect was passed through a 2 mm sieve to remove gravel, roots, and any litter. Prior to drying, a subsample of approximately 12 g of field-moist soil per transect was reserved to quantify plant available inorganic N (ammonium and nitrate). The remaining soil was dried at 60°C for 2–3 days prior to chemical analysis. Field moist subsamples for inorganic N were extracted in 125ml flasks using 1N KCL. Samples were shaken on an orbital shaker for 1 h, allowed to settle, and filtered through Whatman 42 (125mm) filter paper. Extracts were refrigerated until analysis. Chemical analysis of extracts and soil samples was conducted at the Kansas State Soil Testing Laboratory and included pH, exchangeable base cations (Ca, Na, Mg, and K), extractable phosphorus (P), inorganic N, and total soil C and N.

Data Analysis

To account for spatial variability and repeated measures over time, plot-level ANPP measurements were averaged within transects for each watershed $\times$ topographic position $\times$ year combination prior to all analyses. Total productivity was calculated as the sum of graminoid and forb ANPP.

Aboveground net primary productivity (ANPP) of graminoids, forbs, and total biomass was analyzed using linear mixed-effects models (LMMs) fit with the *lmer* function in the *lmerTest* package (Kuznetsova et al. 2017). For each response variable, we fit models with burn season, topographic position, and either year or precipitation, along with their interactions, as fixed effects. Watershed and transect were included as random intercepts to account for shared variation among transects within watersheds and repeated measurements of transects through time. Fixed effects were evaluated using Type III analysis of variance (Fox and Weisberg 2019) with Satterthwaite's approximation for degrees of freedom, and post hoc comparisons were conducted using estimated marginal means with Tukey-adjusted contrasts from the *emmeans* package (Lenth 2020). Long-term directional trends in ANPP were evaluated by including year as a continuous predictor in the LMMs. Slopes of ANPP over time were estimated using *emtrends* from the *emmeans* package for each burn season $\times$ topographic position combination. To meet the assumptions of normality and homoscedasticity, response variables were transformed prior to analysis. Forb ANPP was square-root transformed for all mixed models and graminoid and total ANPP were square-root transformed only in models including precipitation.

We assessed the relationships between precipitation and ANPP for each burn treatment $\times$ topographic position combination. Because growing-season precipitation explained slightly more variation in ANPP than annual precipitation, subsequent analyses used growing season precipitation. Effects of growing-season precipitation on ANPP were evaluated using the mixed

models described above, with precipitation included as a continuous predictor. For visualization and reporting of treatment-specific slopes, separate linear regression models were fit for each treatment combination.

Because summer burns occurred biennially, we considered the possibility that productivity may have been reduced or enhanced in burned years relative to non-burned years. To determine whether productivity responses in summer watersheds were affected by a short-term response to fire in the year of measurement independently of any broader interannual variation (e.g., climate), years in which summer burns were applied were classified as “burned”, and all other years as “non-burned” and applied consistently across all burn season treatments. To assess productivity responses within each seasonal fire treatment, separate LMMs were fit for each burn season with burn classification, topographic position, and year as fixed effects. We also evaluated whether treatment differences among burn seasons varied between burned and non-burned years by fitting models including burn season, topographic position, year, and their interactions separately for burned and non-burned years. To determine whether stochastic differences in precipitation could account for any productivity differences between burned and non-burned years, growing-season precipitation was included as a predictor in models restricted to summer treatments. Differences in precipitation – productivity slopes between burned and non-burned years were evaluated within topographic position using *emtrends* contrasts. Finally, to determine if burned and non-burned differed climatically, we tested whether annual or growing-season precipitation varied between burn classes by fitting separate regression models with burn classification, year, and their interactions as fixed factors.

Treatment effects on soil properties were evaluated using LMMs with burn season and topographic position as fixed effects and watershed as a random intercept. Type III ANOVA was

used to assess main effects and interactions. When significant effects were detected, post hoc comparisons were conducted using *emmeans* with Tukey-adjusted pairwise contrasts. All analyses were performed in R (v. 4.2.2; R Core Team 2022).

Results

Aboveground Net Primary Productivity: Productivity of both graminoids and forbs exhibited high interannual variability, with graminoid ANPP generally fluctuating synchronously across fire treatments, particularly in uplands. While interannual fluctuations in forb productivity were more idiosyncratic and varied with different season-of-fire treatments (Figure 1). Graminoid, forb, and total ANPP were all significantly greater in lowlands than in uplands (Figure 1; Table 1). We also observed some significant directional trends in ANPP over the 30-year study period, with graminoid ANPP increasing under all seasonal fire treatments, while trends in forb ANPP varied with fire treatment and topography (Figure 1; Table B.1). When annual ANPP was averaged across years to assess overall treatment differences, graminoid and total productivity were not significantly affected by burn treatment in the uplands and were not different for fall, winter, and spring fire treatments in the lowlands, but were significantly lower under summer burning in the lowlands (Figure 2). Mean forb ANPP also differed among season of fire treatments in both topographic positions (Figure 2).

Graminoids accounted for the majority of aboveground ANPP across all fire treatments and topographic positions. Graminoid productivity was significantly affected by burn season ($p = 0.022$), topographic position ($p < 0.001$), and their interaction ($p = 0.032$), with consistently greater ANPP in lowlands than uplands (Figure 1, Table 1). In lowlands, graminoid productivity averaged $523 \text{ g m}^{-2} \text{ y}^{-1}$ across all dormant-season burning treatments. There were no significant

differences in mean ANPP among fall, winter, and spring fire treatments (509 to 542 g m⁻² y⁻¹), and all dormant season burning treatments supported greater graminoid production than did summer burning, which averaged 414 g m⁻² y⁻¹ (19-24% lower; Figure 2A). In lowlands, graminoid ANPP under spring burning showed a small, non-significant increase over time (1.54 g m⁻² y⁻¹; $p = 0.07$), whereas graminoid ANPP in summer, fall, and winter burned lowlands exhibited significant increases at twice that rate (3.27, 3.56, and 4.07 g m⁻² y⁻¹, respectively; $p < 0.001$; Table B.1). In uplands, mean productivity ranged from 316 to 364 g m⁻² y⁻¹ and did not differ among burn treatments (Figure 2A). Spring burning again produced a marginal increase in graminoid ANPP over time (1.52 g m⁻² y⁻¹; $p = 0.074$), while ANPP under summer, fall, and winter burns increased at higher rates (2.11, 2.28, and 2.80 g m⁻² y⁻¹, respectively; $p \leq 0.013$; Table B.1).

Forb productivity was significantly affected by burn season ($p = 0.035$), topographic position ($p < 0.001$), but did not exhibit a main effect of year overall ($p = 0.372$; Table 1). However, forb productivity was significantly affected by two- and three-way interactions among burn season, topography, and year. Therefore, temporal trends in forb ANPP differed among burn seasons and with topographic position ($p < 0.001$; Table 1). In lowlands, mean forb productivity was lowest under spring burns (58.3 g m⁻² y⁻¹) and highest under fall burns (88.8 g m⁻² y⁻¹) (Figure 2B). Forb productivity in lowlands exhibited a positive trend over time under all dormant-season burns, with spring, fall, and winter increasing at rates of 1.25, 1.49, 0.74 g m⁻² y⁻¹, respectively ($p < 0.01$; Figure 1; Table B.1). In contrast, summer burning decreased lowland forb productivity by approximately 22% over time (-0.66 g m⁻² y⁻¹; $p < 0.01$; Figure 1; Table 2). In uplands, mean forb productivity was again lowest with spring burning (18.8 g m⁻² y⁻¹), but greatest under summer burns (44.9 g m⁻² y⁻¹; Figure 2B). Forb productivity generally declined

over time across all treatments, although significant decreases were detected only under fall ($-0.65 \text{ g m}^{-2} \text{ y}^{-1}$) and winter burning ($-0.71 \text{ g m}^{-2} \text{ y}^{-1}$; $p < 0.001$; Table B.1), corresponding to overall declines of 45% and 51%, respectively.

The effect of burn season on mean annual total herbaceous productivity varied with topographic position as reflected in a significant two-way interaction ($p = 0.029$; Table 1). In lowlands, mean productivity ranged from 575 to 614 $\text{g m}^{-2} \text{ y}^{-1}$ under fall, winter, and spring burning, with productivity under spring burning significantly lower ($486 \text{ g m}^{-2} \text{ y}^{-1}$) than all dormant season treatments (Figure 2C). Total productivity in lowlands increased through time under all burn treatments (Table B.1). Total ANPP under spring and summer treatments increased at a moderate rate (2.85 and $2.55 \text{ g m}^{-2} \text{ y}^{-1}$, respectively), whereas total ANPP under fall and winter burning increased more rapidly (4.96 and $4.81 \text{ g m}^{-2} \text{ y}^{-1}$, respectively; $p < 0.01$; Figure 1; Table B.1). In uplands, herbaceous productivity averaged $361 - 392 \text{ g m}^{-2} \text{ y}^{-1}$ with no differences among burn seasons (Figure 2C). Productivity increased over time with summer ($1.83 \text{ g m}^{-2} \text{ y}^{-1}$; $p = 0.033$), fall ($1.69 \text{ g m}^{-2} \text{ y}^{-1}$; $p = 0.049$), and winter burns ($2.03 \text{ g m}^{-2} \text{ y}^{-1}$; $p = 0.019$), while no significant change occurred under spring burning ($p = 0.112$; Figure 1; Table B.1). In both uplands and lowlands, interannual variability in graminoid and total productivity closely aligned with growing-season precipitation patterns, with notable high ANPP in wet periods (e.g., 2004-05, 2008-2010) and pronounced declines during the 2012 drought (Figure 1).

Precipitation and ANPP: Growing season precipitation was a significant positive predictor of graminoid and total ANPP across all burn treatments ($p < 0.001$; Figure 3; Table B.2; B.3). Growing season precipitation did not change over time from 1994 to 2024 (Table B.4). There were no two- or three-way interactions, indicating that neither burn treatment nor

topographic position influenced the relationship between precipitation and productivity (Table B.2). Graminoid productivity increased with growing-season precipitation among all treatment combination, with precipitation explaining a moderate amount of the variation in ANPP ($r^2 = 0.18 - 0.34$; Table 3). ANPP responses to precipitation were slightly higher in lowlands ($0.46 - 0.49 \text{ g m}^{-2} \text{ mm}^{-1}$) than in uplands ($0.36 - 0.41 \text{ g m}^{-2} \text{ mm}^{-1}$; Figure 3A, 3B; Table B.3). Despite similar slopes among burn seasons, graminoid productivity was lower under summer burns than dormant-season burns across precipitation levels (Figure 3A, 3B). Forb productivity responded weakly to growing season precipitation, with near-zero slopes and little variation explained across treatment combinations ($r^2 \leq 0.01$; Figure 3C, 3D; Table 2). Total ANPP was driven mainly by graminoid productivity and showed similar relationships with precipitation ($r^2 = 0.19 - 0.34$; Table 3), with slightly greater responses in lowlands ($0.48 - 0.53 \text{ g m}^{-2} \text{ mm}^{-1}$) than in uplands ($0.39 - 0.43 \text{ g m}^{-2} \text{ mm}^{-1}$) (Figure 3E, 3F; Table B.3).

Summer-burned versus non-burned years: Summer burns showed strong differences between burn classifications (burned and non-burned years) in both topographic positions for graminoid and total ANPP ($p < 0.001$) but did not affect forb productivity ($p = 0.83$; Table B.5). To determine whether these differences were unique to the summer burn treatment (i.e., due to biennial burning as opposed to chance variation in climate or other factors between burned and non-burned years), we explored whether comparable differences in ANPP occurred during those same burned and non-burned years within the other seasonal fire treatments. ANPP responses to burn classification were largely restricted to biennial summer burns. Under spring, fall, and winter burns, mean productivity did not differ between burned and non-burned years for graminoids, forbs, or total productivity ($p > 0.05$; Table B.5). In the summer treatment, both

graminoid and total ANPP were 17–23% greater in burned years than non-burned years (Table B.5), resulting in average annual graminoid productivity during burned years comparable to that observed under spring and fall treatments (Figure 4; Table B.6). The mean difference in graminoid and total productivity between dormant and growing-season burns was $\sim 77 \text{ g m}^{-2}$ and $\sim 68 \text{ g m}^{-2}$ in burned years, but increased to $\sim 166 \text{ g m}^{-2}$ and $\sim 157 \text{ g m}^{-2}$ in non-burned years, roughly doubling of the difference between seasons. Although precipitation strongly influenced graminoid and total productivity ($p < 0.001$; Figure B.2, Table B.7), the precipitation – productivity relationship did not differ between burn classes ($p > 0.24$; Table B.8). Additionally, precipitation itself did not differ between burned and non-burned years (Figure B.3; Table B.9). Combined, these results indicate that differences in productivity between burned and non-burned years under the summer treatment were unlikely to be driven by climatic variation.

Soil Properties: After 32 years of seasonal fire treatments, we found no measurable differences in soil properties among burn treatments in either the lowlands or uplands. Of the 11 soil variables examined, three differed by topographic position, and two had burn season $\times$ topography interactions (Table 3; Table B.10). Among the base cations, Mg concentrations were higher in lowlands ($\sim 513 \text{ ppm}$) compared to uplands ($\sim 420 \text{ ppm}$) ($p < 0.001$; Table 3; Table B.10). Extractable inorganic nitrogen also differed with topography, with both NH_4^+ and NO_3^- concentrations higher in the lowlands compared to uplands ($p < 0.01$; Table 3; Table B.10). The interaction between burn season and topographic position was driven by differences in soil %C and %N in lowland and upland positions within summer-burned watersheds, where lowlands had lower concentrations of both soil C and N (Table 3, Table N.10). Soil C:N ratios were similar

across all burn seasons, ranging from 12.5 to 13.4 with a global mean of approximately 13 (Table 3).

Discussion

Prescribed fire is widely used to maintain tallgrass prairie productivity, yet most burning in the Flint Hills and other regions occurs within a narrow window in late spring. Concerns about reduced plant diversity, degraded regional air quality, and logistical constraints associated with simultaneous widespread spring burning have raised questions about whether prescribed fire could be applied more broadly across seasons. Our results suggest that limiting prescribed burning to late spring may not be necessary to maintain the high levels of productivity characteristic of these grasslands. We found that three decades of contrasting seasonal fire treatments had relatively small effects on aboveground net primary productivity (ANPP) regardless of when in the dormant season burning occurred, with fall, winter, and spring fires supporting similar levels of graminoid and total ANPP (Figures 1 and 2). In contrast, summer burning reduced mean annual ANPP in lowland sites, although these reductions were largely associated with lower productivity in non-burned years. Productivity across all burn treatments responded similarly to interannual variability in growing-season precipitation, as indicated by similar slopes among all treatments for the precipitation – productivity relationship, though ANPP per mm precipitation was reduced under summer burning (Figure 3). Despite subtle differences in productivity responses, we found no evidence that the season of fire altered soil properties after decades of contrasting fire regimes. Expanding prescribed fire to other parts of the dormant season, and even into the growing season when appropriate, may provide additional flexibility for land managers without substantially reducing key ecosystem functions.

The greatest differences in productivity occurred between the dormant-season and growing-season fire treatments. In lowlands, dormant-season fires generally resulted in greater graminoid productivity than summer fires, whereas productivity in uplands did not differ among burn treatments. Lower productivity under summer burning was largely driven by differences in ANPP between burned and non-burned years. In years when summer fires were applied, graminoid ANPP was comparable to that observed under spring and fall burning. Prior to burning, the summer fire treatment included litter from post-fire regrowth in the year it was burned and from the prior growing season when fire wasn't applied. Summer fire removes both accumulated litter and standing biomass during a period of active plant growth, temporarily increasing light and potentially soil nutrient availability (Blair 1997), which can stimulate late season regrowth. Because summer fires remove accumulated biomass late in the growing season, they also reduce surface litter at the start of the following year, which might be expected to increase resource availability for subsequent growth. Contrary to this expectation, productivity in non-burned years was substantially lower than under dormant season burns. Similar responses have been observed in other studies where growing-season fires reduced mean ANPP (Dickeson et al. 2017) or produced lagged reductions in productivity in the year following a burn (Engle et al. 1993; Engle and Bidwell 2001), suggesting that the effects of a growing-season fire can extend beyond the year of burning, although the mechanisms driving these reductions remain unclear.

In addition to differences between burned and non-burned years, lower productivity under summer burning may also reflect changes in plant community composition associated with repeated growing-season fire. Other research in these watersheds has shown that summer fire

reduced the relative cover of dominant C₄ grasses with concomitant increases in native plant species richness and diversity relative to dormant-season burns (Glidden et al. in review; Towne and Kemp 2008). Similar compositional differences may also contribute to contrasting forb productivity trajectories among burn seasons, with forb productivity increasing through time under dormant season burns but declining under summer burning in lowlands. Because warm-season grasses account for the majority of aboveground biomass production in tallgrass prairie, reductions in their abundance can lower total productivity even though plant diversity increases (Knapp et al. 2002).

Interannual variation in ANPP under all prescribed fire treatments was related to growing-season precipitation across burn seasons, reflecting the role of precipitation in regulating productivity in grassland ecosystems (Huxman et al. 2004; Sala et al. 1988). Periods of above-average precipitation were associated with high graminoid ANPP across all burn treatments. Drought conditions, such as those observed in 2012 substantially reduced productivity, though ANPP returned to levels comparable to pre-drought years in the subsequent growing season. The rapid recovery of ANPP following precipitous declines in productivity indicates a high degree of ecosystem resilience to periodic droughts (Hoover et al. 2014), regardless of seasonal fire timing. Importantly, the slope of the precipitation - productivity relationships were similar among burn seasons, indicating that the timing of prescribed fire did not alter the sensitivity of graminoid or total ANPP to precipitation. However, forb productivity showed little relationship with precipitation. As expected, lowlands consistently supported greater productivity than uplands for both grasses and forbs, reflecting differences in soil depth and water availability across topographic gradients. In addition to strong interannual variability and no directional increase in precipitation over time, total ANPP increased under all fire

treatments, with more pronounced increases in lowland sites than in uplands, resulting in more distinct differences between landscape positions over the course of the study. Increases in warm-season grass production have been observed in other long-term studies of tallgrass prairie under frequent burning regimes (Collins and Calabrese 2012; Tooley et al. 2025). A similar shift towards greater canopy cover of the dominant C₄ grasses has been documented in these watersheds (Glidden et al. in review, Towne and Kemp 2003; 2008), which together with other changes in environmental conditions, may contribute to increasing graminoid ANPP over time.

Soil properties also differed among landscape positions, with greater concentrations of inorganic N and Mg were found in lowlands compared to the uplands. Greater productivity and downslope movement of organic matter likely contributes to higher nutrient availability in soils at lower landscape positions. However, because soils were sampled only once near the end of the study and no-pretreatment baseline was available, we cannot exclude the possibility that frequent burning influenced soil through gradual changes or homogenization over time. Regardless of fire season, managers should expect considerable year-to-year variation in plant productivity, as interannual climate variables can exert stronger influences on productivity than differences in management practices.

Implications

Fire-dependent grasslands require periodic fire to maintain an open grassland state and limit woody encroachment, making prescribed burning one of the most important tools for conserving and managing tallgrass prairie. Our results indicate that the beneficial effects of prescribed fire are not limited to late-spring burning. Variation in productivity was driven more by climate variability and topography than by the timing of fire, and fire season did not alter

these relationships. These findings suggest that grassland productivity is more constrained by broader environmental controls than the seasonal timing of fire. Expanding prescribed burning beyond late spring may provide a practical and cost-effective approach for maintaining functional ecosystems while increasing opportunities to burn under more favorable weather conditions and distributing smoke emissions more evenly.

Management strategies incorporating growing-season fire may require balancing biodiversity goals with forage production, particularly in productive lowlands where mean ANPP under summer burning was lower relative to dormant-season burns. Expanding the season of fire may also create tradeoffs for the conservation of wildlife species dependent on standing vegetation or litter for habitat and refugia during different parts of the year. Because many rangelands are managed with large herbivores, additional research is needed to determine how interactions between fire timing and grazing influence productivity and ecosystem responses under grazed conditions. Incorporating greater variation in fire timing across the landscape may also offset the homogenizing effects of repeated burning at a single time of year, promoting heterogeneity in vegetation structure and habitat availability while providing a more adaptive approach for managing diverse and functional tallgrass prairie.

ACKNOWLEDGEMENTS

This research was supported by DEB-2025849 and multiple grants from the National Science Foundation's Long-Term Ecological Research Program (LTER) to support the Konza Prairie LTER program. AJG was funded in part by the Grassland Heritage Foundation (#). We thank Amanda Kuhl and many undergraduate students for collecting data. Kansas State Soil Testing lab for processing our samples. Patrick O'Neal and Jim Larkins for overssing the

management of these watersheds and volunteers who helped with prescribed burning over the years. JMB was supported by the Agricultural Experimental Station at Kansas State University. This is contribution number 26-XXX-J from the Kansas Agricultural Experimental Station.

AUTHOR CONTRIBUTIONS

JMB and AJG conceptualized the study. All authors contributed to writing and editing the manuscript.

References

- Abrams, M. D., A. K. Knapp, and L. C. Hulbert. 1986. "A ten-year record of aboveground biomass in a Kansas tallgrass prairie: effects of fire and topographic position." *American Journal of Botany*, 73(10):1509–1515. <https://doi.org/10.1002/j.1537-2197.1986.tb10897.x>.
- Archer, S. R., E. M. Andersen, K. I. Predick, S. Schwinning, R. J. Steidl, and S.R. Woods. 2017. "Woody plant encroachment: causes and consequences." In *Rangeland systems: Processes, management and challenges*, edited by Briske, D, 25–84. Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-46709-2_2
- Blair, J. M., 1997. Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis. *Ecology*, 78(8), 2359–2368. [https://doi.org/10.1890/0012-9658\(1997\)078\[2359:fnaapr\]2.0.co;2](https://doi.org/10.1890/0012-9658(1997)078[2359:fnaapr]2.0.co;2).
- Blair, J. M., and J. B. Nippert. 2025. PAB03 Aboveground primary productivity of tallgrass prairie based on accumulated plant biomass on LTER watersheds burned at different seasons ver 19. Environmental Data Initiative. <https://doi.org/10.6073/pasta/4c65a4dee1f0c04b522ece6703ae33ca>. Accessed December 30, 2025.
- Blair, J. M., J. B. Nippert, and J. M. Briggs. 2014. Grassland ecology. In: Monson, R. (Ed.), *The Plant Sciences—Ecology & the Environment*, Springer Reference Series. Springer-Verlag, Berlin Heidelberg, Germany, pp. 389–423. https://doi-org.er.lib.k-state.edu/10.1007/978-1-4614-7612-2_14-1.
- Briggs, J. M., and A. K. Knapp. 1995. "Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass." *American Journal of Botany*, 82(8): 1024–1030. <https://doi.org/10.1002/j.1537-2197.1995.tb11567.x>.
- Bowman, D. M., J. K. Balch, P. Artaxo, W. J. Bond, J. M. Carlson, M. A. Cochrane, C. M. d'Antonio, et al. 2009. "Fire in the Earth system." *Science*, 324(5926): 481–484. <https://doi.org/10.1126/science.1163886>.
- Buis, G. M., J. M Blair, D. E. Burkepile, C. E. Burns, A. J. Chamberlain, P. L. Chapman, S. L. Collins, et al. 2009. "Controls of aboveground net primary production in mesic savanna grasslands: an inter-hemispheric comparison." *Ecosystems*, 12(6):982–995. <https://doi.org/10.1007/s10021-009-9273-1>.
- Clarke, J. R., T. J. Hovick, B. Geaumont, J. P. Harmon, and K. Sedivec. 2026. "Plant litter as a cornerstone of grassland ecosystem services." *Agriculture, Ecosystems & Environment*, 399: 110171. <https://doi.org/10.1016/j.agee.2025.110171>.

- Collins, S. L., and L. B. Calabrese. 2012. "Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie." *Journal of Vegetation Science*, 23(3): 563–575. <https://doi.org/10.1111/j.1654-1103.2011.01369.x>.
- Connell, R. K., J. B. Nippert, and J. M. Blair. 2020. "Three decades of divergent land use and plant community change alters soil C and N content in tallgrass prairie." *Journal of Geophysical Research: Biogeosciences*, 125(8): e2020JG005723. <https://doi.org/10.1029/2020JG005723>.
- Coppedge, B. R., D. M. Engle, C. S. Toepfer, and J. H. Shaw. 1998. "Effects of seasonal fire, bison grazing and climatic variation on tallgrass prairie vegetation." *Plant Ecology*, 139(2), 235–246. <https://doi.org/10.1023/A:1009728104508>.
- Dickson, T. L., B. A. Hayes, and T. B. Bragg. 2019. "Effects of 34 years of experimentally manipulated burn seasons and frequencies on prairie plant composition." *Rangeland Ecology & Management*, 72(1): 82–91. <https://doi.org/10.1016/j.rama.2018.07.014>.
- Engle, D. M., and T. G. Bidwell. 2001. "Viewpoint: The response of central North American prairies to seasonal fire." *Journal of Range Management*, 54(1): 2–10. <https://doi.org/10.2307/4003519>.
- Engle, D. M., J. F. Stritzke, T. G. Bidwell, and P. L. Claypool. 1993. "Late-summer fire and follow-up herbicide treatments in tallgrass prairie." *Journal of Range Management*, 46: 542–547.
- Ewing, A. L., and D. M. Engle. 1988. "Effects of late summer fire on tallgrass prairie microclimate and community composition." *American Midland Naturalist*, 120(1): 212–223. <https://doi.org/10.2307/2425901>.
- Fuhlendorf, S. D., and D. M. Engle. 2004. "Application of the fire–grazing interaction to restore a shifting mosaic on tallgrass prairie." *Journal of Applied Ecology*, 41(4): 604–614. <https://doi.org/10.1111/j.0021-8901.2004.00937.x>.
- Fay, P. A., J. M. Blair, M. D. Smith, J. B. Nippert, J. D. Carlisle, and A. K. Knapp. 2011. "Relative effects of precipitation variability and warming on tallgrass prairie ecosystem function." *Biogeosciences*, 8(10): 3053–3068. <https://doi.org/10.5194/bg-8-3053-2011>.
- Fox, J., and S. Weisberg. 2018. "An R companion to applied regression." Sage publications.
- Freeman C. C. 1998. "The flora of Konza Prairie: a historical review and contemporary patterns." In: Knapp, A.K., Briggs, J.M., Hartnett, D.C., Collins, S.L., (Ed.), *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie*, New York, NY: Oxford University Press, 69–80.

- Fynn, R. W. S., R. J. Haynes, and T. G. O'Connor. 2003. "Burning causes long-term changes in soil organic matter content of a South African grassland." *Soil Biology and Biochemistry*, 35(5): 677–687. [https://doi.org/10.1016/S0038-0717\(03\)00054-3](https://doi.org/10.1016/S0038-0717(03)00054-3).
- Gibson, D. J., and L. C. Hulbert. 1987. "Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie." *Vegetatio*, 72: 175–185. <https://doi.org/10.1007/BF00039839>.
- Glidden A.J., Z. Ratajczak, J. H. Taylor, and J. M. Blair. *In review*. Long-term plant community dynamics vary with season of fire in tallgrass prairie. *Ecological Applications*.
- Hartnett, D., S. Collins, and Z. Ratajczak. 2025. PVC02 Plant species composition on selected watersheds at Konza Prairie ver 24. Environmental Data Initiative. <https://doi.org/10.6073/pasta/c2dde97352fb0e25ab749765967997b9>. Accessed October 22, 2025.
- Hoover, D. L., A. K. Knapp, and M. D. Smith. 2014. "Resistance and resilience of a grassland ecosystem to climate extremes." *Ecology*, 95(9): 2646–2656. <https://doi.org/10.1890/13-2186.1>.
- Howe, H. F. 2000. "Grass response to seasonal burns in experimental plantings." *Journal of Range Management*. <https://doi.org/10.2307/4003757>.
- Hsu, A., M. W. Jones, J. R. Thurgood, A. J. Smith, R. Carmenta, J. T. Abatzoglou, L. O. Anderson, et al. 2025. "A global assemblage of regional prescribed burn records—GlobalRx." *Scientific Data*, 12(1): 1083. <https://doi.org/10.1038/s41597-025-04941-w>.
- Huxman, T. E., M. D. Smith, P. A. Fay, A. K. Knapp, M. R. Shaw, M. E. Loik, S. D. Smith, et al., 2004. "Convergence across biomes to a common rain-use efficiency." *Nature*, 429(6992): 651–654. <https://doi.org/10.1038/nature02561>.
- KDHE. 2025. Kansas Department of Health and Environment: Flint Hills Wildland Fire Update, 2025 summary. https://ksfire.org/media/Flint_Hills_Update_2025_Summary-77e3962.pdf. Accessed January 11, 2025
- Kirkman, K. P., S. L. Collins, M. D. Smith, A. K. Knapp, D. E. Burkepile, C. E. Burns, R. W. S. Fynn, et al. 2014. "Responses to fire differ between South African and North American grassland communities." *Journal of Vegetation Science*, 25(3): 793–804. <https://doi.org/10.1111/jvs.12130>.
- Kitchen, D. J., J. M. Blair, and M. A. Callaham Jr. 2009. "Annual fire and mowing alter biomass, depth distribution, and C and N content of roots and soil in tallgrass prairie." *Plant and Soil*, 323(1): 235–247. <https://doi.org/10.1007/s11104-009-9931-2>.
- Knapp, A. K., J. M. Briggs, J.M., Blair, and C. L. Turner. 1998. "Patterns and controls of aboveground net primary production in tallgrass prairie." In *Grassland dynamics: Long-term*

- ecological research in tallgrass prairie*, edited by Alan K. Knapp, John M. Briggs, David C. Hartnett, and Scott L. Collins, 193–221. New York, NY: Oxford University Press.
- Knapp, A. K., P. A. Fay, J. M. Blair, S. L. Collins, M. D. Smith, J. D. Carlisle, and C. W. Harper. 2002. “Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland.” *Science*, 298(5601), 2202–2205. <https://doi.org/10.1126/science.1076347>.
- Knapp, A. K., and T. R. Seastedt. 1986. “Detritus accumulation limits productivity of tallgrass prairie.” *BioScience*, 36(10): 662–668. <https://doi.org/10.2307/1310387>.
- Kuznetsova, A., P. B. Brockhoff, and R. H. Christensen. 2017. “lmerTest package: tests in linear mixed effects models.” *Journal of statistical software*, 82: 1–26. <https://doi.org/10.18637/jss.v082.i13>.
- Lenth, R. V., B. Banfai, B. Bolker, P. Buerkner, I. Giné-Vázquez, M. Herve, M. Jung, J. Love, F. Miguez, J. Piaskowski, et al. 2024. Emmeans: estimated marginal means, aka least-squares means. <https://doi.org/10.32614/cran.package.emmeans>. Accessed July 15, 2025.
- Launchbaugh, J. L., and C. E. Owensby. 1978. “Kansas Rangelands: their management, based on half a century of research.” Manhattan, KS. Kansas Agricultural Experiment Station.
- McCain, K. N., S. G. Baer, J. M. Blair, and G. W. Wilson. 2010. “Dominant grasses suppress local diversity in restored tallgrass prairie.” *Restoration Ecology*, 18: 40–49. <https://doi.org/10.1111/j.1526-100X.2010.00669.x>.
- McGranahan, D. A., T. J. Hovick, R. D. Elmore, D. M. Engle, and S. D. Fuhlendorf. 2018. “Moderate patchiness optimizes heterogeneity, stability, and beta diversity in mesic grassland.” *Ecology and Evolution*, 8(10): 5008–5015. <https://doi.org/10.1002/ece3.4081>.
- Nippert, J. 2026. AWE01 Meteorological data from the Konza prairie headquarters weather station ver 25. Environmental Data Initiative. <https://doi.org/10.6073/pasta/645f6ebe7d75869d1b6747174aaa342b>. Accessed February 13, 2026.
- Nippert, J. B., A. K. Knapp, and J. M. Briggs. 2006. “Intra-annual rainfall variability and grassland productivity: can the past predict the future?” *Plant Ecology*, 184(1): 65–74. <https://doi.org/10.1007/s11258-005-9052-9>.
- Nippert, J. B., T. W. Ocheltree, A. M. Skibbe, L. C. Kangas, J. M. Ham, K. B. Shonkwiler Arnold, and N. A. Brunsell. 2011. “Linking plant growth responses across topographic gradients in tallgrass prairie.” *Oecologia*, 166(4): 1131–1142. <https://doi.org/10.1007/s00442-011-1948-6>.
- Ojima, D. S., D. S. Schimel, W. J. Parton, and C. E. Owensby. 1994. “Long-and short-term effects of fire on nitrogen cycling in tallgrass prairie.” *Biogeochemistry*, 24(2): 67–84. <https://doi.org/10.1007/BF02390180>.

- R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Ransom, Michel D., Charles W. Rice, Timothy C. Todd, and William A. Wehmueller. 1998. "Soils and soil biota." In *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie*, edited by Alan K. Knapp, John M. Briggs, David C. Hartnett, and Scott L. Collins, 48–66. New York, NY: Oxford University Press.
- Rappold, A. G., J. Reyes, G. Pouliot, W. E. Cascio, and D. Diaz-Sanchez. 2017. "Community vulnerability to health impacts of wildland fire smoke exposure." *Environmental Science & Technology*, 51(12): 6674–6682. <https://doi.org/10.1021/acs.est.6b06200>.
- Ratajczak, Z., J. B. Nippert, J. M. Briggs, J.M., Blair. 2014. "Fire dynamics distinguish grasslands, shrublands and woodlands as alternative attractors in the Central Great Plains of North America." *Journal of Ecology*, 1374–1385. <https://doi.org/10.1111/1365-2745.12311>.
- Sablan, O., B. Ford, E. Gargulinski, M. S. Hammer, G. Henery, S. Kondragunta, R. V. Martin, et al. 2024. "Quantifying prescribed-fire smoke exposure using low-cost sensors and satellites: Springtime burning in Eastern Kansas." *GeoHealth*, 8(4), e2023GH000982. <https://doi.org/10.1029/2023GH000982>.
- Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth, 1988. "Primary production of the central grassland region of the United States." *Ecology*, 69(1): 40–45. <https://doi.org/10.2307/1943158>.
- Smith, M. D., A. K. Knapp, and S. L. Collins. 2009. "A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change." *Ecology*, 90(12): 3279–3289. <https://doi.org/10.1890/08-1815.1>.
- Tooley, E. G., J. B. Nippert, and A. K. Knapp. 2025. "Revisiting patterns and controls of productivity in a mesic grassland 30 years later: do we know now what we knew then." *Ecosystems*, 28(4): 42. <https://doi.org/10.1007/s10021-025-00985-6>.
- Towne, E. G., and J. M. Craine. 2014. "Ecological consequences of shifting the timing of burning tallgrass prairie." *PLoS One*, 9(7): e103423. <https://doi.org/10.1371/journal.pone.0103423>.
- Towne, E. G., and J. M. Craine. 2016. "A critical examination of timing of burning in the Kansas Flint Hills." *Rangeland Ecology & Management*, 69(1): 28–34. <https://doi.org/10.1016/j.rama.2015.10.008>.
- Towne, E. G., and K. E. Kemp. 2003. "Vegetation dynamics from annually burning tallgrass prairie in different seasons." *Journal of Range Management*, 56(2): 185–192. <https://doi.org/10.2307/4003903>.

- Towne, E. G., and K. E. Kemp 2008. "Long-term response patterns of tallgrass prairie to frequent summer burning." *Rangeland Ecology & Management*, 61(5): 509–520.
<https://doi.org/10.2111/08-043.1>.
- Twidwell, D., A. S. West, W. B. Hiatt, A. L. Ramirez, J. T. Winter, D. M. Engle, S. D. Fuhlendorf, and J. D. Carlson. 2016. "Plant invasions or fire policy: which has altered fire behavior more in tallgrass prairie?" *Ecosystems*, 19(2): 356–368.
<https://doi.org/10.1007/s10021-015-9937-y>.
- Uys, R. G., W. J. Bond, and T. M. Everson. 2004. "The effect of different fire regimes on plant diversity in southern African grasslands." *Biological Conservation*, 118(4): 489–499.
<https://doi.org/10.1016/j.biocon.2003.09.024>.
- Weir, J. R., D. Twidwell, and C. L. Wonkka. 2015. "Prescribed burn association activity, needs, and safety record: a survey of the Great Plains." *Great Plains Fire Science Exchange*. GPE Publication, 6: 1–19.

Table 3.1: Summary ANOVA statistics from linear mixed-effects models evaluating graminoids, forbs, and total herbaceous productivity over time among burn seasons and between topographic positions. Forbs were square-root transformed prior to analysis.

Fun Group	Factor	Sum Sq	Mean Sq	df_n,df_d	F value	Pr(>F)
Graminoids	Burn Season (BS)	422437.86	140812.62	3,4	10.86	0.0216
	Topography (T)	2123536.48	2123536.48	1,52	163.77	< 0.001
	Year (Y)	1004929.08	1004929.08	1,1846	77.50	< 0.001
	BS:T	122940.41	40980.14	3,52	3.16	0.0322
	BS:Y	70028.54	23342.85	3,1846	1.80	0.1451
	T:Y	31031.98	31031.98	1,1846	2.39	0.1220
	BS:T:Y	9925.86	3308.62	3,1846	0.26	0.8577
Forbs	Burn Season (BS)	92.61	30.87	3,4	8.23	0.0347
	Topography (T)	325.66	325.66	1,52	86.87	< 0.001
	Year (Y)	2.99	2.99	1,1846	0.80	0.3717
	BS:T	6.66	2.22	3,52	0.59	0.6226
	BS:Y	96.84	32.28	3,1846	8.61	< 0.001
	T:Y	236.00	236.00	1,1846	62.96	< 0.001
	BS:T:Y	136.99	45.66	3,1846	12.18	< 0.001
Total Herbaceous	Burn Season (BS)	191782.72	63927.57	3,4	4.82	0.0814
	Topography (T)	3259794.76	3259794.76	1,52	245.70	< 0.001
	Year (Y)	1094752.19	1094752.19	1,1846	82.52	< 0.001
	BS:T	129503.63	43167.88	3,52	3.25	0.0289
	BS:Y	54114.13	18038.04	3,1846	1.36	0.2534
	T:Y	152878.95	152878.95	1,1846	11.52	< 0.001
	BS:T:Y	37081.31	12360.44	3,1846	0.93	0.4246

Table 3.2: Coefficient of determination (r^2) depicting the relationship between ANPP and growing season precipitation for each burn season within lowlands and uplands. Values represent the proportion of interannual variation in productivity explained by precipitation and are shown for graminoid, forb, and total productivity.

	Graminoid		Forb		Total	
	(Lowland r^2)	(Upland r^2)	(Lowland r^2)	(Upland r^2)	(Lowland r^2)	(Upland r^2)
Spring	0.18	0.32	NS	NS	0.19	0.34
Summer	0.34	0.27	NS	NS	0.33	0.28
Fall	0.25	0.22	0.01	0.01	0.26	0.25
Winter	0.24	0.30	NS	NS	0.24	0.32

Table 3.3: Mean and standard error for each soil property in the different seasonal burn treatments. Means were calculated across all replicate samples for each burn season × topographic position combination. Global Mean represents the mean across all burn seasons within a topographic position. Different letters indicate significant differences based on Tukey-adjusted pairwise comparison ($\alpha = 0.05$) from mixed-effects models using Kenward-Roger degrees of freedom. Upper-case letters indicate significant topographic differences within a burn season or for the global mean.

Response	Topographic Position	Spring	Summer	Fall	Winter	Global Mean
Ca (ppm)	Upland	3621.86 ± 182.7	3761.04 ± 308.5	3487.26 ± 171.2	3494.62 ± 213.8	3591.2 ± 112.7 ^A
	Lowland	2984.89 ± 137.1	3287.14 ± 92.2	3633.72 ± 166.5	3708.14 ± 241.2	3403.47 ± 84.1
Mg (ppm)	Upland	450.98 ± 14.94	381.54 ± 22.48	441.92 ± 14.44	405.59 ± 14.36	420.01 ± 8.45 ^A
	Lowland	504.35 ± 20.46	491.52 ± 18.47	513.71 ± 10.37	540.68 ± 9.29	512.57 ± 7.72 ^B
K (ppm)	Upland	520.88 ± 24.66	535.82 ± 37.21	526.26 ± 40.16	522.14 ± 14.19	526.28 ± 15.42
	Lowland	494.08 ± 34.14	501.02 ± 24.68	593.59 ± 16.8	569.68 ± 28.14	539.59 ± 13.34
Na (ppm)	Upland	13.56 ± 1.88	11.06 ± 0.29	20.82 ± 4.4	11.74 ± 1.63	14.3 ± 1.27
	Lowland	21.39 ± 4.47	13.04 ± 0.96	17.46 ± 2.28	14.06 ± 1.03	16.49 ± 1.3
pH	Upland	6.49 ± 0.03	6.53 ± 0.03	6.5 ± 0.05	6.54 ± 0.1	6.51 ± 0.03
	Lowland	6.45 ± 0.06	6.59 ± 0.04	6.61 ± 0.04	6.5 ± 0.08	6.54 ± 0.03
C %	Upland	4.88 ± 0.11	5.38 ± 0.49 ^A	4.96 ± 0.28	4.98 ± 0.12	5.05 ± 0.15
	Lowland	4.86 ± 0.2	4.58 ± 0.09 ^B	4.82 ± 0.12	5.51 ± 0.24	4.94 ± 0.09
N %	Upland	0.39 ± 0.01	0.43 ± 0.04 ^A	0.37 ± 0.02	0.39 ± 0.01	0.39 ± 0.01
	Lowland	0.38 ± 0.01	0.35 ± 0.01 ^B	0.36 ± 0.01	0.41 ± 0.02	0.37 ± 0.01
NH ₄ (mg/kg)	Upland	1.77 ± 0.14	1.72 ± 0.27	1.02 ± 0.1	1.65 ± 0.15	1.54 ± 0.09 ^A
	Lowland	2 ± 0.11	1.91 ± 0.26	1.89 ± 0.32	2.53 ± 0.48	2.08 ± 0.16 ^B
NO ₃ (mg/kg)	Upland	1.03 ± 0.2	1.69 ± 0.6	0.51 ± 0.16	0.49 ± 0.16	0.93 ± 0.17 ^A
	Lowland	1.57 ± 0.24	2.66 ± 0.45	1.07 ± 0.3	2.12 ± 0.4	1.85 ± 0.18 ^B
NO ₃ + NH ₄ (mg/kg)	Upland	2.81 ± 0.26	3.42 ± 0.76	1.53 ± 0.23	2.14 ± 0.28	2.47 ± 0.22 ^A
	Lowland	3.57 ± 0.33	4.57 ± 0.58	2.95 ± 0.51	4.65 ± 0.78	3.94 ± 0.29 ^B
P (ppm)	Upland	5.27 ± 0.38	5.46 ± 0.48	4.81 ± 0.42	5.09 ± 0.44	5.16 ± 0.22
	Lowland	6.16 ± 0.83	6.24 ± 0.83	5.96 ± 0.45	5.36 ± 0.43	5.93 ± 0.33

Note: C:N = range from 12.5 to 13.4 for each burn season and average ~13 global.

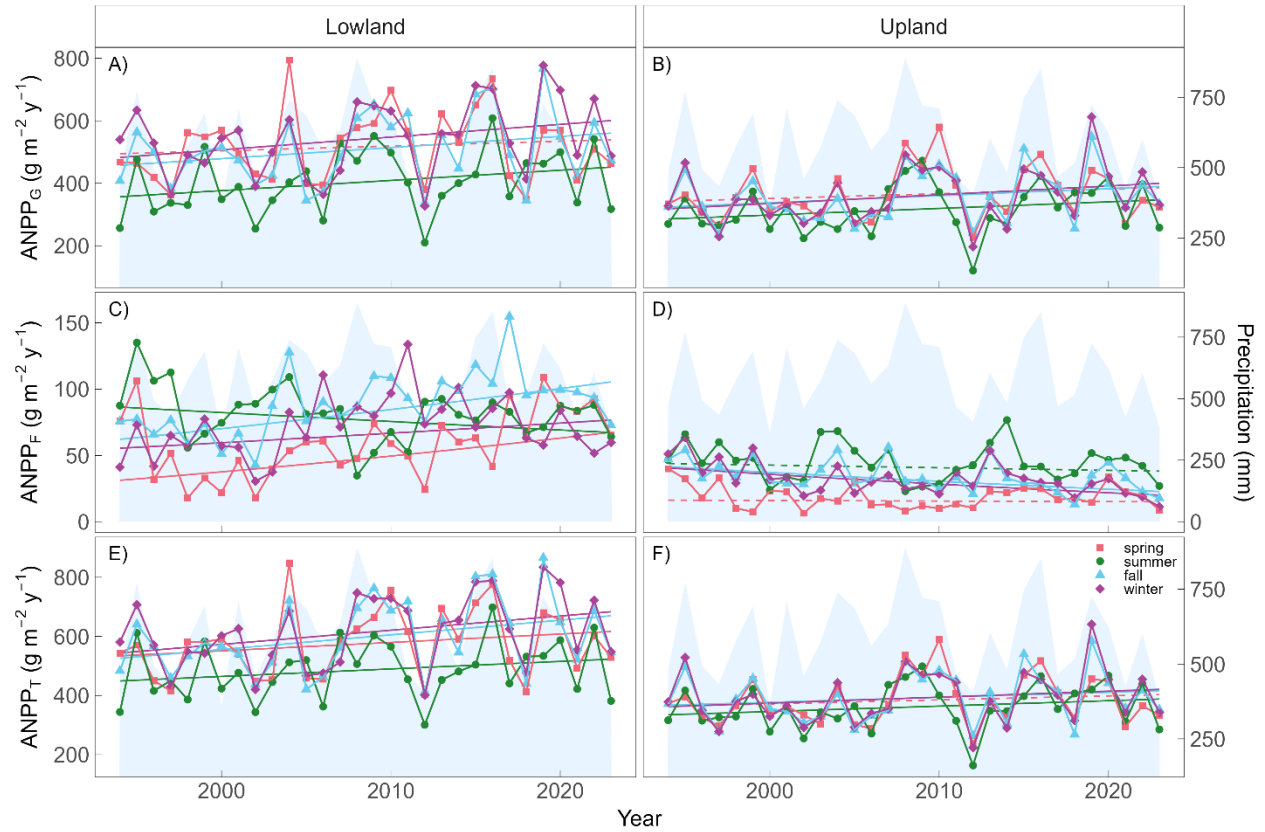


Figure 3-1: Annual net primary productivity for graminoids (ANPP_G) (A, B), forbs (ANPP_F) (C, D), and combined herbaceous groups (ANPP_H) (E, F) in lowlands and uplands from 1994 to 2023. Solid lines represent significant linear mixed model trends, with dashed lines for non-significant trends. Growing season (April – September) precipitation is shown as shaded background.

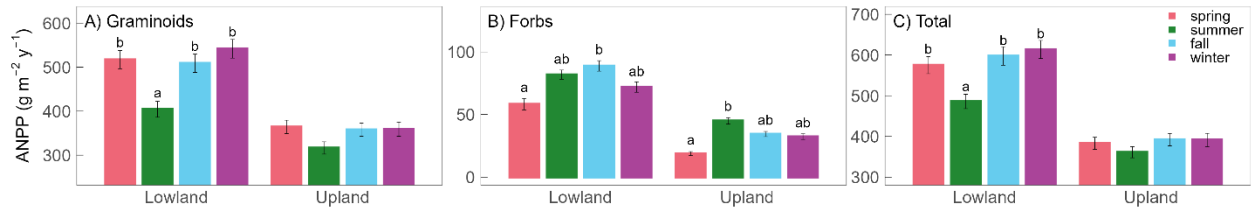


Figure 3-2: Mean ($\pm$ SE) annual productivity for graminoids (A), forbs (B), and total productivity (C). Values represent means averaged across 30 years for each burn season and topographic position combination. Different letters indicate significant differences ($p < 0.05$) among burn seasons within each topographic position, derived from linear mixed models using the transect-level dataset (Table 3.1).

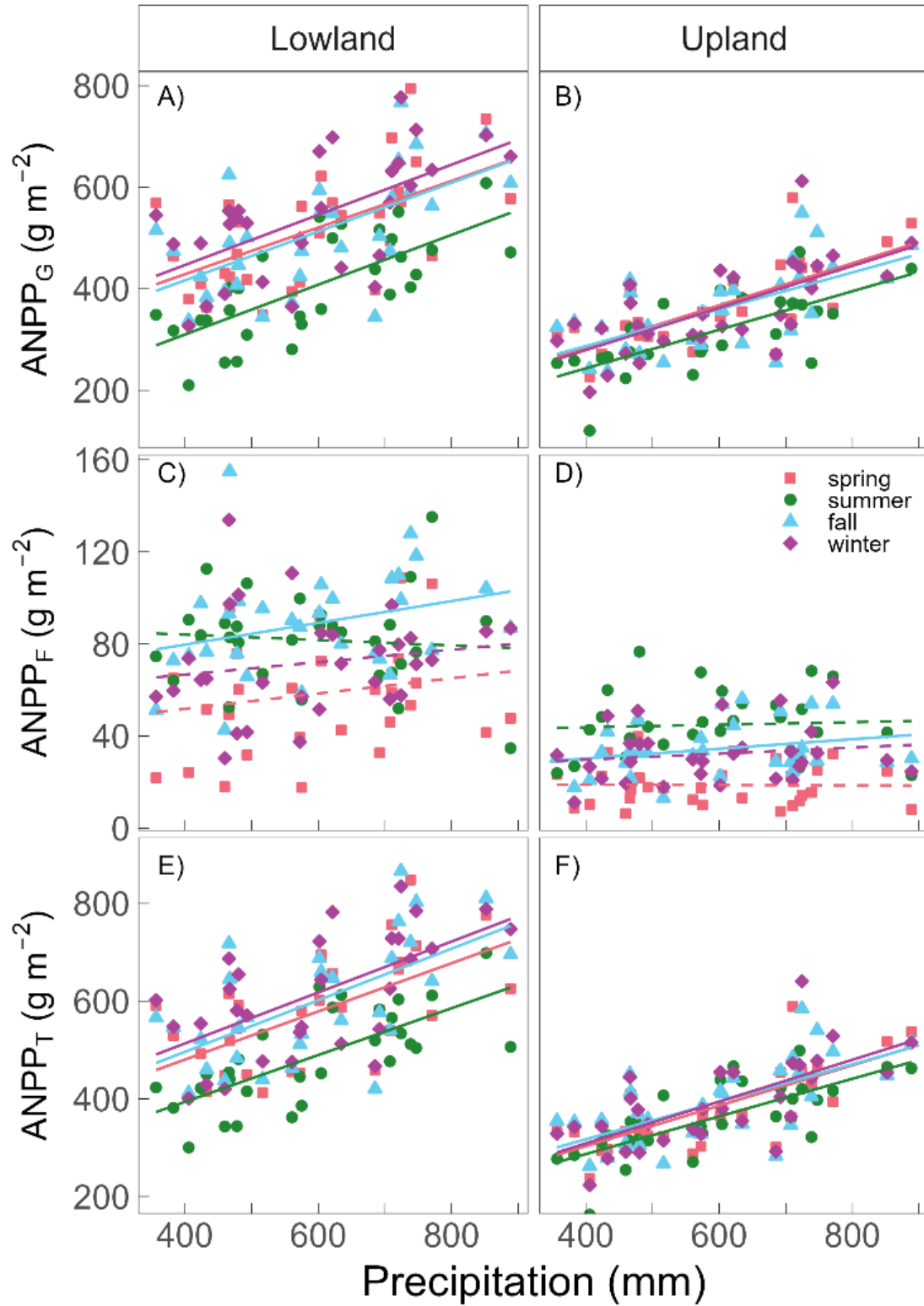


Figure 3-3: Linear regressions of ANPP and growing season precipitation for each burn season and topographic position combination for graminoids (A, B), forbs (C, D), and total herbaceous (E, F). Solid lines represent significant relationships ($p < 0.05$), while dashed lines represent non-significant relationships.

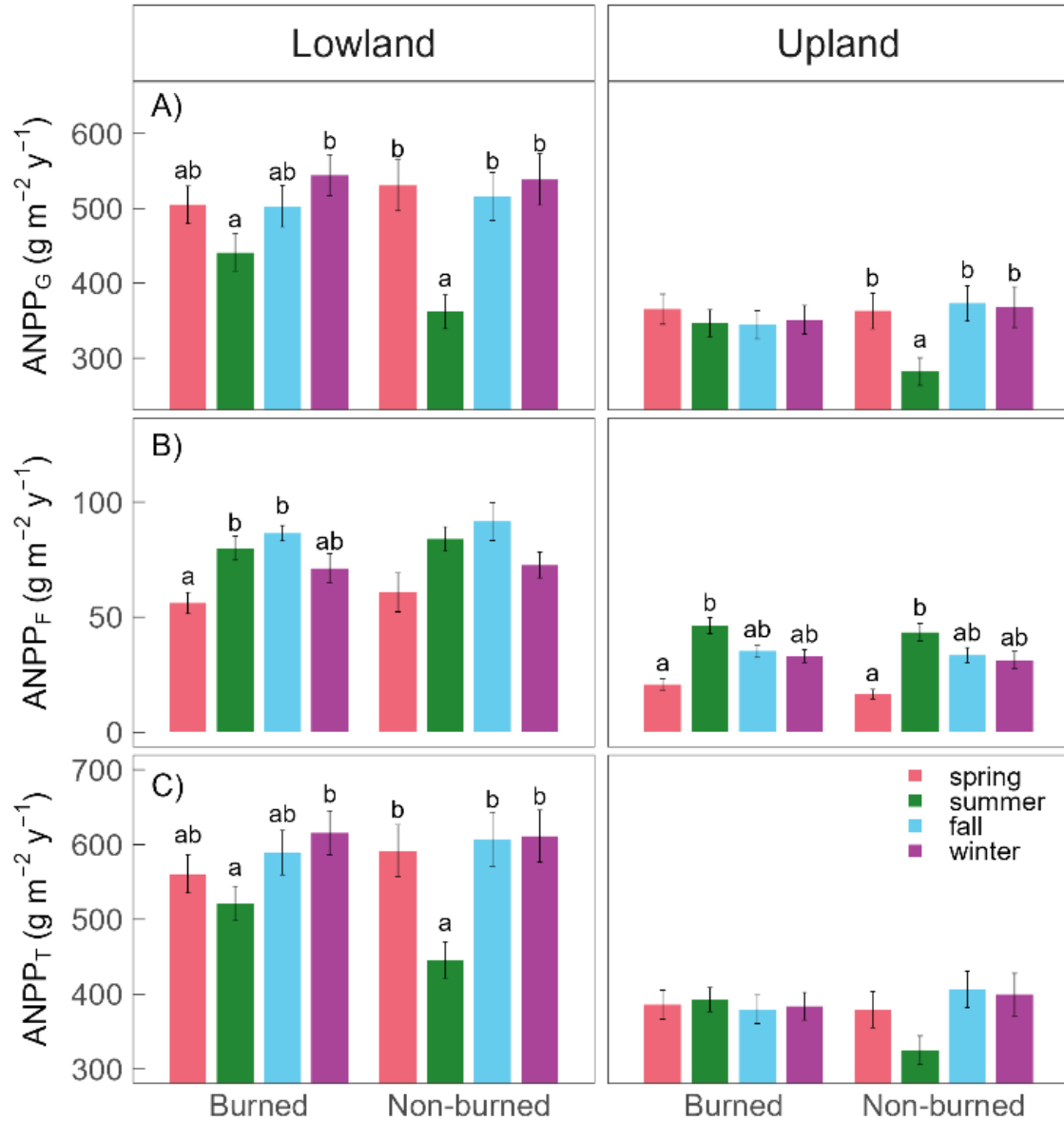


Figure 3-4: Mean ($\pm$ SE) annual aboveground net primary productivity for graminoids (A), forbs (B), and total productivity (C) by burn classifications (burned and non-burned) for each burn season and topographic combination. Different letters indicate significant differences ($p < 0.05$) among burn season within each burn category, derived from linear mixed models (Table B.6).

Chapter 4 - Reintroducing Frequent Seasonal Fire to Shrub-Encroached Bison-Grazed Grasslands

Abstract

Woody encroachment threatens grassland ecosystems worldwide. Frequent prescribed fire, particularly spring burning, is often recommended to restore grassland structure and function. However, established clonal shrubs persist despite repeated spring fire, and little is known about whether altering fire seasonality can improve restoration outcomes in shrub-encroached, grazed grasslands. We evaluated the initial (two-year) effects of reintroducing annual spring and late-summer fire in a bison-grazed tallgrass prairie watershed that had experienced severe shrub expansion under a 4-year fire return interval. Responses were assessed at the landscape scale through vegetation transects and shrub mapping, and at the shrub-island scale using targeted combinations of burn season, grazing exclusion, and mowing. Herbaceous communities responded similarly under both spring and summer burning. Warm-season grass cover increased across the watershed, native species richness increased through time, and differences in community composition were driven more strongly by topographic position than by burn season. In contrast, shrub responses differed by species and burn treatment. Following the initial fire, *Cornus drummondii* increased in size, whereas *Rhus aromatica* declined. After the second fire, both species contracted under spring burning, whereas summer-burned shrubs either maintained their expanded size or recovered to their original size. At the shrub-island scale, the effects of two years of annual burning on reducing aboveground biomass of *C. drummondii* were offset by increases in stem density, particularly along shrub edges. Excluding bison increased graminoid cover around shrub islands but did not reduce shrub stem densities. Despite complete top-kill, the effects of mowing were limited to a transient increase in stem recruitment. These

results suggest that both annual spring and summer fire promote herbaceous recovery in shrub-encroached, bison-grazed grasslands. However, because these findings only represent the initial two years after annual fire reintroduction, continued monitoring is necessary to determine whether fire seasonality can shift these systems towards a more open, grass-dominated state.

Introduction

Woody plant encroachment is a serious and growing threat to grassland ecosystems globally. The persistence and spread of woody plants alters community composition and many ecosystem services that these grasslands provide. This process occurs when shrubs and trees increase in abundance and cover at the expense of the herbaceous vegetation that has historically dominated grasslands (Archer et al., 2017; Van Auken, 2009). As woody plants expand, they shift species composition, change disturbance regimes, and alter local resource availability, leading to broad changes in ecosystem processes (Archer & Predick, 2014; Briggs et al., 2005; Ratajczak et al., 2012). These ecological changes have direct consequences for rangeland ecosystem services, including declines in forage production and substantial economic losses (Anadón et al., 2014). Across North America alone, woody plant encroachment has been associated with estimated reductions in cattle production valued between \$4.1–5.6 billion (Morford et al., 2022). These ecological and economic impacts have increased the need for management interventions aimed at not only limiting but also reversing woody expansion (Symstad & Leis, 2017).

Across the North American Great Plains, woody plant cover has increased by approximately 1–2% annually (Barger et al., 2011), with transitions from grassland to shrubland- and eventually woodland-dominated states occurring within as little as 40 years (Ratajczak et al.,

2016). These transitions appear to be accelerating in North America and other regions (Stevens et al., 2017) as a result of increased propagule pressure and interacting global drivers, including land use change, rising atmospheric CO₂, climate variability, and altered disturbance regimes (Archer et al., 2017; Bond and Midgley, 2012; Scholtz et al. 2018; Van Auken, 2009). Once established, woody plants are often difficult to remove because reinforcing feedback mechanisms promote their persistence (Collins et al., 2021; Ling et al., 2023; Miller et al., 2017). As woody plant cover increases, it can form dense canopies that reduce light availability and suppress herbaceous vegetation, disrupting the continuity of fine fuels needed to carry fire and weakening the grass-fire feedback (Ratajczak et al., 2011; Tooley et al., 2024). Responses to fire vary among woody plant functional types, as many tree species experience higher mortality following fire, while clonal species can persist by resprouting from belowground reserves (Bond & Midgley, 2001; O’Conner et al., 2020). This ability to resprout allows some woody plants to survive through repeated disturbance events and even under interacting stressors such as drought and fire (Keen et al., 2024). As a result, the restoration of shrub encroached grasslands can be quite challenging, and there is a need to identify management methods that facilitate reductions in woody plant cover and the recovery of a grassland state (Ding and Eldridge, 2023).

Prescribed fire is the most widely used tool to limit woody expansion in tallgrass prairie and other mesic grasslands because it emulates an important historical disturbance and can be applied across large spatial scales at relatively low cost (Rowe 2010). In these ecosystems, fire removes accumulated litter and alters light and resource availability, influencing plant growth and community composition (Gibson & Hulbert, 1987; Knapp et al., 1999). Plant community composition in fire-dependent grasslands is strongly influenced by variation in fire frequency, with frequent burning maintaining a herbaceous, grass-dominated state and less frequent burning

allowing woody plants to establish (Briggs et al., 2005). Following initial establishment of woody species in a grass matrix, encroachment often develops as discrete patches that can expand and coalesce across the landscape, particularly in the case of clonal shrubs (Connell et al., 2021; Ratajczak et al., 2011). As these patches expand, they compete with and increasingly suppress herbaceous vegetation, reducing the amount of fine fuel available and leading to patchy and often less effective fires. As woody plants increase in size and abundance, fire effectiveness continues to decline, and even with the return of more frequent burning, fire alone is often insufficient for substantially reducing shrub cover (Collins et al., 2021; Nippert et al., 2021; Noble & Ratajczak, 2025; Ratajczak et al., 2017). While much of the research on use of fire in grassland restoration and shrub control has focused on the fire frequency, other aspects of fire regimes (e.g., timing) remain understudied (Towne & Craine, 2016; Twidwell et al., 2021).

In tallgrass prairie, prescribed fire is most commonly applied during the spring, with millions of acres burned annually in regions such as the Flint Hills (KDHE 2025). Burning at this time of year promotes growth and cover of the dominant perennial warm-season grasses and increases forage production for grazers (Engle & Bidwell, 2001). Increased grass cover also enhances fine fuel availability for subsequent fires, helping sustain frequent fire and maintain a grass-dominated state. However, repeated spring burning can reduce native species richness and diversity, particularly among C_3 graminoids, and contribute to more homogenous grasslands (Collins et al., 1998; Glidden et al., in review; Towne & Kemp, 2003). In contrast, historical fire regimes were not as temporally confined as current practices; rather, ignitions occurred throughout the year from both lightning and use of fire by Native Americans (Bragg, 1982; Stambough et al., 2013; Stewart, 2002). This included growing season fires, including late-summer burns, which occur during warmer conditions that coincide with periods of active plant

growth and aboveground resource allocation. Summer fires can be more variable in intensity and spatial extent due to differences in fuel and weather conditions. Warmer and drier conditions can increase fire intensity, while high plant moisture can limit combustion and promote less intense, patchier fires, leading to less predictable outcomes across the landscape (Engle & Bidwell, 2001; Yurkonis et al., 2019). At the same time, summer burning can alter plant community composition in ways that differ from spring fire, often resulting in a reduction of warm-season grasses but much higher richness and diversity (Glidden et al., in review; Howe, 2000; Towne & Kemp, 2008). Timing of summer fires can also affect fire intensity, with later summer fires generally occurring when some plants have begun to senesce and fuel conditions are more optimal. Prescribed burning later in summer, but before woody plants senesce, may increase the susceptibility of woody plants to fire by disrupting photosynthetic activity and reducing stored resources before they are translocated to belowground tissues.

Native ungulate grazers were historically abundant and important in tallgrass prairie (Shaw & Lee, 1997; Stebbins, 1997) and much of the remaining tallgrass prairie is now managed as rangeland. Therefore, understanding how fire timing interacts with grazing is critical for predicting plant community responses and woody control. Large grazers such as bison are a co-dominant driver of tallgrass prairie structure and function (Collins & Calabrese, 2012). By preferentially consuming C₄ grasses, bison can limit increases in grass cover, alter competitive interactions, and maintain high plant diversity in even annually burned prairies, counteracting the homogenizing effects of frequent burning (Collins et al., 1998; Ratajczak et al., 2022). However, the reductions in grass cover and subsequent fuel loads can also constrain the ability of fire to suppress woody plants, allowing shrubs to persist or expand even under frequent burning (Briggs et al., 2002; Knapp et al., 1999). Recent research suggests that reintroducing spring fire to areas

with a historically low fire frequency improves bison habitat but does little to reduce shrub cover (Noble & Ratajczak, 2025). In some studies, bison grazing even under frequent spring burning has also been associated with increased woody plant cover (Briggs et al., 2002), suggesting that fire and grazing alone may be insufficient to limit shrub expansion. While previous work has examined herbaceous plant responses to seasonal fire and bison grazing (Coppedge et al., 1998), less is known about how fire timing interacts with grazing to influence woody plant responses.

Many previous studies have reported the high resilience of established clonal shrubs to fire (Collins et al., 2020; Ling et al., 2023; Nippert et al., 2021; O’Conner et al., 2020), suggesting that additional management practices may need to be integrated with prescribed fire to reduce woody plant cover. One option is mowing shrubs prior to burning. Mowing removes aboveground biomass and nutrients and alters shrub structure, but many resprouting species can recover, which can limit the effectiveness of a single mowing treatment (Charton & Damschen, 2023; Ding and Eldridge, 2023; Watson et al., 2019). Despite this, mowing temporarily alters shrub structure by reducing stem height and canopy cover, and converting standing biomass into a layer of surface litter that can act as fuel for future fires. These changes can increase light availability, enhance herbaceous plant growth, and allow fire to more effectively penetrate shrub islands, where dense canopies would otherwise suppress herbaceous fuels and limit fire spread (Gaskin et al., 2021).

In this study, we evaluated how reintroducing annual fire in contrasting seasons (spring and late-summer) influences tallgrass prairie plant communities and the effect of woody plant control within a shrub-encroached, bison-grazed watershed previously managed under a 4-year fire return interval at Konza Prairie Biological Station. We evaluated plant community responses at the subcatchment scale by establishing vegetation transects in lowland and upland positions.

We also tracked changes in cover of established clonal shrubs through time to assess how spring and summer fires alter shrub cover and patterns of woody expansion. Finally, we assessed the impact of targeted management on selected individual shrub islands to test how fire timing, grazing (with and without bison exclosures), and mechanical removal (i.e., mowing) influence shrub persistence and shrub cover across the grassland-shrub boundary (outside, edge, and interior of shrub islands). Our specific objectives were to 1) determine how burn season influences plant community composition, including functional group cover, species richness, and diversity, and how these responses vary across topographic positions, 2) evaluate how burn season influences changes in shrub size and area at the landscape scale, and 3) assess how fire timing, grazing, and mowing interact to influence shrub stem density, biomass, recruitment, and herbaceous recovery at the shrub island scale.

Methods

Study Site

This study took place at Konza Prairie Biological Station (KPBS), a 3,487-ha native tallgrass prairie in the Flint Hills of Kansas. This landscape consists of rolling topography with deeper, fine-textured lowlands characterized by colluvial and alluvial deposits (Pachic Argiustolls), and shallow, rocky uplands composed of silty clay loams overlying layers of limestone and shale (Udic Argiustolls). KPBS is topographically divided into distinct watersheds, with each assigned a specific prescribed fire and grazing treatment. Vegetation consists primarily of C₄ grasses (*Andropogon gerardii*, *Panicum virgatum*, *Sorghastrum nutans*, *Schizachyrium scoparium*), with a mix of subdominant C₃ graminoids and forbs. In bison-grazed areas, C₄ dominance and cover is reduced with concomitant increases in diversity and cover of

forbs (Ratajczak et al., 2022). Bison grazing at KPBS began in 1987 with 30 animals introduced to a 469-ha area that included the study watershed. The herd was allowed to grow and the bison grazed area was increased to ~980 ha in 1992, with a target stocking rate of 213 animal units (AUs) or ~ 4.6 ha/AU. Bison graze year-round and are free to move through the entire area, which is divided into 10 watershed units assigned different fire treatments. The target stocking rate is based on 25% removal of herbaceous aboveground annual net primary productivity (ANPP) averaged across the area, though the spatial distribution of grazing activity varies with landscape position and fire (Raynor et al., 2015; 2016). Cover of woody species varies greatly with fire return interval and grazing treatment. Woody encroachment at this site is typically concentrated along riparian corridors and in infrequently burned watersheds (4-20 yr fire frequency), where encroaching species include *Cornus drummondii*, *Rhus aromatica*, and *Rhus glabra*, with *Juniper virginiana* more common in ungrazed areas. Mean annual temperature is ~12.5 °C and mean annual precipitation is ~817 mm, with high interannual variability.

Our study focused on watershed N4C, which has been managed under a 4-yr spring fire return interval since 1986 and with bison grazing since 1987. Prior to the start of this study, the watershed last burned in spring of 2022 (Table C.1). Woody vegetation within this watershed has expanded over time under a 4-year spring fire regime and occurs in patches ranging from discrete shrub islands to larger interconnected stands, primarily composed of *C. drummondii* and *R. aromatica*. In 2023, N4C was divided along its midpoint into two experimental subcatchments designated for annual burning in different seasons: a 34-ha western subcatchment assigned to annual spring burning (initiated in spring 2024) and a 42-ha eastern subcatchment assigned to annual late-summer burning (initiated in late summer 2023) (Figure 4.1; Table C.1).

Plant Community Composition at the Subcatchment Scale

Vegetation Transects

Experimental design & data collection

To evaluate broader (i.e., landscape-scale) plant community responses and provide a baseline for future assessments to prescribed annual burning in different seasons, we established permanent vegetation transects in upland and lowland positions within each of the newly initiated burn treatments. Each subcatchment (spring and late-summer burn treatments) contained eight transects (four in lowlands and four in uplands). Each 50-m transect included five permanent circular sampling plots (10 m²) spaced at regular intervals. All vascular plant species within each plot were recorded during three annual sampling surveys (May, July, and August–September) using a modified Daubenmire cover scale (1 = 0-1%, 2 = 1-5%, 3 = 5-25%, 4 = 25-50%, 5 = 50-75%, 6 = 75-95%, 7 = 95-100%) (Bailey & Poulton, 1968). Midpoint values for each cover class were used in subsequent analyses. Sampling began in July 2023. Late-season sampling in the summer burn treatment always occurred prior to burning. When a species was recorded multiple times within a year, in a given plot, only the highest observed cover value was retained (similar to many past analyses in this ecosystem; e.g., Collins and Calabrese, 2012). Prior to analysis, cover values were converted to relative cover based on total plant cover within each plot.

Data analysis

To evaluate treatment effects on plant community functional composition, species were aggregated into functional groups (warm-season grasses, cool-season graminoids, and forbs, and woody cover), and relative cover values were averaged at the transect level prior to analysis.

Functional group cover, native species richness, and the effective number of species ($e^{H'}$) from Shannon's index (H') (Jost, 2006) were analyzed using linear mixed-effects models (LMMs) fit with the *lmer* function in the *lmerTest* package (Kuznetsova et al. 2017). For each response, burn season, topographic position, year, and their interactions were included as fixed effects. For functional group cover, transect was included as a random intercept to account for repeated measures through time. For species richness and diversity, which were assessed at the plot scale, plot nested within transect was included as a random intercept. Fixed effects were evaluated using Type III analysis of variance with Satterthwaite's approximation for degrees of freedom, and post hoc comparisons were conducted using estimated marginal means with Tukey-adjusted contrasts from the *emmeans* package (Lenth 2020). To meet model assumptions, both warm- and cool-season graminoid cover were $\log(x + 1)$ transformed.

Effects of burn season and topographic position on multivariate community composition were evaluated using non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity of square-root transformed species cover data (Warton & Hui, 2017). Species occurring in less than 5% of samples were excluded prior to analysis. Ordinations were performed using the metaMDS function in the *vegan* package (Oksanen et al., 2024). Differences in community composition were tested using permutational multivariate analysis of variance (PERMANOVA) with the same fixed effects described above.

Clonal Shrub Cover

Shrub Mapping

To evaluate responses of individual clonal shrub cover to fire timing, entire shrub island boundaries were mapped annually from 2023 to 2025. Within each subcatchment, we mapped

discrete shrub islands of *C. drummondii* (spring n = 59, summer n = 66) and *R. aromatica* (spring n = 113, summer n = 139) using high-precision Trimble GPS units (~0.5 m accuracy) by walking the perimeter and recording boundary vertices. Boundaries were defined as the grass-shrub edge where approximately 50% shrub cover existed. The same shrub islands were mapped each year. For each island and year, we calculated area (m²) and perimeter (m).

Data Analysis

Changes in shrub size for *C. drummondii* and *R. aromatica* were evaluated using relative area standardized to initial (2023) shrub area. For each shrub, relative area was indexed as A_t/A_{2023} and log-transformed prior to analysis. Relative area change from 2023 was analyzed for 2024–2025 using the same mixed-effects model structure described above, with burn season, year, and their interaction included as fixed effects and shrub island included as a random intercept. To evaluate whether shrub responses depended on initial size, which may be used as a proxy for shrub island age, baseline shrub area (log-transformed 2023 area) and its interaction with year were included as fixed effects in models of relative area change. In addition, because fire interacts differently with distinct parts of a canopy, shrub shape was evaluated using an irregularity index calculated as $P^2/4\pi A$ where P is perimeter and A is area. An increased surface area may indicate a potential weakening of the shrub to fire, as convoluted boundaries allow flames to isolate and ignite vulnerable or more isolated sections. Values equal to 1 represent a perfect circle, with increasing values showing greater deviation from circular form (i.e., more complex and less compact shapes). Irregularity was log-transformed prior to analysis and modeled as a function of burn season, year, and their interaction, with log-transformed shrub area included as a covariate to account for the relationship between shrub size and measured

shape. All shrub analyses were conducted separately for each species using the same inferential framework described above.

Shrub Island Responses to Fire, Grazing, and Mowing

Experimental design

To evaluate the effects of fire timing, grazing, and mowing on individual shrub islands, we used a split-plot design with prescribed fire applied at the subcatchment scale and grazing and mowing treatments applied to shrub islands. In each subcatchment, we identified 16 *C. drummondii* shrub islands, which were grouped into four spatial blocks of four nearby islands with broadly similar initial sizes. Blocks were located in comparable areas of each subcatchment to minimize variation in site conditions. Within each block, two islands were randomly selected for grazer exclusion using 14 m × 14 m cattle-panel fences, while the remaining two islands remained accessible to grazers. Cattle panels were installed in January 2024. Within each block, one island per grazing treatment (one grazed and one in an exclosure) was assigned to mowing, where shrubs were cut to ~20 cm height using a tractor-mounted rotary cutter. Mowing was conducted once near the end of the first growing season (early September 2023) following initial vegetation surveys. All thatch (cut stems and leaves) was left in place and burned with the next scheduled fire. Prescribed burning was conducted annually beginning in late 2023, with late-summer burns in late September and spring burns in early April.

Data Collection

Vegetation sampling in each shrub island was conducted annually along three 4 m transects that began in the surrounding grassland and extended into the interior of each shrub

island. Transects were oriented roughly 120° apart around the island's center. Along each transect, four evenly spaced 0.5 m × 0.5 m permanent quadrats were established at 1 m intervals: one located at the shrub edge (edge), defined as the grass-shrub boundary with approximately 50% shrub cover, one in the surrounding grassland (outside), and two within the shrub interior (inside). Within each quadrat, we recorded stem density of all woody species and estimated aboveground biomass of *C. drummondii*. We identified and counted all *C. drummondii* stems greater than 15 cm in height; stems below this threshold were counted separately and classified as recruits to distinguish individuals not included in biomass estimates. For each stem, we used digital calipers to record the diameter at 15 cm above the ground surface to the nearest hundredth of a millimeter. Stem diameters were used to estimate aboveground biomass using a species-specific allometric equation: $\ln(\text{mass}) = 2.53099 \ln(\text{diameter}) - 1.29768$, where diameter is basal stem diameter (mm) (Keen et al., 2024). We also estimated percent cover of all plant functional groups (graminoid, forb, woody, and bare ground) in each quadrat using the same modified Daubenmire cover scale described above.

Data Analysis

Response variables were evaluated at multiple spatial scales. *C. drummondii* stem density and biomass were assessed at the quadrat level. Cover of plant functional groups (including bare ground) was averaged across transects within each proximity position (outside, edge, inside) for each shrub island prior to analysis, as the coarse resolution of the Daubenmire cover scale limits the reliability of quadrat-level estimates. *C. drummondii* recruitment (stems <15 cm in height) was summarized at the island level by averaging across all quadrats within each island. Shrub island was treated as the primary unit of replication for all analyses, with transect- and quadrat-

level measurements incorporated as nested or averaged observations depending on the response variable.

We analyzed all response variables using linear mixed-effects models (LMMs) following the same framework described above. Analyses were conducted separately for each proximity position (outside, edge, inside) for quadrat- and cover-level responses. For each response, burn season, grazing, mowing, year, and their interactions were included as fixed effects. Shrub island was included as a random intercept to account for repeated measures through time. For stem density and biomass, transect nested within island was also included as a random intercept; this term was not included in cover or recruitment models due to averaging prior to analysis.

Alternative random-effect structures incorporating the block design were evaluated, but island-level random effects provided improved model fit based on AIC and explained greater variance. To meet model assumptions, response variables were transformed as follows: stem density and bare ground (outside and edge) were $\log(x + 1)$ transformed; aboveground biomass was cube-root transformed; graminoid cover, forb cover, and recruitment were square-root transformed; and woody cover (outside) and bare ground (interior) were also square-root transformed. All analyses were conducted in R (v. 4.2.2; R Core Team, 2022).

Results

Plant Community Composition at the Subcatchment Scale

Vegetation Transects

Across herbaceous functional groups (warm-season grasses, cool-season graminoids, and forbs), there were no detectable main or interactive effects of spring vs. summer annual burning ($p \geq 0.11$; Table C.2). However, there was a significant year $\times$ topographic position interaction (p

< 0.01; Table C.2) indicating topographically-dependent changes in herbaceous cover following the initiation of an annual fire return interval regardless of season. Warm-season grasses showed a slight increase in average cover in lowlands from ~42% to 48%, while warm-season grass cover in the uplands increased from ~28% to ~38% (Figure 4.2A). Cool-season graminoid cover in lowlands declined from ~5% to <2% by 2025, whereas cool-season graminoid cover in uplands remained between ~7 and ~9% (Figure 4.2B). Forb cover remained relatively high (~47 to ~54%) in lowlands but declined from ~47% to 36% in uplands (Figure 4.2C). Woody cover did not differ between topographic positions ($p = 0.07$; Table C.2) but showed a burn season $\times$ year interaction ($p = 0.042$; Table C.2). Under summer burning woody cover declined by ~3% from 2023 to 2024, and remained at ~7% in 2025, whereas under spring burning, woody cover showed little consistent change over time, maintaining ~ 8% cover (Figure 4.2D).

Native species richness at the plot-level (# spp. 10 m⁻²) varied over time ($p < 0.001$) and between topographic positions ($p = 0.029$), with trajectories differing between spring and summer burning ($p < 0.001$; Table C.2). Initial richness ranged from ~20-21 species per plot in lowlands and ~22-24 species in uplands and increased across both burn treatments through time. By 2025, richness reached ~27-32 species in lowlands and ~31-34 species in uplands (Figure 4.3A). Increases were greater under summer burning than spring burning. Uplands maintained higher richness than lowlands across all years, with the highest values observed under summer burning in 2025 (~34 species per plot). Native species diversity was also higher in uplands than in lowlands ($p < 0.01$; Table C.2). In 2023, diversity ranged from approximately 12-13 effective species per plot in lowlands and ~13-16 in uplands. Diversity increased across all treatments in 2024 before declining in 2025, with summer burning maintaining higher diversity than spring burning across both topographic positions (Figure 4.3B).

Community composition in ordination space differed significantly among topographic position, year, and burn season ($p < 0.022$; Table C.3). Topographic position explained the greatest proportion of variation ($R^2 = 0.20$), followed by year ($R^2 = 0.056$) and burn season ($R^2 = 0.039$; Table C.3). Interaction terms were not significant ($p > 0.1$; Table C.3). Ordination patterns showed a clear separation between lowland and upland communities, whereas separation by burn season was comparatively weak (Figure C.1).

Clonal Shrub Cover

Cornus drummondii and *Rhus aromatica* showed contrasting changes in shrub area over time, with significant burn season $\times$ year interactions ($p < 0.01$; Table C.4, S5). Following the initial switch to annual burning, shrub area increased for *C. drummondii* islands and decreased for *R. aromatica*, with subsequent trajectories differing between burn seasons (Figure 4.4A, 4.4B; Table C.5). Under both spring and summer burning, *C. drummondii* area was ~15-17% larger in 2024 than in 2023. By 2025, this difference persisted under summer burning but not under spring burning (~2% greater than 2023 levels). In contrast, the size of *R. aromatica* shrubs continuously declined under spring burning with a combined reduction of ~25% relative to 2023, while under summer burning it was only ~11% lower in 2024 and returned to initial size by 2025. Changes in shrub area were not related to initial shrub size ($p \geq 0.096$; Table C.6). Over time, shrubs became less compact and more complex ($p < 0.001$; Table C.7) as reflected by increases in the irregularity index. These changes were greater in *C. drummondii*, increasing from ~1.5 to ~2, while *R. aromatica* remained less irregular overall (~1.1 to ~1.3) (Figure 4.4C, 4.4D).

Shrub Island Responses to Fire, Grazing, and Mowing

Stem Density and Aboveground Biomass:

Initial analysis of shrub island responses detected no main or interactive effects of mowing on *C. drummondii* stem density, aboveground biomass, or functional group composition, and data from mowed and unmowed shrub islands were subsequently pooled for all analyses except *C. drummondii* recruitment. *C. drummondii* stem density varied across shrub island positions (outside, edge, interior) and changed over time but was not influenced by burn season or its interactions (Table C.8). Outside of shrub islands, stem density remained higher in grazed plots (~ 11 stems m^{-2}) than when grazers were excluded (~ 7 stems m^{-2}) ($p = 0.038$; Table C.8). At shrub edges, stem density increased over time and showed a grazing $\times$ year interaction ($p < 0.01$; Table C.8). In grazed areas, stem density increased by $\sim 50\%$ from ~ 28 to ~ 42 stems m^{-2} , while stem density in bison-exlosures increased by $\sim 31\%$ from ~ 39 to ~ 51 stems m^{-2} before declining to ~ 42 stems m^{-2} . Within shrub interiors, stem density increased by ~ 11 stems m^{-2} over time ($p < 0.001$; Table C.8) with most increases occurring after the first year, however grazing did not have an effect within interiors (Figure 4.5A; Table C.8).

In contrast to stem density, aboveground biomass of *C. drummondii* generally declined following initiation of annual burning, with responses varying among outside, edge, and interior positions. Outside of shrub islands, biomass diverged between burn seasons with time ($p = 0.019$; Table C.8). Under spring burning, biomass declined by approximately 50% between 2023 and 2025 (from 102 to 50 g m^{-2}), with most reductions occurring after the first fire. Under summer burning, biomass remained relatively unchanged from 2023 to 2024 before increasing from ~ 95 to ~ 127 g m^{-2} in 2025 (Figure 4.5B). Despite these contrasting trajectories, biomass did not differ between burn seasons within individual years. At shrub edges, biomass varied with

both burn season $\times$ year and grazing $\times$ year interactions ($p < 0.001$; Table C.8). Under spring burning, biomass declined by $\sim 60\%$ (from 1185 g m^{-2} to $\sim 436 \text{ g m}^{-2}$) between 2023 and 2025. Under summer burning, biomass declined by $\sim 50\%$ (from ~ 1130 to $\sim 579 \text{ g m}^{-2}$), before partially recovering to $\sim 752 \text{ g m}^{-2}$. By 2025, biomass was lower under spring burning than summer burning. Grazing effects showed similar temporal patterns, with *C. drummondii* biomass declining more consistently in grazer-exclusion plots, while grazed plots showed little change after an initial reduction in the first year. Differences between grazing treatments diminished by 2025. Within shrub interiors, biomass declined from 2023 to 2024 under both burn treatments. Under spring burning, biomass decreased from ~ 1066 to $\sim 650 \text{ g m}^{-2}$ and remained similar through 2025. Under summer burning, biomass initially dropped from ~ 930 to $\sim 476 \text{ g m}^{-2}$ before partially recovering to $\sim 795 \text{ g m}^{-2}$. A marginal grazing $\times$ year interaction was observed ($p = 0.052$; Table C.8), but differences between grazing treatments were not detected.

Shrub Island: Functional Group Compositions:

Graminoid cover in shrub islands varied over time and was influenced by interactions between year and both burn season and grazing treatments, with effects varying among shrub island positions (Figure 4.6A, Table C.9). Under spring burning, graminoid cover showed little change over time, remaining near $\sim 50\%$, 27% , and 16% from the outside to shrub interiors. In contrast, under summer burning, graminoid cover increased significantly across positions. Outside of shrub islands, graminoid cover increased from $\sim 45\%$ to $\sim 68\%$, while interior cover increased from $\sim 22\%$ to $\sim 31\%$; cover at shrub edges remained relatively constant ($\sim 35\%$). Grazing effects followed a similar temporal pattern but were independent of burn season. In grazed plots, graminoid cover was stable or declined slightly over time, with a significant

decrease from 34% to 27% at shrub edges and little change outside or within shrub interiors. In contrast, grazer-exclusion plots showed consistent increases in graminoid cover across positions, rising from ~46% to ~64% outside shrub islands, ~29 to ~32% at edges, and ~15 to ~25% within interiors. As a result, differences between grazing treatments became more pronounced with time.

Forb cover in shrub islands increased under spring burning but remained relatively unchanged under summer burning across all shrub island positions ($p \leq 0.011$; Table C.9). Under spring burning, forb cover increased from 2023 to 2025 across all positions, rising from ~14% to ~21% outside shrub islands, ~11% to ~24% at edges, and ~7% to ~23% within interiors. These increases occurred in both grazed and fenced plots but were more pronounced in grazed areas, particularly by 2025 (e.g., ~11% to ~27% in grazed plots versus ~10% to ~14% in exclosures under spring burning). Under summer burning, forb cover remained relatively stable (~12–13%) across all positions, and grazing effects were minimal. By 2025, forb cover was greater under spring burning than summer burning, with the highest values observed in spring-burned grazed plots (Figure 4.6B).

Woody cover consisted primarily of *C. drummondii* across all shrub island positions (66–89% of total woody cover), with lower proportions outside shrub islands. Across all positions, woody cover declined with time ($p \leq 0.038$; Table C.9) and showed a significant three-way interaction outside shrub islands ($p < 0.04$; Table C.9). Outside shrub islands, woody cover in grazed plots declined from 2023 to 2024 and increased by 2025, resulting in little net change over time, whereas grazer-exclusion plots decreased cover steadily from ~12% to ~7%. Across edge and interior positions, woody cover declined from ~50–59% to ~43%, with the greatest reduction occurring between 2023 and 2024 (Figure 4.6C).

Bare ground was lowest outside of shrub islands, intermediate at edges, and highest within shrub interiors, averaging ~9%, ~11%, and ~30%, respectively. A burn season $\times$ year interaction occurred ($p < 0.01$; Table C.9), where bare ground increased by 4-7% under spring burning at and outside of shrub edges, while summer burning decreased bare ground cover by ~5-7%. Differences between burn seasons were not evident in 2023 but emerged at the edge in 2024 and were evident at both positions by 2025. Within shrub interiors, bare ground declined from ~46% to ~34% under spring burning and from ~32% to 15% under summer burning (Figure 4.6D).

Shrub Island - Recruitment:

Across shrub islands, recruitment of stems < 15 cm in height was low in 2023 (~0.2-0.3 stems m^{-2}) and increased over time ($p < 0.001$; Table C.10). Recruitment varied with both burn season and mowing ($p = 0.03$; Table C.10). Under both burn treatments, recruitment increased from 2023 to 2024, with values remaining high through 2025. By the final year, recruitment was twice as high under spring burning (~3.2 stems m^{-2}) than under summer burning (~1.6 stems m^{-2}). Mowing influenced recruitment in 2024, with higher densities in mowed plots (~3 stems m^{-2}) than unmowed plots (1.3 stems m^{-2}), but this effect diminished in the final growing season (Figure 4.7).

Discussion

Reduced fire frequency coupled with changing environmental drivers has led to widespread woody plant encroachment that impacts ecosystem services and can be difficult to reverse. Reintroducing more frequent fire has been suggested as an approach to limit and

potentially reduce woody encroachment, but clonal resprouting shrubs may be difficult to control with fire alone (Heisler et al., 2003). Previous studies that have assessed responses to increased fire frequency in encroached tallgrass prairie have found that returning annual fire can promote herbaceous recovery and limit woody expansion but often fail to reverse established shrubs (Collins et al. 2021; Miller et al., 2017). However, these studies have largely been done in the absence of large grazers and have not assessed responses to annual prescribed fires outside of the traditional spring burning season. The overarching objective of this study was to evaluate the initial tallgrass prairie plant community responses to reintroducing annual fire in contrasting seasons (spring and late-summer) in a shrub-encroached, bison-grazed watershed previously managed under a 4-year fire return interval.

Reintroducing annual fire did not reduce woody encroachment in the initial two years of the new fire regimes. Instead, our results revealed decoupled herbaceous and woody responses to fire reintroduction. At the functional group level, herbaceous communities responded similarly to annual burning in spring and summer over the duration of our study, suggesting that prescribed fire in either season may be used to maintain grassland structure and function in grazed systems. In contrast, clonal shrubs persisted and responded variably across burn season and spatial scales. Across the landscape at the subcatchment scale, shrubs showed species-specific and burn season-dependent changes in size, with more predictable reductions under spring burning, but persistence or transient reductions and recovery under summer burning. At the scale of individual *C. drummondii* shrub islands, fire effects were primarily structural, with declines in biomass accompanied by increases in stem density, particularly at shrub edges. Grazing further constrained fire effectiveness by reducing grass cover and maintaining higher stem densities outside shrub patches, while mowing had only transient effects despite complete initial

aboveground biomass removal. Not surprisingly, our findings indicate that increased fire frequency alone is insufficient to reduce shrub encroachment in grazed grasslands, particularly when woody species are capable of rapid post-fire recovery.

Vegetation Transects

Herbaceous plant community responses to fire were largely insensitive to burn season, despite strong and persistent differences between lowland and upland communities. These compositional differences align well with well-established variations in soil depth and water availability across topographic gradients in tallgrass prairie (Briggs & Knapp, 1995; Ransom et al., 1998). Across both positions, functional group trajectories were similar under spring and summer burning, suggesting that fire timing exerts relatively weak short-term controls over herbaceous composition in grazed grasslands. Two years of annual burning increased the cover of dominant warm-season grasses but reduced cover of cool season graminoids and forbs. Although increases in warm-season grass cover are often associated with lower richness (Collins and Calabrese, 2012; Ratajczak et al., 2022), richness in this study increased concurrently with warm-season grasses. This pattern may reflect the already high-diversity of bison-grazed relative to ungrazed prairie, where grazing-driven spatial heterogeneity can help maintain local richness (Hartnett et al., 1996). While our results also showed a greater accumulation of species occurring under summer burns than spring burns, congruent with comparisons of spring- vs. summer-burned ungrazed prairie (Glidden et al., in review; Towne & Kemp, 2008), this may partially reflect improved species detection over time. Over short timeframes, the return of frequent fire may exert stronger influences on herbaceous communities than the seasonal timing of fire in working lands (Spasojevic et al., 2010; Vermeire et al., 2018). However, other studies examining

prescribed fire in contrasting seasons indicate that divergence in plant community composition accumulates over time (Glidden et al., in review, Towne & Kemp, 2008), and longer-term monitoring is needed to determine whether repeated application of fire in different seasons produces more pronounced compositional shifts.

Clonal Shrub Cover

At the landscape (subcatchment) scale, fire season did not produce consistent reductions in shrub cover, with shrubs instead showing species-specific and temporally variable changes in area under repeated burning. Across three years, neither *C. drummondii* nor *R. aromatica* exhibited mortality, in line with previous work showing high survival of clonal shrubs across topographic positions and size classes (Nippert et al., 2021). The absence of size-dependent responses further indicates that survival was not limited to larger or more established individuals; rather, innate resprouting capacity allowed shrubs to withstand repeated burning regardless of initial size. This resilience is likely supported by extensive belowground reserves and access to deep water, which buffer shrubs against both fire and environmental stress (Keen et al., 2024; Nippert et al., 2021). The initial response to fire was a strong pulsed increase in size of *C. drummondii* islands, while *R. aromatica* constricted regardless of fire season. Following the second fire, both species contracted under spring burning, while under summer burning *C. drummondii* islands maintained their initial expansion and *R. aromatica* shrubs recovered to their original size. The recovery of shrubs under repeated summer burning may reflect reduced fuel accumulation following the initial summer fire, limiting the effectiveness of subsequent fires (Chapter 3; Twidwell et al., 2016). Even relatively small increases in shrub expansion may contribute to cumulative reductions in herbaceous vegetation, and their associated ecosystem

services, when repeated across numerous shrub islands. Shrubs also became increasingly irregular in shape over time, particularly *C. drummondii*, suggesting that repeated burning may have altered the spatial boundaries and potential dynamics of shrub islands and their interactions with surrounding grassland vegetation.

Shrub Island Responses

We also performed a more detailed and mechanistic assessment of *C. drummondii* responses to combinations of fire, grazing, and mowing at the individual shrub island scale. Despite complete initial removal of aboveground biomass, mowing had no lasting effects on stem density, aboveground biomass, or functional group cover across shrub island positions, even when combined with annual fire and grazing. Rather than reducing shrub vigor, mowing appeared to temporarily alter shrub structure while allowing rapid recovery within a year. Similar responses were recently observed following mowing and annual fire in tallgrass prairie encroached by *C. drummondii* and other resprouting shrubs, where single mechanical treatments failed to produce lasting reductions in shrub cover (O'Connor et al., 2026). Although mowing did not reduce existing shrubs, we found increased recruitment in the year following treatment, suggesting that disturbance and temporary canopy opening may create conditions favorable for new ramet emergence in established shrub islands (Heisler et al., 2004). However, the limited herbaceous response following canopy removal may also reflect shrub legacy effects (Lett & Knapp, 2003, 2005). Increased recruitment following disturbance further highlights the strong regenerative capacity of *C. drummondii*; repeated applications or integration with alternative management approaches may be necessary to achieve sustained reductions in shrub cover (Wedel et al., 2024; O'Conner et al., 2026).

Fire and grazing interacted to affect dogwood responses. Initial reductions in aboveground biomass following fire were offset by subsequent increases in stem density and recruitment. Responses also varied across shrub island positions. The greatest biomass reductions occurred at shrub edges, where fire intensity on shrub tissues was likely greatest. Under spring burning, edge biomass declined more consistently through time, whereas summer-burned edges partially recovered following the second fire. In contrast, shrub interiors maintained relatively high woody cover despite declines in biomass. Reduced understory fuel loads within established shrub interiors may have limited fire penetration, while post-fire regrowth contributed to recovery of woody cover over the growing season. Stem density increased across all shrub island positions, with the largest responses occurring after the first treatment, resulting in shorter shrubs with greater stem densities. Grazing further mediated these dynamics. Outside shrub islands, grazed areas maintained higher stem densities and showed negligible increases in graminoid cover over time compared to areas that excluded grazers. This suggests that continued bison grazing reduced fuel accumulation surrounding shrub islands, potentially limiting fire intensity around shrub patches. In contrast, grazer exclusion represented a temporary release from grazing pressure that promoted greater graminoid accumulation and potentially increased fuel loads surrounding shrub patches. However, the absence of bison did not translate into meaningful effect, as stem density increased across both grazed and ungrazed treatments.

Conclusion

The continued expansion of woody plants into grasslands reinforces the need to better understand how encroached grasslands respond to restoration. Our study only reflects the initial

two years following the reintroduction of annual fire, a timeframe too short to capture long-term dynamics of these treatments. However, short-term responses to returning frequent annual spring and late-summer fire demonstrated divergent patterns among herbaceous and woody vegetation. Herbaceous communities were broadly similar between burn seasons, suggesting that expanding fire beyond spring may provide a practical and cost-effective approach for managing rangelands. While we observed noticeable increases in warm-season grass cover, which may indicate heightened forage availability, previous studies suggest that productivity can decline in the year following summer fire in both ungrazed (Chapter 3) and grazed (Engle et al., 1993) tallgrass prairie. Broadening the seasonal fire window may also help distribute smoke concentrations associated with temporally compressed spring burning.

The responses of clonal shrubs to repeated summer fire across the watershed further support this broader seasonal window; however, a second summer burn appears less effective than a second spring burn. The effectiveness of summer fires may depend heavily on fuel loads and the specific burn timing, which could be altered to increase their impact (e.g., burning biennially or earlier or later in the season). Furthermore, we did not detect any additive or synergistic effects of burn season, grazing (with or without bison), or mowing on *C. drummondii* shrub islands, nor did we document a single shrub mortality across the entire watershed. While this lack of mortality highlights the resilient nature of clonal shrubs, the divergent behaviors of *C. drummondii* and *R. aromatica* indicate that restoration will likely require management approaches customized to the dominant encroaching species (Wedel et al., 2025). Successful reduction of shrub cover may require repeated or compounded disturbances that limit post-disturbance recovery and progressively weaken shrub vigor over time.

In either case, long-term monitoring is needed to determine whether repeated applications of fire in different seasons, alone or in combination with other interventions, can shift shrub-encroached prairie toward a more open grass-dominated state. These results further emphasize the importance of preventing woody species from establishing in the first place, as restoration following establishment will likely be a high-cost, long-term endeavor. In landscapes where management is difficult or resource-intensive, developing plans to optimize existing ecosystem services may require alternative conservation approaches (Hobbs et al., 2009, 2011), such as the resist-accept-direct framework (Nippert et al., 2026), to determine the most viable ecological trajectory.

References

- Anadón, J. D., O. E. Sala, B. L. Turner, and E. M. Bennett. 2014. "Effect of woody-plant encroachment on livestock production in North and South America." *Proceedings of the National Academy of Sciences*, 111(35): 12948–12953. <https://doi.org/10.1073/pnas.132058511>.
- Archer, S. R., E. M. Andersen, K. I. Predick, S. Schwinning, R. J. Steidl, and S. R. Woods. 2017. "Woody plant encroachment: causes and consequences." In *Rangeland systems: Processes, management and challenges*, edited by Briske, D, 25–84. Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-46709-2_2.
- Archer, S. R., and K. I. Predick, K. I. 2014. "An ecosystem services perspective on brush management: research priorities for competing land-use objectives." *Journal of Ecology*, 102(6): 1394–1407. <https://doi.org/10.1111/1365-2745.12314>.
- Bailey, A. W., and C. E. Poulton. 1968. "Plant communities and environmental interrelationship in a portion of the Tillamook burn, northwestern Oregon." *Ecology*, 49(1): 1–13. <https://doi.org/10.2307/1933554>.
- Barger, N. N., S. R. Archer, J. L. Campbell, C. Y. Huang, J. A. Morton, and A. K. Knapp. 2011. "Woody plant proliferation in North American drylands: a synthesis of impacts on ecosystem carbon balance." *Journal of Geophysical Research: Biogeosciences*, 116(G4). <https://doi.org/10.1029/2010JG001506>.
- Bond, W. J., and G. F. Midgley. 2012. "Carbon dioxide and the uneasy interactions of trees and savannah grasses." *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1588): 601–612. <https://doi.org/10.1098/rstb.2011.0182>
- Bond, W. J., and J. J. Midgley. 2001. "Ecology of sprouting in woody plants: the persistence niche." *Trends in ecology & evolution*, 16(1): 45–51. [https://doi.org/10.1016/S0169-5347\(00\)02033-4](https://doi.org/10.1016/S0169-5347(00)02033-4)
- Bragg, T. B. 1982. "Seasonal variations in fuel and fuel consumption by fires in a bluestem prairie." *Ecology*, 63(1): 7–11. <https://doi.org/10.2307/1937024>
- Briggs, J. M., A. K. Knapp, J. M. Blair, J. L. Heisler, G. A. Hoch, M. S. Lett, and J. K. McCarron. 2005. "An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland." *BioScience*, 55(3): 243–254. [https://doi.org/10.1641/0006-3568\(2005\)055\[0243:AEITCA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[0243:AEITCA]2.0.CO;2)
- Briggs, J. M., A. K. Knapp, and B. L. Brock. 2002. "Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing interactions." *The American Midland Naturalist*, 147(2): 287–294. [https://doi.org/10.1674/0003-0031\(2002\)147\[0287:EOWPIT\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2002)147[0287:EOWPIT]2.0.CO;2)

- Charton, K. T., and E. I. Damschen. 2024. "Grassland woody plant management rapidly changes woody vegetation persistence and abiotic habitat conditions but not herbaceous community composition." *Journal of Applied Ecology*, 61(9): 2020–2032. <https://doi.org/10.1111/1365-2664.14716>.
- Collins, S. L., and L. B. Calabrese, 2012. "Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie." *Journal of Vegetation Science*, 23(3): 563–575. <https://doi.org/10.1111/j.1654-1103.2011.01369.x>
- Collins, S. L., A. K. Knapp, J. M. Briggs, J. M. Blair, E. M. Steinauer. 1998. "Modulation of diversity by grazing and mowing in native tallgrass prairie." *Science*, 280(5364): 745–747. <https://doi.org/10.1126/science.280.5364.745>
- Collins, S. L., J. B. Nippert, J. M. Blair, J. M., Briggs, P. Blackmore, and Z. Ratajczak. 2021. "Fire frequency, state change and hysteresis in tallgrass prairie." *Ecology Letters*, 24(4): 636–647. <https://doi.org/10.1111/ele.13676>.
- Connell, R. K., R. C. O'Connor, J. B. Nippert, and J. M. Blair. 2021. "Spatial variation in soil microbial processes as a result of woody encroachment depends on shrub size in tallgrass prairie." *Plant and Soil*, 460(1): 359–373. <https://doi.org/10.1007/s11104-020-04813-9>.
- Coppedge, B. R., D. M. Engle, C. S. Toepfer, and J. H. Shaw. 1998. "Effects of seasonal fire, bison grazing and climatic variation on tallgrass prairie vegetation." *Plant Ecology*, 139(2): 235–246. <https://doi.org/10.1023/A:1009728104508>.
- Ding, J., and D. Eldridge. 2023. "The success of woody plant removal depends on encroachment stage and plant traits." *Nature Plants*, 9(1): 58–67. <https://doi.org/10.1038/s41477-022-01307-7>.
- Engle, D. M., J. F. Stritzke, T. G. Bidwell, and P. L. Claypool. 1993. "Late-summer fire and follow-up herbicide treatments in tallgrass prairie." *Journal of Range Management*, 46:542–547.
- Engle, D. M., and T. G. Bidwell. 2001. "The response of central North American prairies to seasonal fire." *Journal of Rangeland Management*. 54(1): 2–10. <https://doi.org/10.2307/4003519>.
- Gaskin, J. F., E. Espeland, C. D. Johnson, D. L. Larson, J. M. Mangold, R. A. McGee, R. A. Milner, et al. 2021. "Managing invasive plants on Great Plains grasslands: A discussion of current challenges." *Rangeland Ecology & Management*, 78: 235–249. <https://doi.org/10.1016/j.rama.2020.04.003>.
- Gibson, D. J., and L. C. Hulbert. 1987. "Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie." *Vegetatio*, 72(3): 175–185. <https://doi.org/10.1007/BF00039839>.

- Glidden A.J., Z. Ratajczak, J. H. Taylor, and J. M. Blair. *In review*. “Long-term Plant Community Dynamics Vary with Season of Fire in Tallgrass Prairie.” *Ecological Applications*.
- Hartnett, D. C., K. R. Hickman, and L. E. Walter. 1996. “Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie.” *Journal of Range Management*, 49(5): 413–420. <https://doi.org/10.2307/4002922>.
- Heisler, J. L., J. M. Briggs, and A. K. Knapp. 2003. “Long-term patterns of shrub expansion in a C4-dominated grassland: fire frequency and the dynamics of shrub cover and abundance.” *American Journal of Botany*, 90(3): 423–428. <https://doi.org/10.3732/ajb.90.3.423>.
- Heisler, J. L., J. M. Briggs, A. K. Knapp, J. M. Blair, and A. Seery. 2004. “Direct and indirect effects of fire on shrub density and aboveground productivity in a mesic grassland.” *Ecology*, 85(8): 2245–2257. <https://doi.org/10.1890/03-0574>.
- Hobbs, R. J., E. Higgs, and J. A. Harris. 2009. “Novel ecosystems: implications for conservation and restoration.” *Trends in ecology & evolution*, 24(11): 599–605. <https://doi.org/10.1016/j.tree.2009.05.012>.
- Hobbs, R. J., L. M. Hallett, P. R. Ehrlich, and H. A. Mooney. 2011. “Intervention ecology: applying ecological science in the twenty-first century.” *BioScience*, 61(6): 442–450. <https://doi.org/10.1525/bio.2011.61.6.6>.
- Howe, H. F. 2000. “Grass response to seasonal burns in experimental plantings.” *Journal of Range Management*, 53(4): 437–441. <https://doi.org/10.2307/4003757>.
- Jost, L. 2006. “Entropy and diversity.” *Oikos* 113(2): 363–375. <https://doi.org/10.1111/j.2006.0030-1299.14714.x>.
- KDHE. 2025. Kansas Department of Health and Environment: Flint Hills wildland fire update, 2025 summary. https://ksfire.org/media/Flint_Hills_update_2025_summary-77e3962.pdf. (accessed 8 May 2026).
- Keen, R. M., S. Bachle, M. Bartmess, and J. B. Nippert. 2024. “Combined effects of fire and drought are not sufficient to slow shrub encroachment in tallgrass prairie.” *Oecologia*, 204(4): 727–742. <https://doi.org/10.1007/s00442-024-05526-x>.
- Knapp, A. K., J. M. Blair, J. M., Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. “The keystone role of bison in North American tallgrass prairie: Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes.” *BioScience*, 49(1): 39–50. <https://doi.org/10.1525/bisi.1999.49.1.39>.

- Kuznetsova, A., P. B. Brockhoff, and R. H. Christensen. 2017. “lmerTest package: tests in linear mixed effects models.” *Journal of Statistical Software*, 82: 1–26. <https://doi.org/10.18637/jss.v082.i13>.
- Lenth, R. V., B. Banfai, B. Bolker, P. Buerkner, I. Giné-Vázquez, M. Herve, M. Jung, J. Love, F. Miguez, J. Piaskowski, et al. 2024. Emmeans: estimated marginal means, aka least-squares means. <https://doi.org/10.32614/cran.package.emmeans>. Accessed July 15, 2025.
- Lett, M. S., and A. K. Knapp. 2003. “Consequences of shrub expansion in mesic grassland: resource alterations and graminoid responses.” *Journal of Vegetation Science*, 14(4): 487–496. <https://doi.org/10.1111/j.1654-1103.2003.tb02175.x>
- Lett, M. S., and A. K. Knapp. 2005. “Woody plant encroachment and removal in mesic grassland: production and composition responses of herbaceous vegetation.” *The American Midland Naturalist*, 153(2): 217–231. [https://doi.org/10.1674/0003-0031\(2005\)153\[0217:wpeari\]2.0.co;2](https://doi.org/10.1674/0003-0031(2005)153[0217:wpeari]2.0.co;2)
- Ling, H., G. Wang, W. Wu, A. Shrestha, and J. L. Innes. 2023. “Grassland resilience to woody encroachment in North America and the effectiveness of using fire in national parks.” *Climate*, 11(11): 219. <https://doi.org/10.3390/cli11110219>.
- Miller, J. E., E. I. Damschen, Z. Ratajczak, and M. Özdoğan. 2017. “Holding the line: three decades of prescribed fires halt but do not reverse woody encroachment in grasslands.” *Landscape Ecology*, 32(12): 2297–2310. <https://doi.org/10.1007/s10980-017-0569-9>.
- Morford, S. L., B. W. Allred, D. Twidwell, M. O. Jones, J. D. Maestas, C. P. Roberts, and D. E. Naugle. 2022. “Herbaceous production lost to tree encroachment in United States rangelands.” *Journal of Applied Ecology*, 59(12): 2971–2982. <https://doi.org/10.1111/1365-2664.14288>
- Nippert, J. B., M. A. Ahlering, S. D. Fuhlendorf, C. J. Helzer, N. A. McMillan, and Z. Ratajczak. 2026. “Rethinking grassland management in the Great Plains during the era of woody plant encroachment.” *BioScience*, biag033. <https://doi.org/10.1093/biosci/biag033>.
- Nippert, J. B., L. Telleria, P. Blackmore, J. H. Taylor, and R. C. O'Connor. 2021. “Is a prescribed fire sufficient to slow the spread of woody plants in an infrequently burned grassland? A case study in tallgrass prairie.” *Rangeland Ecology & Management*, 78: 79–89. <https://doi.org/10.1016/j.rama.2021.05.007>
- Noble, S., and Z. Ratajczak. 2025. “Restoring Frequent Fire Results in Habitat Improvement for Bison but Minimal Early Reduction of Woody Encroachment.” *Ecological Restoration*, 43(4): 288–301. <https://doi.org/10.3368/er.43.4.288>.
- O'Connor, R. C., J. H. Taylor, and J. B. Nippert. 2020. “Browsing and fire decreases dominance of a resprouting shrub in woody encroached grassland.” *Ecology*, 101(2): e02935. <https://doi.org/10.1002/ecy.2935>.

- O'Connor, R. C., K. R. Wilcox, S. E. Koerner, K. J. Komatsu, E. R. Wedel, and M. L. Avolio. 2026. "Cutting, herbicide, and fire: a case study for managing woody plants in tallgrass prairies." *Restoration Ecology*, e70403. <https://doi.org/10.1111/rec.70403>.
- Oksanen, J., R. Kindt, P. Legendre, B. O'Hara, G. L. Simpson, M. Solymos, H. H. Stevens, and H. Wagner 2007. The vegan package. *Community ecology package*, 10(631-637): 719. <https://cran.r-project.org/web/packages/vegan/index.html>. (Accessed June 22, 2025).
- R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Ransom, Michel D., Charles W. Rice, Timothy C. Todd, and William A. Wehmueller. 1998. "Soils and soil biota." In *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie*, edited by Alan K. Knapp, John M. Briggs, David C. Hartnett, and Scott L. Collins, 48–66. New York, NY: Oxford University Press.
- Ratajczak, Z., J. M. Briggs, D. G. Goodin, L. Luo, R. L. Mohler, J. B. Nippert, and B. Obermeyer. 2016. "Assessing the potential for transitions from tallgrass prairie to woodlands: are we operating beyond critical fire thresholds?" *Rangeland Ecology & Management*, 69(4): 280–287. <https://doi.org/10.1016/j.rama.2016.03.004>.
- Ratajczak, Z., S. L. Collins, J. M. Blair, S. E., Koerner, A. M. Louthan, M. D. Smith, M. D., J. H. Taylor, and J. B. Nippert. 2022. "Reintroducing bison results in long-running and resilient increases in grassland diversity." *Proceedings of the National Academy of Sciences*, 119(36): e2210433119. <https://doi.org/10.1073/pnas.221043311>.
- Ratajczak, Z., P. D'Odorico, J. B. Nippert, S. L. Collins, N. A. Brunsell, and S. Ravi. 2017. "Changes in spatial variance during a grassland to shrubland state transition." *Journal of Ecology*, 105(3): 750–760. <https://doi.org/10.1111/1365-2745.12696>.
- Ratajczak, Z., J. B. Nippert, and S. L. Collins. 2012. "Woody encroachment decreases diversity across North American grasslands and savannas." *Ecology*, 93(4): 697–703. <https://doi.org/10.1890/11-1199.1>.
- Ratajczak, Z., J. B. Nippert, J. C. Hartman, and T. W. Ocheltree. 2011. "Positive feedbacks amplify rates of woody encroachment in mesic tallgrass prairie." *Ecosphere*, 2(11): 1–14. <https://doi.org/10.1890/ES11-00212.1>.
- Raynor, E. J., A. Joern, and J. M. Briggs. 2015. "Bison foraging responds to fire frequency in nutritionally heterogeneous grassland." *Ecology*, 96(6): 1586–1597. <https://doi.org/10.1890/14-2027.1>.
- Raynor, E. J., A. Joern, J. B. Nippert, and J. M. Briggs. 2016. "Foraging decisions underlying restricted space use: effects of fire and forage maturation on large herbivore nutrient uptake." *Ecology and Evolution*, 6(16): 5843–5853. <https://doi.org/10.1002/ece3.2304>.

- Rowe, H. I. 2010. "Tricks of the trade: techniques and opinions from 38 experts in tallgrass prairie restoration." *Restoration Ecology*, 18: 253–262. <https://doi.org/10.1111/j.1526-100X.2010.00663.x>.
- Scholtz, R., S. D. Fuhlendorf, and S. R. Archer. 2018. "Climate–fire interactions constrain potential woody plant cover and stature in North American Great Plains grasslands." *Global Ecology and Biogeography*, 27(8): 936–945. <https://doi.org/10.1111/geb.12752>.
- Shaw, J. H., and M. Lee. 1997. "Relative abundance of bison, elk, and pronghorn on the southern plains, 1806-1857". *Plains Anthropologist*, 42(159): 163–172. <https://doi.org/10.1080/2052546.1997.11931844>.
- Spasojevic, M. J., R. J. Aicher, G. R. Koch, E. S. Marquardt, N. Mirotchnick, T. G. Troxler, and S. L. Collins. 2010. "Fire and grazing in a mesic tallgrass prairie: impacts on plant species and functional traits." *Ecology*, 91(6): 1651–1659. <https://doi.org/10.1890/09-0431.1>.
- Stambaugh, M. C., R. P. Guyette, and J. Marschall. 2013. "Fire history in the Cherokee Nation of Oklahoma." *Human Ecology*, 41(5): 749–758. <https://doi.org/10.1007/s10745-013-9571-2>.
- Stebbins, G. L. 1981. "Coevolution of grasses and herbivores." *Annals of the Missouri Botanical Garden*, 68(1): 75–86. <https://doi.org/10.2307/2398811>.
- Stewart, O. C. 2002. *Forgotten Fires: Native Americans and the Transient Wilderness*. Norman: University of Oklahoma Press.
- Symstad, A. J., and S. A. Leis. 2017. "Woody encroachment in northern Great Plains grasslands: perceptions, actions, and needs." *Natural Areas Journal*, 37(1): 118–127. <https://www.jstor.org/stable/90009260>.
- Tooley, E. G., J. B. Nippert, and Z. Ratajczak. 2024. "Evaluating methods for measuring the leaf area index of encroaching shrubs in grasslands: From leaves to optical methods, 3-D scanning, and airborne observation." *Agricultural and Forest Meteorology*, 349: 109964. <https://doi.org/10.1016/j.agrformet.2024.109964>.
- Towne, E. G., and J. M. Craine. 2016. "A critical examination of timing of burning in the Kansas Flint Hills." *Rangeland Ecology & Management*, 69(1): 28–34. <https://doi.org/10.1016/j.rama.2015.10.008>.
- Towne, E. G., and K.E. Kemp. 2003. "Vegetation dynamics from annually burning tallgrass prairie in different seasons." *Journal of Range Management*, 56(2): 185–192. <https://doi.org/10.2307/4003903>.
- Towne, E. G., and K.E. Kemp. 2008. "Long-term response patterns of tallgrass prairie to frequent summer burning." *Rangeland Ecology & Management*, 61(5): 509–520. <https://doi.org/10.2111/08-043.1>.

- Twidwell, D., C. H. Bielski, R. Scholtz, and S. D. Fuhlendorf. 2021. “Advancing fire ecology in 21st century rangelands.” *Rangeland Ecology & Management*, 78: 201–212. <https://doi.org/10.1016/j.rama.2020.01.008>.
- Twidwell, D., W. E. Rogers, C. L. Wonkka, C. A. Taylor Jr, and U. P. Kreuter. 2016. “Extreme prescribed fire during drought reduces survival and density of woody resprouters.” *Journal of Applied Ecology*, 53(5): 1585–1596. <https://doi.org/10.1111/1365-2664.12674>.
- Van Auken, O. W. 2009. “Causes and consequences of woody plant encroachment into western North American grasslands.” *Journal of environmental management*, 90(10): 2931–2942. <https://doi.org/10.1016/j.jenvman.2009.04.023>.
- Vermeire, L. T., and M. L. Russell. 2018. “Seasonal timing of fire alters biomass and species composition of northern mixed prairie.” *Rangeland Ecology & Management*, 71(6): 714–720. <https://doi.org/10.1016/j.rama.2018.06.005>.
- Warton, D. I., and F. K. Hui. 2017. “The central role of mean-variance relationships in the analysis of multivariate abundance data: A response to Roberts (2017).” *Methods in Ecology and Evolution*, 8(11): 1408–1414. <https://doi.org/10.1111/2041-210X.12843>.
- Watson, P. A., H. D. Alexander, H. D., and J. D. Moczygemba. 2019. “Coastal prairie recovery in response to shrub removal method and degree of shrub encroachment.” *Rangeland Ecology & Management*, 72(2): 275–282. <https://doi.org/10.1016/j.rama.2018.11.005>.
- Wedel, E. R., J. B. Nippert, R. C. O'Connor, P. Nkuna, and A. M. Swemmer. 2024. “Repeated clearing as a mechanism for savanna recovery following bush encroachment.” *Journal of Applied Ecology*, 61(7): 1520–1530. <https://doi.org/10.1111/1365-2664.14666>.
- Wedel, E. R., Z. Ratajczak, E. G. Tooley, and J. B. Nippert. 2025. “Divergent resource-use strategies of encroaching shrubs: Can traits predict encroachment success in tallgrass prairie?” *Journal of Ecology*, 113: 339–352. <https://doi.org/10.1111/1365-2745.14456>.
- Yurkonis, K. A., J. Dillon, D. A. McGranahan, D. Toledo, and B. J. Goodwin. 2019. “Seasonality of prescribed fire weather windows and predicted fire behavior in the northern Great Plains, USA.” *Fire Ecology*, 15(1): 7. <https://doi.org/10.1186/s42408-019-0027-y>.

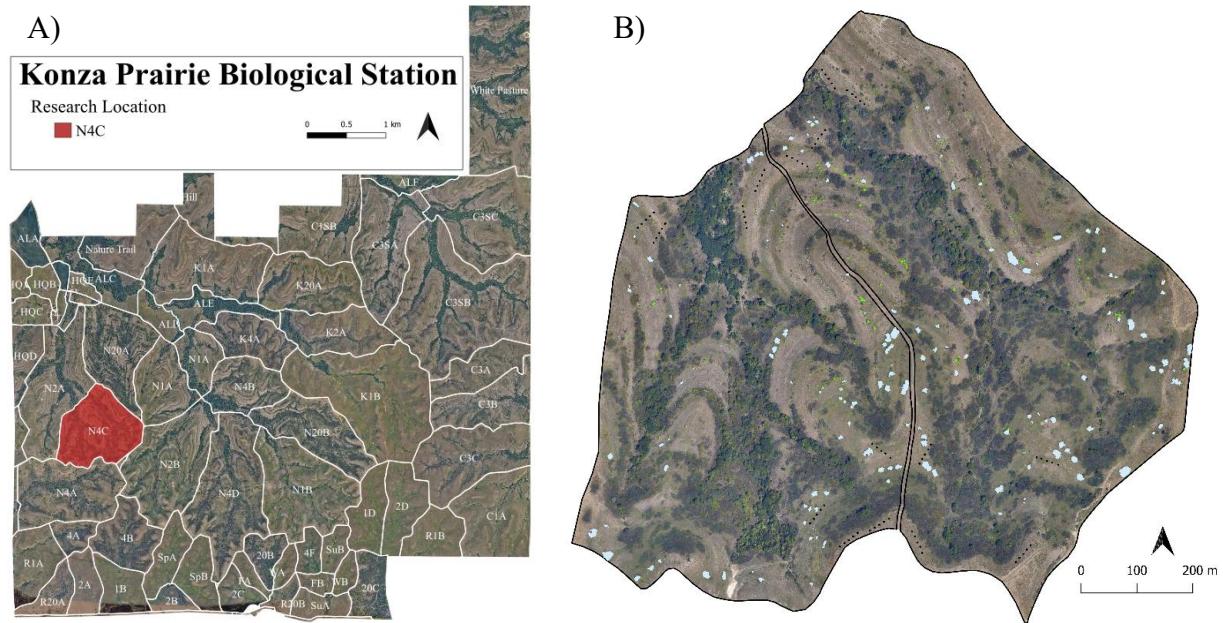


Figure 4-1: Site map of watershed N4C at KPBS (A) and GPS mapping conducted on N4C (B) of *C. drummondii* (white), *R. aromatica* (yellow), and the species composition transects (black circles). Upland transects are on the south side of the map. Annual spring burning occurred on the west side of the fire break, and late-summer burning occurred on the east side of the fire break.

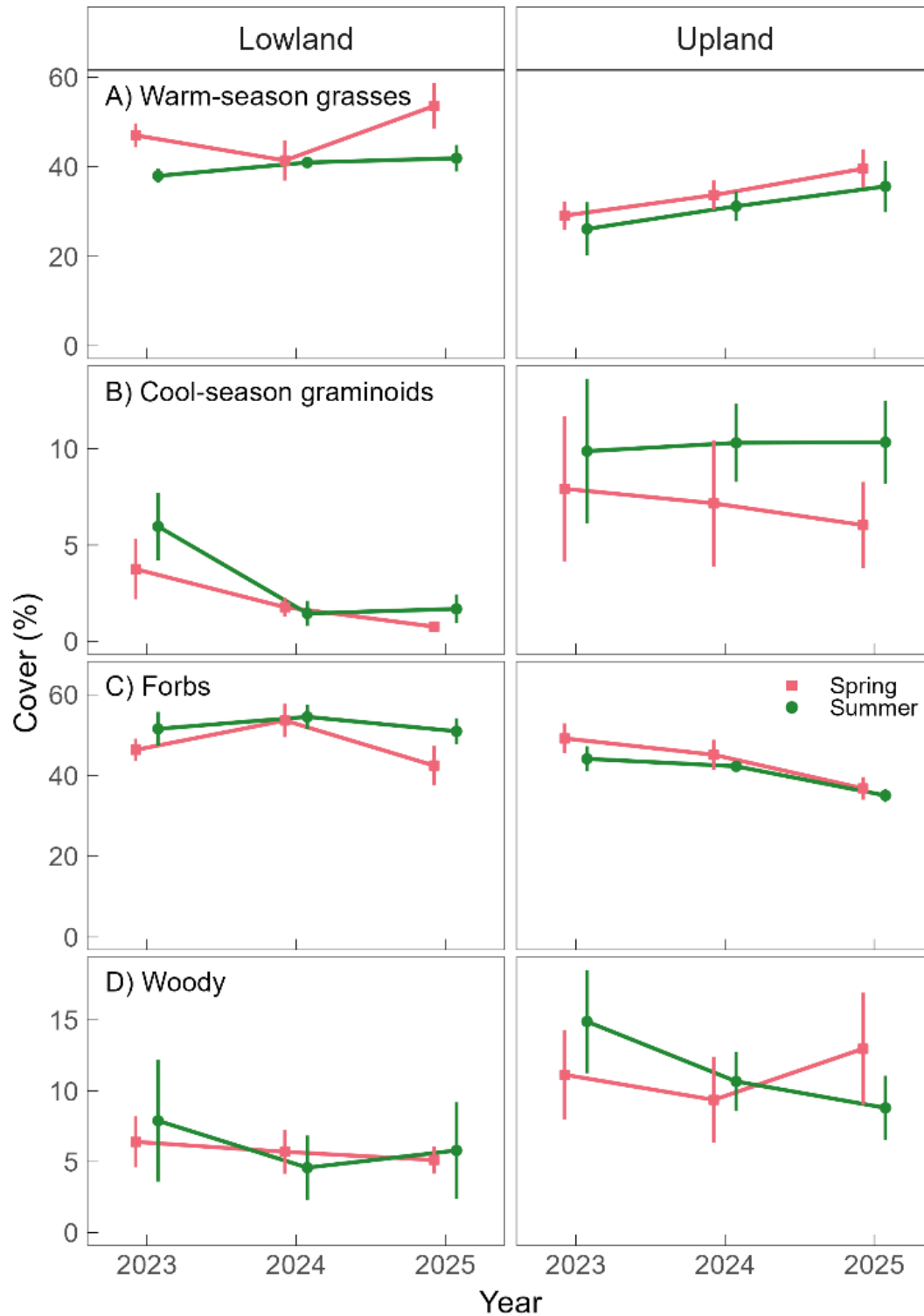


Figure 4-2: Relative percent cover of warm-season grasses (A), cool-season graminoids (B), forbs (C) and woody (D) from vegetation surveys under spring and summer burns in both the lowland (left) and upland (right) topographic positions.

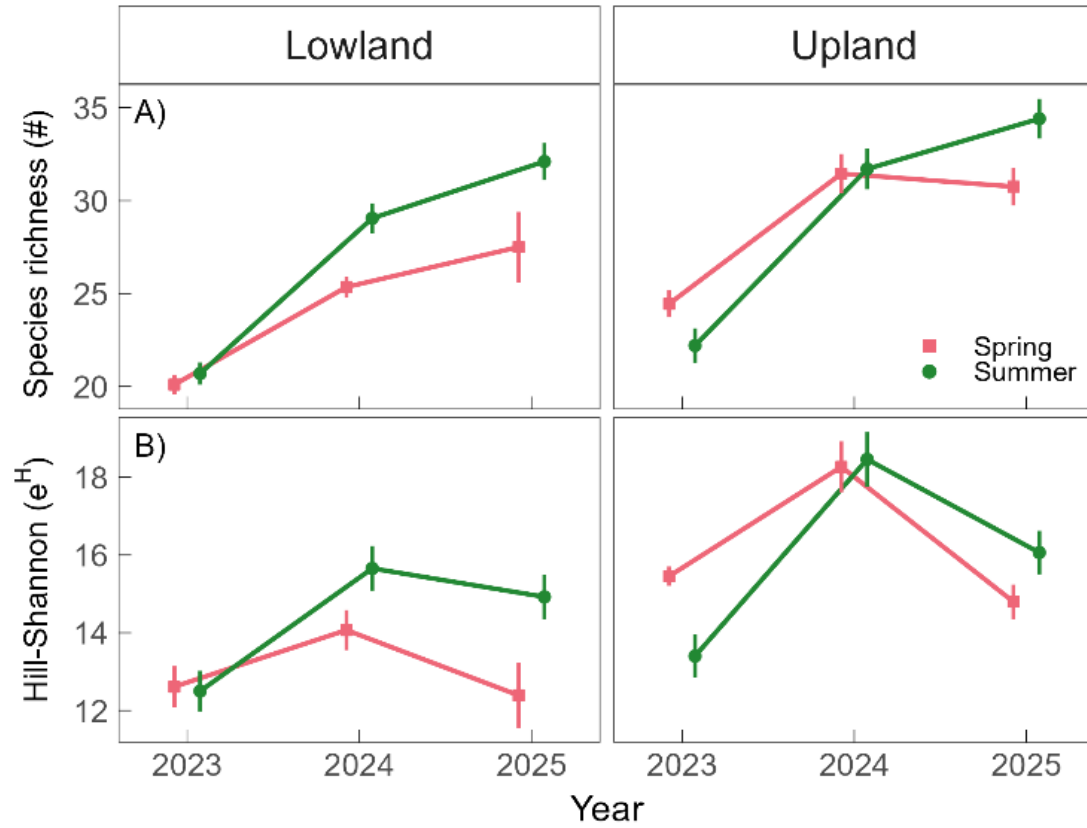


Figure 4-3: Native species richness (A) and Shannon diversity (B) at the plot scale (10 m²) from vegetation surveys under contrasting spring and summer burns in both the lowland (left) and upland (right) topographic positions.

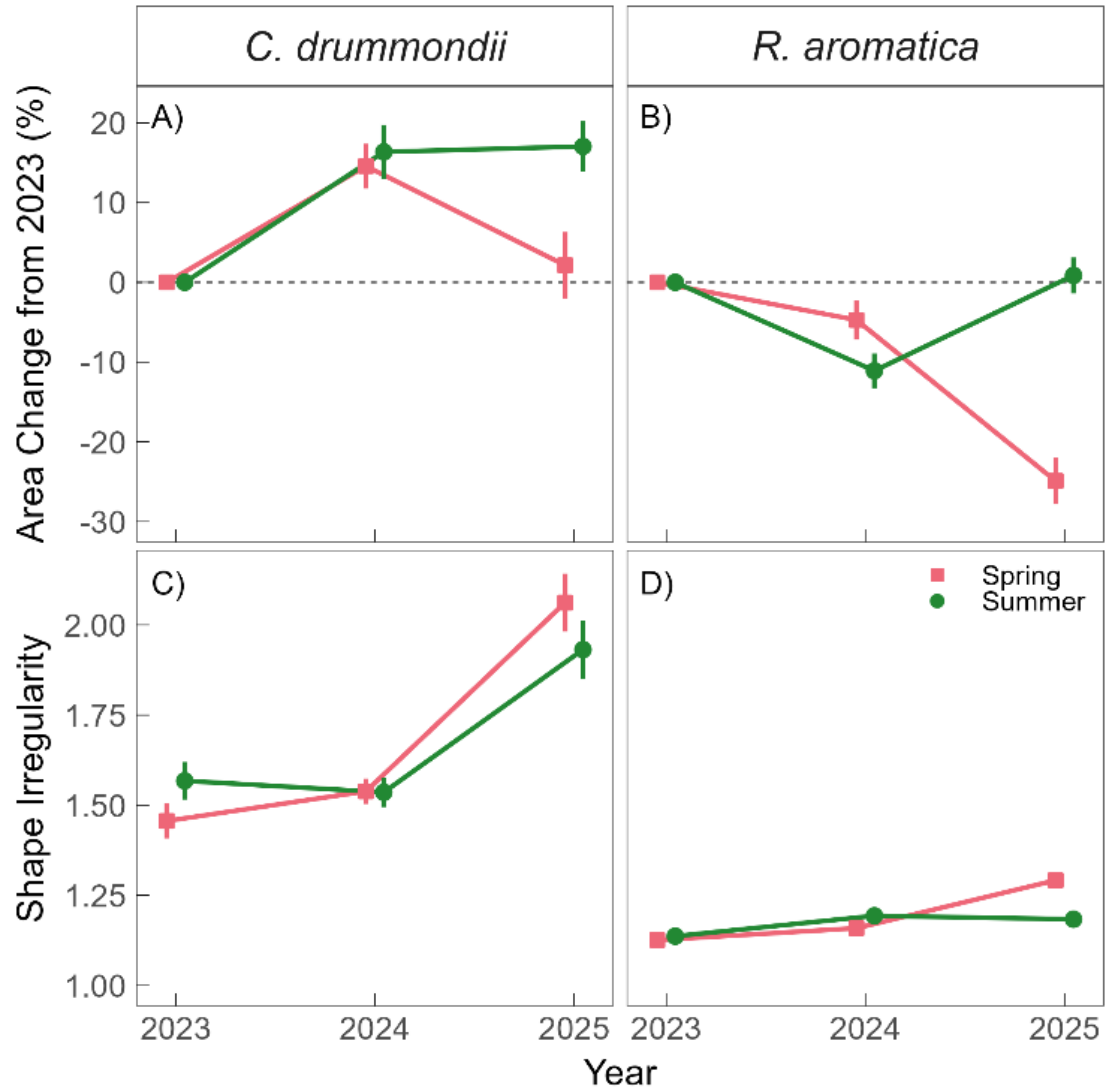


Figure 4-4: Percent change in shrub area relative to 2023 and changes in shrub irregularity from 2023 to 2025 under prescribed spring and summer burning for *C. drummondii* (A, C) and *R. aromatica* (B, D). Points represent means $\pm$ SE for each species within each year and burn season.

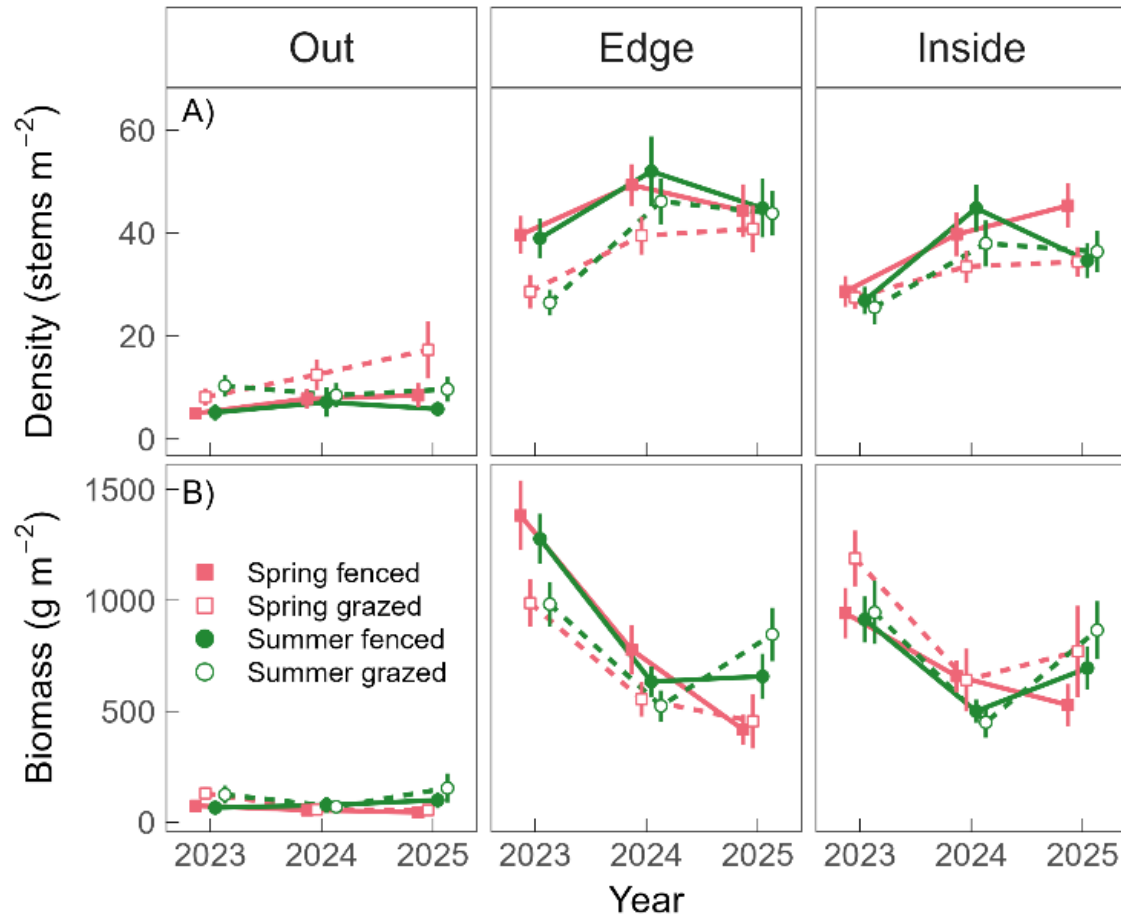


Figure 4-5: Stem density (A) and aboveground biomass (B) of *C. drummondii* from 2023 to 2025 across outside, edge, and interior of shrub islands. Points represent means $\pm$ SE for spring (square) and summer (circle) burn treatments, with bison present (dashed, open symbols) or excluded (filled symbols).

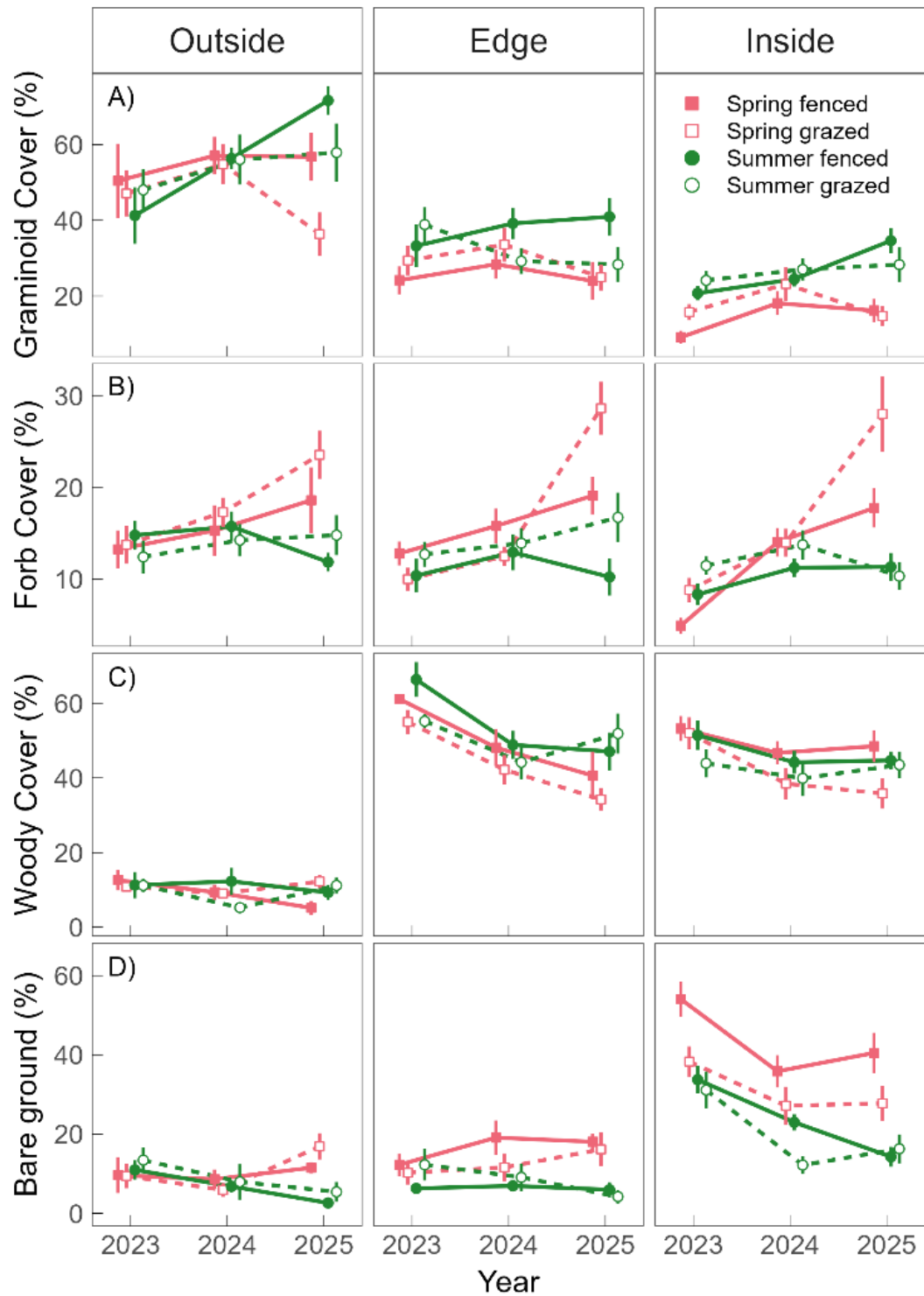


Figure 4-6: Percent cover of graminoids (A), forbs (B), woody vegetation (C) and bare ground (D) from 2023 to 2025 across outside, edge, and interior of shrub islands. Points represent means $\pm$ SE for spring (square) and summer (circle) burn treatments, with bison present (dashed, open symbols) or excluded (filled symbols).

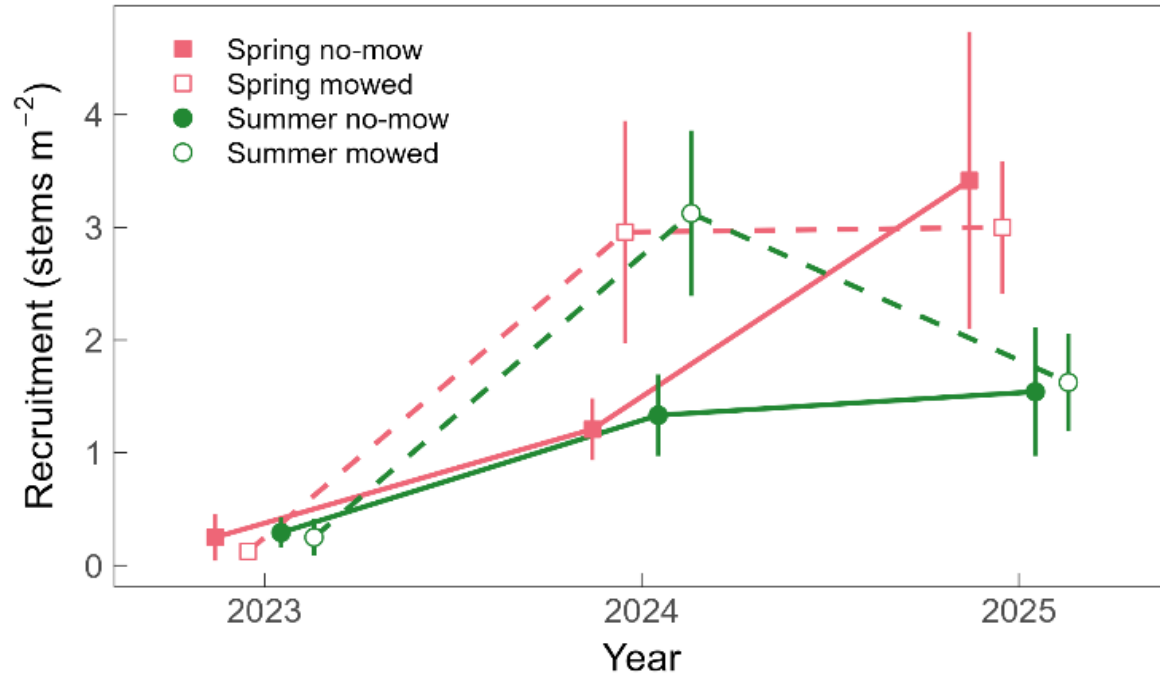


Figure 4-7: Stem density of *C. drummondii* recruits (< 0.15 cm in height) from 2023 to 2025. Points represent means $\pm$ SE averaged across of shrub island positions (outside, edge, and interior) for spring (square) and summer (circle) burn treatments, with (dashed, open symbols) and without (filled symbols) mowing.

Chapter 5 - Conclusion

Tallgrass prairie ecosystems developed under highly variable disturbance regimes, with fire, grazing, and climatic variability interacting to create and maintain diverse and heterogeneous grasslands. However, widespread agricultural conversion, fragmentation, fire suppression, and the replacement of native megafauna with domesticated cattle have altered many of the ecological processes that historically maintained prairie. Current management practices in the Great Plains often utilize uniform disturbance regimes, particularly frequent spring burning to maximize livestock production and limit woody encroachment. Although annual spring burning is a cost-effective way to manage productive grasslands at scale, burning half of the region in a span of a few short weeks poses significant logistical and environmental problems (e.g., regional air quality). Furthermore, the associated homogenizing effect of frequent burning reduces ecosystem services that these prairies provide. At the same time, much of the remaining grassland is either infrequently burned or not burned at all. These land use changes, coupled with other environmental drivers, have increased the opportunities for the successful expansion of woody species into grasslands. Incorporating seasonal variability into our current management practices may provide a cost-effective path to address current loss of grassland diversity and the threat of woody expansion. In this dissertation, I evaluated how the seasonal timing of prescribed fire influences tallgrass prairie ecosystems by using a combination of long- and short-term experiments conducted at Konza Prairie Biological Station. Specifically, I aimed to understand how contrasting seasonal fire regimes influence plant community composition, ecosystem productivity, and the restoration of a shrub-encroached grassland in the presence of large grazers (e.g., bison).

In **Chapter 2**, I used a 31-year experiment to evaluate the long-term effects of seasonal prescribed fire on plant communities across topographic positions. I found that the timing of fire, and its interaction with topography, strongly influence community dynamics. Across all treatment combinations, relative cover of warm-season grasses increased over time, while non-legume forb cover declined. However, the effects of topography were much stronger than those of burn season, particularly for legumes and sedges, where legumes had a strong preference for lowland positions and sedges preferred uplands. The effects of burn season on plant communities were most distinct in ordination space, where spring and summer burns were completely separated while fall and winter communities were intermediate and overlapped with one another. Spring burns had a more pronounced effect on warm-season grasses relative to non-spring burns, particularly among *A. gerardii*, *S. nutans*, and *P. virgatum*. In contrast, summer burning opens the canopy and suppresses warm-season grasses, which led to greater richness, diversity, and cool-season graminoid cover than dormant-season burns. Notably, while annual forb richness was much higher in summer-burned watersheds, the overall increase in richness was driven by perennial species. While fall and winter burns are also conducted in the dormant season, the shift to an earlier burn relative to spring resulted in higher richness and greater cool-season graminoid cover. However, fall and winter burns also exhibited a substantial shift from non-legume forb cover to greater legume cover, particularly in lowland areas. Because many of these responses were characterized by transient and non-linear dynamics (e.g., cool-season graminoids), the results from this study highlight the necessity of long-term monitoring, as conclusions drawn from different time points during the experiment may lead to different interpretations of ecosystem responses. However, these results clearly show that tallgrass prairie communities respond differently to prescribed fire applied in different seasons.

In **Chapter 3**, I used 30 years of annual biomass data collected from the same experimental watersheds as Chapter 2 to examine the effects of fire timing on aboveground net primary productivity (ANPP) and its interaction with topography. Because productivity in mesic grasslands is strongly influenced by precipitation variability, I also assessed the relationships between precipitation and ANPP. Lowland positions in this study were much more productive than uplands for both graminoid and forb ANPP. Lower water availability in the uplands also diminished the differences of ANPP between dormant- and growing-season treatments. Despite the strong differences in plant community composition observed in Chapter 2, ANPP responses to dormant-season fires were negligible across topographic positions. However, even though summer burns had similar cover of cool- and warm-season graminoids in lowlands, ANPP was on average 19-24% lower, which was largely a result of lowered productivity in non-burned years. Across all burn treatments, productivity remained strongly linked to growing-season precipitation, and fire timing did not change this relationship. Similarly, soil properties from samples at the end of the 2025 growing season did not show any differences among seasonal burns, only among topographic positions. These results indicate that while fire timing can strongly influence plant community composition, its effects on long-term ecosystem productivity and soil properties are ultimately overridden by regional climate variability and localized topographic gradients.

In **Chapter 4**, I initiated a new experiment on Konza to evaluate the effects of reintroducing annual fire (applied in spring and late-summer) on a bison-grazed watershed that had experienced shrub encroachment while under a 4-year fire return interval. The main goal of

this study was to determine whether changing the timing of reintroduced annual prescribed fire could facilitate reduction in woody cover and the recovery of a grassland state. In contrast to Chapter 2, the herbaceous communities responded similarly to annual spring and summer burning. Both burn regimes increased warm-season grass cover and had positive effects on native species richness. However, responses to clonal shrubs diverged with repeated treatments. Specifically, reduced intensity under a second summer burn allowed shrubs to persist and recover. Among shrub islands, I did not detect any additive or synergistic effects of burn season, grazing, or mowing on *C. drummondii*. Instead, the reductions in biomass from returning fire were quickly replaced by increased stem density, with the strongest responses occurring at the grass-shrub boundary. A one-time mowing event transiently increased shrub recruitment but had no effects otherwise. Shrub stem densities rose regardless of bison presence, even though graminoid cover increased in the absence of bison. These results indicate that incorporating variation in burn timing into grazed grasslands is a viable option, however, the less than ideal results from a repeated summer burn suggest that expanding the timing to target more ideal weather and fuel conditions may be necessary to effectively impact shrubs. The lack of shrub mortality across the watershed highlights that restoring these grasslands after establishment will likely be a long-term endeavor. Because these findings only represent the initial two years following fire reintroduction, long-term monitoring will be necessary to determine the role of fire seasons in the restoration of shrub-encroached, grazed grasslands.

Appendix A - Chapter 2 supplementary material

Table A.1: Burn history data by year. Prescribed burns on watersheds not planned to burn that year (PU). Wildfire on a watershed planned to be burned that year (WP). Wildfire on a watershed that was not planned to burn that year (WU).

	Spring		Summer		Fall		Winter	
	SpA	SpB	SuA	SuB	FA	FB	WA	WB
Hectares	33.5	36	23	15.6	27.5	26.5	11.6	30.5
Year								
1994	5/5	5/5	9/2	9/7	11/23	11/23	2/15	2/15
1995	4/25	4/13			11/21	11/21	2/21	2/21
1996	4/9	5/13	2/25 (WP), 4/23 (PU)	2/25 (WP), 4/23 (PU)		11/7	2/9	2/9
1997	4/15, 4/17 (PU), 3/24 (WU)	4/15	7/31	7/31	11/21	11/21	2/25	2/25
1998	5/4	4/23			12/1	12/1	2/20	2/20
1999	4/20	4/20	7/26	7/26	12/10	12/10	2/9	2/9
2000	4/12	4/26			11/21	11/21	2/8	2/8
2001	4/24	4/24	8/14	8/14	11/21	11/21	3/6	3/6
2002	5/2	4/29			12/10	12/10	2/13	2/13
2003	4/12	5/5	7/24	7/24			2/17	2/17
2004	4/27	4/13			2/26	2/26, 12/8	2/26	2/26
2005	4/15	4/15	7/29	7/29	11/22	11/22	2/4	2/4
2006	4/27	4/27			11/2	11/20	2/21	2/21
2007	4/30	4/30	7/26	7/26			2/22	2/22
2008	4/14	4/14	7/26	7/26	3/14, 12/12	3/14, 12/12	3/14	3/14
2009	4/22	4/21	7/27	7/27	11/11	11/11	2/4	2/4
2010	4/20	4/20			11/18	11/18	2/18	2/18
2011	4/26	4/26	7/20 (WU), 8/18	8/19	11/23	7/20 (WU), 11/23	2/18, 7/20(WP)	2/18
2012	4/17	4/17			11/14	11/14	2/1	2/1
2013	4/13	4/13			11/14	11/14	3/6	3/6
2014	4/11	4/11	7/24	7/24	11/25	11/25	2/23	2/23
2015	4/14	4/14			11/13	11/13	1/30	1/30
2016	5/3	5/3	7/26	7/26	11/10	11/10	1/29	1/29
2017	4/13	4/13			11/10	11/10	2/6	2/6
2018	3/14 (WP)	3/14	8/1	8/1	11/16	11/16	2/14	2/14
2019	4/15	4/15			11/5	11/5	2/1	2/1
2020	4/21	4/21	8/4	8/4	11/4	11/4	2/6	2/6
2021	4/22	4/22			11/8	11/9	2/26	2/26
2022	4/26	4/26	8/1	8/1	11/21	11/21	2/19	2/19
2023	4/25	4/25			11/7	11/7	2/8	2/8
2024	4/12	4/12	8/7	8/7			2/6	2/6

Table A.2: Summary of Generalized Additive Model Performance for functional group cover.

Response Variable	Burn Season	Topographic Position	Model R²
Warm-season Grass Cover (%)	Spring	Lowland	0.08
Warm-season Grass Cover (%)	Spring	Upland	0.38
Warm-season Grass Cover (%)	Summer	Lowland	0.39
Warm-season Grass Cover (%)	Summer	Upland	0.29
Warm-season Grass Cover (%)	Fall	Lowland	0.16
Warm-season Grass Cover (%)	Fall	Upland	0.16
Warm-season Grass Cover (%)	Winter	Lowland	0.23
Warm-season Grass Cover (%)	Winter	Upland	0.35
Cool-season Graminoid Cover (%)	Spring	Lowland	0.78
Cool-season Graminoid Cover (%)	Spring	Upland	0.62
Cool-season Graminoid Cover (%)	Summer	Lowland	0.15
Cool-season Graminoid Cover (%)	Summer	Upland	0.63
Cool-season Graminoid Cover (%)	Fall	Lowland	0.32
Cool-season Graminoid Cover (%)	Fall	Upland	0.08
Cool-season Graminoid Cover (%)	Winter	Lowland	0.25
Cool-season Graminoid Cover (%)	Winter	Upland	0.21
Non-legume Forb Cover (%)	Spring	Lowland	0.19
Non-legume Forb Cover (%)	Spring	Upland	0.22
Non-legume Forb Cover (%)	Summer	Lowland	0.69
Non-legume Forb Cover (%)	Summer	Upland	0.37
Non-legume Forb Cover (%)	Fall	Lowland	0.36
Non-legume Forb Cover (%)	Fall	Upland	0.56
Non-legume Forb Cover (%)	Winter	Lowland	0.57
Non-legume Forb Cover (%)	Winter	Upland	0.53
Legume Cover (%)	Spring	Lowland	0.06
Legume Cover (%)	Spring	Upland	0.02
Legume Cover (%)	Summer	Lowland	0.32
Legume Cover (%)	Summer	Upland	0.12
Legume Cover (%)	Fall	Lowland	0.27
Legume Cover (%)	Fall	Upland	0.16
Legume Cover (%)	Winter	Lowland	0.67
Legume Cover (%)	Winter	Upland	0.03
Native Species Richness (spp. 10 m ²)	Spring	Lowland	0.37
Native Species Richness (spp. 10 m ²)	Spring	Upland	0.07
Native Species Richness (spp. 10 m ²)	Summer	Lowland	0.21
Native Species Richness (spp. 10 m ²)	Summer	Upland	0.33
Native Species Richness (spp. 10 m ²)	Fall	Lowland	0.11
Native Species Richness (spp. 10 m ²)	Fall	Upland	0.10
Native Species Richness (spp. 10 m ²)	Winter	Lowland	0.19
Native Species Richness (spp. 10 m ²)	Winter	Upland	0.13
Native Species Richness (spp. 200 m ²)	Spring	Lowland	0.67

Native Species Richness (spp. 200 m ²)	Spring	Upland	0.30
Native Species Richness (spp. 200 m ²)	Summer	Lowland	0.04
Native Species Richness (spp. 200 m ²)	Summer	Upland	0.49
Native Species Richness (spp. 200 m ²)	Fall	Lowland	0.40
Native Species Richness (spp. 200 m ²)	Fall	Upland	0.15
Native Species Richness (spp. 200 m ²)	Winter	Lowland	0.50
Native Species Richness (spp. 200 m ²)	Winter	Upland	0.37
Shannon Index (e ^H) (spp. 10 m ²)	Spring	Lowland	0.38
Shannon Index (e ^H) (spp. 10 m ²)	Spring	Upland	0.30
Shannon Index (e ^H) (spp. 10 m ²)	Summer	Lowland	0.09
Shannon Index (e ^H) (spp. 10 m ²)	Summer	Upland	0.09
Shannon Index (e ^H) (spp. 10 m ²)	Fall	Lowland	0.30
Shannon Index (e ^H) (spp. 10 m ²)	Fall	Upland	0.18
Shannon Index (e ^H) (spp. 10 m ²)	Winter	Lowland	0.16
Shannon Index (e ^H) (spp. 10 m ²)	Winter	Upland	0.22
Shannon Index (e ^H) (spp. 200 m ²)	Spring	Lowland	0.56
Shannon Index (e ^H) (spp. 200 m ²)	Spring	Upland	0.77
Shannon Index (e ^H) (spp. 200 m ²)	Summer	Lowland	0.18
Shannon Index (e ^H) (spp. 200 m ²)	Summer	Upland	0.03
Shannon Index (e ^H) (spp. 200 m ²)	Fall	Lowland	0.70
Shannon Index (e ^H) (spp. 200 m ²)	Fall	Upland	0.44
Shannon Index (e ^H) (spp. 200 m ²)	Winter	Lowland	0.44
Shannon Index (e ^H) (spp. 200 m ²)	Winter	Upland	0.75

Table A.3: Summary of Generalized Additive Model Performance for species.

Response Variable	Burn Season	Topographic Position	Model R²
<i>Andropogon gerardii</i> Cover (%)	Spring	Lowland	0.15
<i>Andropogon gerardii</i> Cover (%)	Spring	Upland	0.16
<i>Andropogon gerardii</i> Cover (%)	Summer	Lowland	0.13
<i>Andropogon gerardii</i> Cover (%)	Summer	Upland	0.28
<i>Andropogon gerardii</i> Cover (%)	Fall	Lowland	0.17
<i>Andropogon gerardii</i> Cover (%)	Fall	Upland	0.12
<i>Andropogon gerardii</i> Cover (%)	Winter	Lowland	0.43
<i>Andropogon gerardii</i> Cover (%)	Winter	Upland	0.00
<i>Schizachyrium scoparium</i> Cover (%)	Spring	Lowland	0.06
<i>Schizachyrium scoparium</i> Cover (%)	Spring	Upland	0.00
<i>Schizachyrium scoparium</i> Cover (%)	Summer	Lowland	0.11
<i>Schizachyrium scoparium</i> Cover (%)	Summer	Upland	0.09
<i>Schizachyrium scoparium</i> Cover (%)	Fall	Lowland	0.00
<i>Schizachyrium scoparium</i> Cover (%)	Fall	Upland	0.12
<i>Schizachyrium scoparium</i> Cover (%)	Winter	Lowland	0.08
<i>Schizachyrium scoparium</i> Cover (%)	Winter	Upland	0.20
<i>Sorghastrum nutans</i> Cover (%)	Spring	Lowland	0.24
<i>Sorghastrum nutans</i> Cover (%)	Spring	Upland	0.12
<i>Sorghastrum nutans</i> Cover (%)	Summer	Lowland	0.01
<i>Sorghastrum nutans</i> Cover (%)	Summer	Upland	0.01
<i>Sorghastrum nutans</i> Cover (%)	Fall	Lowland	0.17
<i>Sorghastrum nutans</i> Cover (%)	Fall	Upland	0.03
<i>Sorghastrum nutans</i> Cover (%)	Winter	Lowland	0.00
<i>Sorghastrum nutans</i> Cover (%)	Winter	Upland	0.23
<i>Panicum virgatum</i> Cover (%)	Spring	Lowland	0.11
<i>Panicum virgatum</i> Cover (%)	Spring	Upland	0.07
<i>Panicum virgatum</i> Cover (%)	Summer	Lowland	0.00
<i>Panicum virgatum</i> Cover (%)	Summer	Upland	0.03
<i>Panicum virgatum</i> Cover (%)	Fall	Lowland	0.26
<i>Panicum virgatum</i> Cover (%)	Fall	Upland	0.04
<i>Panicum virgatum</i> Cover (%)	Winter	Lowland	0.14
<i>Panicum virgatum</i> Cover (%)	Winter	Upland	0.06
<i>Sporobolus compositus</i> Cover (%)	Spring	Lowland	0.47
<i>Sporobolus compositus</i> Cover (%)	Spring	Upland	0.39
<i>Sporobolus compositus</i> Cover (%)	Summer	Lowland	0.13
<i>Sporobolus compositus</i> Cover (%)	Summer	Upland	0.04
<i>Sporobolus compositus</i> Cover (%)	Fall	Lowland	0.27
<i>Sporobolus compositus</i> Cover (%)	Fall	Upland	0.26
<i>Sporobolus compositus</i> Cover (%)	Winter	Lowland	0.11
<i>Sporobolus compositus</i> Cover (%)	Winter	Upland	0.10
<i>Carex inops</i> Cover (%)	Spring	Lowland	0.17

<i>Carex inops</i> Cover (%)	Spring	Upland	0.31
<i>Carex inops</i> Cover (%)	Summer	Lowland	0.23
<i>Carex inops</i> Cover (%)	Summer	Upland	0.49
<i>Carex inops</i> Cover (%)	Fall	Lowland	0.19
<i>Carex inops</i> Cover (%)	Fall	Upland	0.33
<i>Carex inops</i> Cover (%)	Winter	Lowland	0.13
<i>Carex inops</i> Cover (%)	Winter	Upland	0.58
<i>Carex meadii</i> Cover (%)	Spring	Lowland	0.02
<i>Carex meadii</i> Cover (%)	Spring	Upland	0.04
<i>Carex meadii</i> Cover (%)	Summer	Lowland	0.39
<i>Carex meadii</i> Cover (%)	Summer	Upland	0.05
<i>Carex meadii</i> Cover (%)	Fall	Lowland	0.32
<i>Carex meadii</i> Cover (%)	Fall	Upland	0.02
<i>Carex meadii</i> Cover (%)	Winter	Lowland	0.28
<i>Carex meadii</i> Cover (%)	Winter	Upland	0.04
<i>Koeleria macrantha</i> Cover (%)	Spring	Lowland	0.06
<i>Koeleria macrantha</i> Cover (%)	Spring	Upland	0.11
<i>Koeleria macrantha</i> Cover (%)	Summer	Lowland	0.07
<i>Koeleria macrantha</i> Cover (%)	Summer	Upland	0.51
<i>Koeleria macrantha</i> Cover (%)	Fall	Lowland	0.04
<i>Koeleria macrantha</i> Cover (%)	Fall	Upland	0.01
<i>Koeleria macrantha</i> Cover (%)	Winter	Lowland	0.15
<i>Koeleria macrantha</i> Cover (%)	Winter	Upland	0.29
<i>Symphyotrichum ericoides</i> Cover (%)	Spring	Lowland	0.33
<i>Symphyotrichum ericoides</i> Cover (%)	Spring	Upland	0.28
<i>Symphyotrichum ericoides</i> Cover (%)	Summer	Lowland	0.60
<i>Symphyotrichum ericoides</i> Cover (%)	Summer	Upland	0.33
<i>Symphyotrichum ericoides</i> Cover (%)	Fall	Lowland	0.58
<i>Symphyotrichum ericoides</i> Cover (%)	Fall	Upland	0.22
<i>Symphyotrichum ericoides</i> Cover (%)	Winter	Lowland	0.67
<i>Symphyotrichum ericoides</i> Cover (%)	Winter	Upland	0.33
<i>Solidago altissima</i> Cover (%)	Spring	Lowland	0.01
<i>Solidago altissima</i> Cover (%)	Spring	Upland	0.00
<i>Solidago altissima</i> Cover (%)	Summer	Lowland	0.12
<i>Solidago altissima</i> Cover (%)	Summer	Upland	0.04
<i>Solidago altissima</i> Cover (%)	Fall	Lowland	0.00
<i>Solidago altissima</i> Cover (%)	Fall	Upland	0.00
<i>Solidago altissima</i> Cover (%)	Winter	Lowland	0.12
<i>Solidago altissima</i> Cover (%)	Winter	Upland	0.08
<i>Symphyotrichum oblongifolium</i> Cover (%)	Spring	Lowland	0.03
<i>Symphyotrichum oblongifolium</i> Cover (%)	Spring	Upland	0.14
<i>Symphyotrichum oblongifolium</i> Cover (%)	Summer	Lowland	0.00
<i>Symphyotrichum oblongifolium</i> Cover (%)	Summer	Upland	0.07
<i>Symphyotrichum oblongifolium</i> Cover (%)	Fall	Lowland	0.07
<i>Symphyotrichum oblongifolium</i> Cover (%)	Fall	Upland	0.15

<i>Symphyotrichum oblongifolium</i> Cover (%)	Winter	Lowland	0.00
<i>Symphyotrichum oblongifolium</i> Cover (%)	Winter	Upland	0.05
<i>Lespedeza violacea</i> Cover (%)	Spring	Lowland	0.09
<i>Lespedeza violacea</i> Cover (%)	Spring	Upland	0.03
<i>Lespedeza violacea</i> Cover (%)	Summer	Lowland	0.20
<i>Lespedeza violacea</i> Cover (%)	Summer	Upland	0.05
<i>Lespedeza violacea</i> Cover (%)	Fall	Lowland	0.32
<i>Lespedeza violacea</i> Cover (%)	Fall	Upland	0.05
<i>Lespedeza violacea</i> Cover (%)	Winter	Lowland	0.56
<i>Lespedeza violacea</i> Cover (%)	Winter	Upland	0.06
<i>Amorpha canescens</i> Cover (%)	Spring	Lowland	0.03
<i>Amorpha canescens</i> Cover (%)	Spring	Upland	0.01
<i>Amorpha canescens</i> Cover (%)	Summer	Lowland	0.01
<i>Amorpha canescens</i> Cover (%)	Summer	Upland	0.05
<i>Amorpha canescens</i> Cover (%)	Fall	Lowland	0.22
<i>Amorpha canescens</i> Cover (%)	Fall	Upland	0.07
<i>Amorpha canescens</i> Cover (%)	Winter	Lowland	0.03
<i>Amorpha canescens</i> Cover (%)	Winter	Upland	0.07
<i>Poa pratensis</i> Cover (%)	Spring	Lowland	0.42
<i>Poa pratensis</i> Cover (%)	Spring	Upland	0.43
<i>Poa pratensis</i> Cover (%)	Summer	Lowland	0.25
<i>Poa pratensis</i> Cover (%)	Summer	Upland	0.45
<i>Poa pratensis</i> Cover (%)	Fall	Lowland	0.54
<i>Poa pratensis</i> Cover (%)	Fall	Upland	0.48
<i>Poa pratensis</i> Cover (%)	Winter	Lowland	0.13
<i>Poa pratensis</i> Cover (%)	Winter	Upland	0.44
<i>Rhus glabra</i> Cover (%)	Spring	Lowland	0.12
<i>Rhus glabra</i> Cover (%)	Spring	Upland	0.13
<i>Rhus glabra</i> Cover (%)	Summer	Lowland	0.09
<i>Rhus glabra</i> Cover (%)	Summer	Upland	0.28
<i>Rhus glabra</i> Cover (%)	Fall	Lowland	0.05
<i>Rhus glabra</i> Cover (%)	Fall	Upland	0.00
<i>Rhus glabra</i> Cover (%)	Winter	Lowland	0.03
<i>Rhus glabra</i> Cover (%)	Winter	Upland	0.02

Table A.4: Estimated yearly trends (Slope (β)) from linear mixed effects models using Kenward-Roger method. Slopes represent the estimated annual change in the transformed response variable.

Warm-season Graminoid Cover (%)							
Burn Season	Topographic Position	df	Slope (β)	SE	95% CI	t	p-value
Spring	Lowland	1960	0.129	0.076	[-0.02, 0.28]	1.703	0.0887
Summer	Lowland	1960	0.592	0.076	[0.44, 0.74]	7.807	< 0.001
Fall	Lowland	1960	0.178	0.076	[0.03, 0.33]	2.352	0.0188
Winter	Lowland	1960	-0.170	0.076	[-0.32, -0.02]	-2.241	0.0251
Spring	Upland	1960	0.339	0.076	[0.19, 0.49]	4.470	< 0.001
Summer	Upland	1960	0.531	0.076	[0.38, 0.68]	6.996	< 0.001
Fall	Upland	1960	0.484	0.076	[0.33, 0.63]	6.373	< 0.001
Winter	Upland	1960	0.460	0.076	[0.31, 0.61]	6.063	< 0.001
Cool-season Graminoid Cover (%)							
Burn Season	Topographic Position	df	Slope (β)	SE	95% CI	t	p-value
Spring	Lowland	1960	-0.078	0.004	[-0.09, -0.07]	-20.399	< 0.001
Summer	Lowland	1960	0.008	0.004	[0, 0.02]	2.114	0.0347
Fall	Lowland	1960	-0.015	0.004	[-0.02, -0.01]	-3.848	< 0.001
Winter	Lowland	1960	-0.002	0.004	[-0.01, 0.01]	-0.488	0.6257
Spring	Upland	1960	-0.059	0.004	[-0.07, -0.05]	-15.232	< 0.001
Summer	Upland	1960	0.041	0.004	[0.03, 0.05]	10.757	< 0.001
Fall	Upland	1960	0.009	0.004	[0, 0.02]	2.354	0.0187
Winter	Upland	1960	0.014	0.004	[0.01, 0.02]	3.751	0.0002
Non-legume Forb Cover (%)							
Burn Season	Topographic Position	df	Slope (β)	SE	95% CI	t	p-value
Spring	Lowland	1960	-0.014	0.006	[-0.03, 0]	-2.234	0.0256
Summer	Lowland	1960	-0.084	0.006	[-0.1, -0.07]	-13.603	< 0.001
Fall	Lowland	1960	-0.058	0.006	[-0.07, -0.05]	-9.326	< 0.001
Winter	Lowland	1960	-0.093	0.006	[-0.1, -0.08]	-15.051	< 0.001
Spring	Upland	1960	-0.022	0.006	[-0.03, -0.01]	-3.625	< 0.001
Summer	Upland	1960	-0.026	0.006	[-0.04, -0.01]	-4.283	< 0.001
Fall	Upland	1960	-0.076	0.006	[-0.09, -0.06]	-12.254	< 0.001
Winter	Upland	1960	-0.069	0.006	[-0.08, -0.06]	-11.175	< 0.001
Legume Cover (%)							
Burn Season	Topographic Position	df	Slope (β)	SE	95% CI	t	p-value
Spring	Lowland	1960	0.018	0.003	[0.01, 0.02]	6.309	< 0.001
Summer	Lowland	1960	0.023	0.003	[0.02, 0.03]	8.102	< 0.001
Fall	Lowland	1960	0.027	0.003	[0.02, 0.03]	9.472	< 0.001
Winter	Lowland	1960	0.046	0.003	[0.04, 0.05]	15.767	< 0.001
Spring	Upland	1960	-0.003	0.003	[-0.01, 0]	-0.871	0.3837
Summer	Upland	1960	0.013	0.003	[0.01, 0.02]	4.422	< 0.001
Fall	Upland	1960	0.009	0.003	[0, 0.01]	3.193	0.0014
Winter	Upland	1960	0.008	0.003	[0, 0.01]	2.885	0.0040
Native Species Richness (spp. 10 m ²)							
Burn Season	Topographic Position	df	Slope (β)	SE	95% CI	t	p-value
Spring	Lowland	9880	-0.025	0.001	[-0.03, -0.02]	-20.182	< 0.001
Summer	Lowland	9880	0.014	0.001	[0.01, 0.02]	11.370	< 0.001
Fall	Lowland	9880	-0.004	0.001	[-0.01, 0.00]	-3.060	0.0022
Winter	Lowland	9880	-0.001	0.001	[0.00, 0.00]	-1.092	0.2747

Spring	Upland	9880	-0.005	0.001	[-0.01, 0.00]	-4.240	< 0.001
Summer	Upland	9880	0.019	0.001	[0.02, 0.02]	15.483	< 0.001
Fall	Upland	9880	-0.001	0.001	[0.00, 0.00]	-0.532	0.5946
Winter	Upland	9880	0.003	0.001	[0.00, 0.01]	2.176	0.0296
Native Species Richness (spp. 200 m²)							
Burn Season	Topographic Position	df	Slope (β)	SE	95% CI	t	p-value
Spring	Lowland	475	0.000	0.000	[0.00, 0.00]	8.222	< 0.001
Summer	Lowland	475	-0.0000020	0.000	[0.00, 0.00]	-0.092	0.9266
Fall	Lowland	475	0.000	0.000	[0.00, 0.00]	4.536	< 0.001
Winter	Lowland	475	0.000	0.000	[0.00, 0.00]	2.849	0.0046
Spring	Upland	475	0.000	0.000	[0.00, 0.00]	4.444	< 0.001
Summer	Upland	475	-0.00011	0.000	[0.00, 0.00]	-5.240	< 0.001
Fall	Upland	475	0.000	0.000	[0.00, 0.00]	1.195	0.2327
Winter	Upland	475	-0.0000045	0.000	[0.00, 0.00]	-0.209	0.8347
Shannon Index (e^H) (spp. 10 m²)							
Burn Season	Topographic Position	df	Slope (β)	SE	95% CI	t	p-value
Spring	Lowland	9880	-0.008	0.000	[-0.01, -0.01]	-16.291	< 0.001
Summer	Lowland	9880	0.000	0.000	[0.00, 0.00]	0.597	0.5506
Fall	Lowland	9880	-0.006	0.000	[-0.01, 0.00]	-11.737	< 0.001
Winter	Lowland	9880	-0.002	0.000	[0.00, 0.00]	-4.982	< 0.001
Spring	Upland	9880	-0.007	0.000	[-0.01, -0.01]	-15.148	< 0.001
Summer	Upland	9880	0.001	0.000	[0.00, 0.00]	2.780	0.0054
Fall	Upland	9880	-0.005	0.000	[-0.01, 0.00]	-10.632	< 0.001
Winter	Upland	9880	-0.006	0.000	[-0.01, -0.01]	-12.617	< 0.001
Shannon Index (e^H) (spp. 200 m²)							
Burn Season	Topographic Position	df	Slope (β)	SE	95% CI	t	p-value
Spring	Lowland	475	-0.015	0.002	[-0.02, -0.01]	-7.148	< 0.001
Summer	Lowland	475	0.001	0.002	[0.00, 0.01]	0.549	0.5835
Fall	Lowland	475	-0.009	0.002	[-0.01, 0.00]	-4.016	< 0.001
Winter	Lowland	475	-0.004	0.002	[-0.01, 0.00]	-1.820	0.0693
Spring	Upland	475	-0.012	0.002	[-0.02, -0.01]	-5.611	< 0.001
Summer	Upland	475	0.004	0.002	[0.00, 0.01]	1.715	0.0870
Fall	Upland	475	-0.009	0.002	[-0.01, -0.01]	-4.427	< 0.001
Winter	Upland	475	-0.012	0.002	[-0.02, -0.01]	-5.637	< 0.001

Table A.5: Summary table of linear regression on native forb richness based on life history (annual versus perennial).

Burn Season	Topographic Position	Life History	Slope (β)	Model R²	p-value
Spring	Lowland	Annual	-0.148	0.364	< 0.001
Spring	Lowland	Perennial	-0.219	0.751	< 0.001
Spring	Upland	Annual	-0.061	0.181	0.0170
Spring	Upland	Perennial	-0.139	0.427	< 0.001
Summer	Lowland	Annual	-0.051	0.010	0.5915
Summer	Lowland	Perennial	0.049	0.034	0.3196
Summer	Upland	Annual	0.067	0.027	0.3734
Summer	Upland	Perennial	0.200	0.383	< 0.001
Fall	Lowland	Annual	-0.120	0.494	< 0.001
Fall	Lowland	Perennial	-0.163	0.308	< 0.001
Fall	Upland	Annual	-0.104	0.418	< 0.001
Fall	Upland	Perennial	0.007	0.003	0.7815
Winter	Lowland	Annual	-0.057	0.122	0.0537
Winter	Lowland	Perennial	-0.170	0.298	0.0015
Winter	Upland	Annual	-0.062	0.231	0.0061
Winter	Upland	Perennial	0.090	0.307	0.0012

Table A.6: Relative cover and absences (-) of each species averaged across the first five (1994-98) and last five (2020-24) years within the lowlands. Species are categorized into broad functional groups and organized alphabetically. Total indicates the sum relative cover percent of each burn treatment within each functional group.

Lowlands		Spring		Summer		Fall		Winter	
Species		Start	End	Start	End	Start	End	Start	End
Warm-season Graminoids									
<i>Andropogon gerardii</i>		31.89	31.47	23.96	29.69	32.29	30.12	44.27	31.26
<i>Bouteloua curtipendula</i>		0.36	0.10	0.26	0.57	0.16	0.12	0.04	0.14
<i>Cyperus lupulinus</i>		0.11	0.04	0.01	0.03	-	0.01	-	0.01
<i>Digitaria cognata</i>		-	-	-	0.00	-	-	-	-
<i>Eragrostis spectabilis</i>		0.32	0.27	0.02	0.05	0.01	0.01	0.02	0.01
<i>Muhlenbergia racemosa</i>		-	-	-	-	-	0.01	-	0.01
<i>Panicum capillare</i>		0.02	0.01	-	-	0.00	-	-	-
<i>Panicum virgatum</i>		2.60	9.07	0.79	0.84	2.71	11.70	3.78	11.03
<i>Schizachyrium scoparium</i>		9.90	5.84	2.61	6.12	6.57	6.20	2.49	2.73
<i>Sorghastrum nutans</i>		10.83	17.30	5.97	8.07	8.57	6.51	8.05	8.37
<i>Sporobolus compositus</i>		3.38	0.64	4.93	6.73	2.91	0.83	2.26	1.01
<i>Sporobolus heterolepis</i>		1.00	0.14	4.11	5.90	0.04	0.04	0.39	0.36
<i>Tridens flavus</i>		0.00	0.01	-	-	0.02	-	-	-
Total		60.41	64.88	42.66	58.01	53.27	55.53	61.29	54.92
Cool-season Graminoids									
<i>Agrostis hyemalis</i>		0.26	0.00	0.02	0.00	0.01	-	-	-
<i>Carex austrina</i>		-	-	-	0.00	-	-	-	-
<i>Carex bicknellii</i>		-	0.01	-	0.04	-	0.01	-	-
<i>Carex brevior</i>		0.80	0.20	0.91	0.72	0.84	0.91	0.45	0.45
<i>Carex gravida</i>		0.04	0.07	0.17	0.29	0.05	0.10	0.06	0.17
<i>Carex inops</i>		-	-	0.09	1.90	-	0.63	0.02	0.21
<i>Carex meadii</i>		0.49	0.67	1.15	3.35	1.01	2.33	1.32	3.86
<i>Carex spp.</i>		4.79	-	2.74	-	3.55	-	3.06	-
<i>Dichanthelium oligosanthes</i>		1.39	0.13	1.29	0.46	0.83	0.33	1.13	0.31
<i>Dichanthelium ovale</i>		0.90	0.11	0.30	0.47	0.13	0.04	0.03	0.04
<i>Eleocharis compressa</i>		-	-	0.20	0.31	0.39	0.16	0.17	0.05
<i>Elymus canadensis</i>		0.01	-	0.01	-	0.07	0.00	0.00	0.00
<i>Juncus interior</i>		0.03	-	0.01	0.01	0.01	0.00	0.01	0.00
<i>Koeleria macrantha</i>		0.03	-	0.10	0.39	0.15	0.10	0.10	0.07
<i>Sphenopholis obtusata</i>		0.54	-	0.42	0.02	0.07	-	0.01	0.00
<i>Vulpia octoflora</i>		-	-	-	0.02	-	-	-	-
Total		9.29	1.19	7.41	7.98	7.10	4.60	6.37	5.16
Non-Legume Forbs									
<i>Acalypha virginica</i>		0.02	0.02	0.00	0.00	0.01	-	0.00	-
<i>Achillea millefolium</i>		0.13	-	0.09	0.10	0.23	0.06	0.12	0.04
<i>Ageratina altissima</i>		-	0.00	-	-	-	-	-	-
<i>Ambrosia artemisiifolia</i>		0.27	0.12	0.10	0.07	0.01	-	0.00	0.22
<i>Ambrosia psilostachya</i>		2.68	3.81	1.43	0.64	2.23	1.82	2.75	1.68
<i>Antennaria neglecta</i>		0.11	-	0.00	0.00	0.01	0.00	0.03	-
<i>Apocynum cannabinum</i>		-	0.01	-	0.01	0.06	0.04	0.01	0.00
<i>Arnoglossum plantagineum</i>		-	0.00	0.02	0.02	-	-	-	-
<i>Artemisia ludoviciana</i>		0.66	0.02	0.78	3.66	0.75	3.21	0.16	0.88
<i>Asclepias stenophylla</i>		0.06	0.00	0.05	0.02	0.02	0.01	0.01	0.01
<i>Asclepias sullivantii</i>		-	0.00	0.04	0.02	0.29	0.03	0.08	0.01
<i>Asclepias syriaca</i>		0.22	0.23	0.54	0.01	0.19	-	0.09	0.00
<i>Asclepias tuberosa</i>		0.04	0.05	0.04	0.01	0.01	-	0.01	0.01
<i>Asclepias verticillata</i>		0.41	0.37	0.05	0.04	0.08	0.04	0.10	0.07

<i>Asclepias viridiflora</i>	0.00	-	0.01	-	0.01	-	-	-
<i>Asclepias viridis</i>	1.04	0.40	0.27	0.02	0.26	0.23	0.31	0.06
<i>Brickellia eupatorioides</i>	0.06	0.01	0.21	0.62	0.08	0.02	0.09	0.11
<i>Callirhoe involucrata</i>	-	-	0.09	0.07	-	-	-	-
<i>Calystegia macounii</i>	-	-	-	0.01	0.01	-	-	-
<i>Cirsium altissimum</i>	0.39	-	0.29	0.07	0.25	-	0.06	0.00
<i>Conyza canadensis</i>	-	-	0.02	0.04	-	-	-	-
<i>Corydalis micrantha</i>	-	-	0.00	-	-	-	-	-
<i>Croton monanthogynus</i>	-	-	0.00	-	-	-	-	-
<i>Cuscuta indecora</i>	-	-	-	-	-	-	-	0.00
<i>Draba reptans</i>	-	-	0.00	-	-	-	-	-
<i>Erigeron philadelphicus</i>	-	-	0.00	0.02	0.00	-	-	0.00
<i>Erigeron strigosus</i>	0.06	0.01	-	-	0.00	-	0.00	-
<i>Eupatorium altissimum</i>	0.30	0.00	0.16	-	0.09	-	0.04	0.01
<i>Euphorbia glyptosperma</i>	0.01	0.01	-	-	-	-	-	-
<i>Euphorbia maculata</i>	-	0.00	-	-	-	-	-	-
<i>Euphorbia marginata</i>	0.04	0.00	0.04	0.00	0.02	-	0.01	0.00
<i>Euphorbia missurica</i>	-	-	-	-	0.00	-	-	-
<i>Euphorbia nutans</i>	0.01	0.02	-	-	-	-	-	-
<i>Euphorbia serpens</i>	0.03	-	-	-	-	-	-	-
<i>Euphorbia spathulata</i>	0.00	-	0.23	0.06	0.02	-	0.00	-
<i>Galium aparine</i>	-	-	0.02	-	-	-	-	-
<i>Geranium carolinianum</i>	-	-	0.02	0.02	-	-	0.00	-
<i>Helianthus annuus</i>	-	-	-	-	0.00	-	-	-
<i>Hieracium longipilum</i>	-	-	0.12	0.02	0.03	0.01	0.01	-
<i>Krigia cespitosa</i>	0.03	0.00	-	-	-	-	-	-
<i>Lactuca ludoviciana</i>	0.00	-	0.00	-	0.00	-	-	0.00
<i>Liatris punctata</i>	-	-	-	0.00	-	-	-	-
<i>Linum sulcatum</i>	0.04	-	0.09	0.17	0.12	0.01	0.04	0.02
<i>Mirabilis albida</i>	-	-	-	-	-	-	-	0.00
<i>Oenothera biennis</i>	-	-	0.00	-	-	-	-	-
<i>Oenothera curtiflora</i>	0.01	-	0.01	-	-	-	-	-
<i>Oenothera glaucifolia</i>	-	-	-	-	0.00	-	-	-
<i>Oenothera speciosa</i>	0.00	-	0.22	0.03	0.27	0.00	0.11	0.01
<i>Oenothera villosa</i>	-	-	-	0.01	-	-	-	-
<i>Oxalis dillenii</i>	-	0.00	-	0.03	-	-	-	-
<i>Oxalis stricta</i>	0.23	-	0.12	-	0.05	-	0.02	-
<i>Oxalis violacea</i>	0.31	0.14	0.05	0.03	0.57	0.05	0.40	0.02
<i>Packera plattensis</i>	0.00	-	0.02	0.03	0.01	-	-	-
<i>Parietaria pensylvanica</i>	-	-	0.00	-	-	-	-	-
<i>Physalis heterophylla</i>	0.02	-	0.17	0.01	-	-	0.04	0.03
<i>Physalis longifolia</i>	-	-	-	0.00	-	-	-	-
<i>Physalis pumila</i>	1.02	0.08	0.87	0.07	0.80	0.01	0.86	0.01
<i>Physalis virginiana</i>	-	0.29	0.00	0.27	-	0.07	-	0.07
<i>Plantago rhodosperma</i>	0.01	-	0.00	-	0.00	-	-	-
<i>Plantago virginica</i>	-	-	-	0.01	-	-	-	-
<i>Ratibida columnifera</i>	0.00	-	0.00	0.01	-	-	-	-
<i>Ruellia humilis</i>	1.14	0.91	1.73	0.20	0.69	0.14	0.49	0.10
<i>Rumex altissimus</i>	-	-	0.03	-	-	-	-	-
<i>Salvia azurea</i>	0.00	-	0.10	0.11	0.04	0.02	0.04	0.01
<i>Scutellaria parvula</i>	-	-	-	0.00	-	0.00	-	0.00
<i>Silene antirrhina</i>	0.00	-	0.11	0.04	-	-	-	-
<i>Sisyrinchium campestre</i>	0.03	0.00	0.10	0.10	0.05	0.03	0.05	0.01
<i>Solanum carolinense</i>	-	0.02	-	0.01	-	-	-	-
<i>Solidago altissima</i>	4.49	6.29	5.15	1.34	5.91	6.92	1.45	1.84
<i>Solidago missouriensis</i>	1.38	1.10	4.42	1.93	2.07	1.99	0.53	0.48

<i>Solidago rigida</i>	0.63	1.02	0.37	0.01	0.22	0.70	0.03	0.22
<i>Spermolepis inermis</i>	-	-	0.01	0.05	-	-	-	-
<i>Spiranthes vernalis</i>	0.00	0.00	0.02	0.00	0.00	-	0.00	-
<i>Symphyotrichum ericoides</i>	0.96	0.16	17.02	4.16	10.87	2.60	13.28	1.53
<i>Symphyotrichum lanceolatum</i>	0.13	-	0.03	-	0.05	0.01	0.02	0.00
<i>Symphyotrichum oblongifolium</i>	-	-	-	-	-	-	0.01	0.01
<i>Symphyotrichum sericeum</i>	-	-	0.03	0.01	-	-	0.01	-
<i>Teucrium canadense</i>	0.66	0.06	0.26	0.54	0.11	0.12	0.05	0.07
<i>Tradescantia bracteata</i>	-	-	0.01	0.01	-	0.02	-	-
<i>Tragia betonicifolia</i>	-	-	-	0.00	-	-	-	-
<i>Triodanis leptocarpa</i>	-	-	-	0.00	-	-	-	-
<i>Triodanis perfoliata</i>	-	-	0.04	0.01	-	-	-	-
<i>Verbena stricta</i>	0.00	-	0.02	-	0.00	-	-	-
<i>Vernonia baldwinii</i>	0.47	0.29	0.66	0.31	0.34	0.58	0.50	0.37
<i>Viola bicolor</i>	-	-	0.08	0.00	-	-	-	-
<i>Viola missouriensis</i>	-	-	-	-	-	-	-	0.01
<i>Viola nephrophylla</i>	0.00	-	-	-	-	-	-	-
<i>Viola pedatifida</i>	0.17	0.00	0.05	0.02	0.05	0.02	0.04	0.04
Total	18.29	15.44	36.41	15.11	26.89	18.77	21.86	7.96
Legumes								
<i>Amorpha canescens</i>	4.29	2.43	4.21	4.95	2.80	1.48	3.15	3.06
<i>Astragalus crassicaupus</i>	-	-	-	-	-	-	0.01	-
<i>Baptisia australis</i>	0.24	0.12	0.03	0.01	0.03	0.01	0.03	0.04
<i>Baptisia bracteata</i>	0.06	0.01	0.19	0.09	0.22	0.12	0.23	0.16
<i>Dalea candida</i>	0.49	0.17	0.12	0.09	0.54	0.38	0.61	0.21
<i>Dalea multiflora</i>	-	-	-	-	-	-	0.01	-
<i>Dalea purpurea</i>	-	-	0.03	0.02	0.03	0.01	0.11	0.02
<i>Desmodium canescens</i>	-	-	-	-	0.74	0.03	-	-
<i>Desmodium illinoense</i>	0.12	0.00	0.02	0.05	0.01	0.02	0.24	0.04
<i>Desmodium sessilifolium</i>	0.01	0.01	-	0.09	0.02	0.02	-	0.00
<i>Lespedeza capitata</i>	0.96	1.64	0.22	3.54	0.48	0.68	1.02	0.19
<i>Lespedeza violacea</i>	3.90	13.87	0.71	5.89	4.91	17.22	3.44	27.35
<i>Lespedeza x manniana</i>	-	-	-	-	-	0.05	-	-
<i>Mimosa quadrivalvis</i>	0.22	0.05	0.07	0.22	0.16	0.25	0.08	0.16
<i>Pedimelum argophyllum</i>	-	-	0.14	0.15	0.05	0.19	0.20	0.45
<i>Pedimelum esculentum</i>	-	-	0.00	0.00	0.00	-	0.00	0.00
<i>Pedimelum tenuiflorum</i>	0.08	0.04	0.25	0.20	0.20	0.19	0.08	0.10
<i>Strophostyles leiosperma</i>	0.04	-	0.03	0.00	0.00	-	0.00	-
<i>Vicia americana</i>	-	-	-	-	0.02	-	0.01	0.00
Total	10.41	18.34	6.03	15.31	10.22	20.67	9.23	31.78
Introduced								
<i>Bromus inermis</i>	-	-	0.72	0.91	-	-	0.00	-
<i>Chenopodium album</i>	0.00	-	-	-	-	-	-	-
<i>Lactuca saligna</i>	-	-	-	0.00	-	-	-	-
<i>Lactuca serriola</i>	-	-	0.03	-	0.00	-	-	-
<i>Lepidium densiflorum</i>	0.01	-	0.05	0.00	-	-	-	-
<i>Melilotus officinalis</i>	-	-	-	-	-	-	0.01	-
<i>Poa pratensis</i>	0.98	-	4.47	2.40	2.08	0.17	0.36	0.16
<i>Setaria faberi</i>	-	0.00	-	-	-	-	-	-
<i>Taraxacum officinale</i>	-	-	0.00	-	-	-	-	-
<i>Tragopogon dubius</i>	-	-	0.00	-	-	-	-	-
Total	0.99	0.00	5.28	3.31	2.08	0.17	0.38	0.16
Woody								
<i>Ceanothus herbaceus</i>	0.02	0.00	0.00	0.00	0.02	-	0.05	0.01
<i>Cornus drummondii</i>	0.02	0.10	0.00	0.14	0.02	0.23	-	0.01
<i>Prunus americana</i>	-	-	0.04	0.00	-	-	-	-

<i>Rhus glabra</i>	0.50	0.05	1.96	-	-	-	0.76	0.00
<i>Rosa arkansana</i>	0.01	-	0.00	0.10	0.30	0.02	-	0.00
<i>Rubus pensilvanicus</i>	-	-	-	-	-	0.01	-	-
<i>Symphoricarpos orbiculatus</i>	0.05	-	0.20	0.03	0.10	0.01	0.07	0.00
<i>Ulmus americana</i>	-	-	0.01	0.00	-	-	-	-
<i>Ulmus rubra</i>	0.01	0.00	-	-	-	-	-	-
Total	0.61	0.15	2.22	0.27	0.45	0.27	0.88	0.02
Richness	90	69	110	106	91	69	83	80

Table A.7: Relative cover and absences (-) of each species averaged across the first five (1994-98) and last five (2020-24) years within the uplands. Species are categorized into broad functional groups and organized alphabetically. Total indicates the sum relative cover percent of each burn treatment within each functional group.

Uplands	Species	Spring		Summer		Fall		Winter	
		Start	End	Start	End	Start	End	Start	End
Warm-season Graminoids									
	<i>Andropogon gerardii</i>	27.80	38.14	27.00	29.04	32.63	28.42	26.40	26.26
	<i>Bouteloua curtipendula</i>	6.83	5.20	1.30	5.36	2.07	0.91	1.45	0.75
	<i>Bouteloua dactyloides</i>	-	-	-	-	-	-	0.00	-
	<i>Bouteloua gracilis</i>	0.16	0.28	0.02	0.09	0.07	0.24	0.25	0.47
	<i>Bouteloua hirsuta</i>	0.00	-	-	-	-	-	-	-
	<i>Cyperus lupulinus</i>	0.08	0.12	0.03	0.07	0.01	0.02	0.03	0.07
	<i>Cyperus x mesochorus</i>	-	-	-	0.00	-	-	-	-
	<i>Digitaria cognata</i>	0.00	-	0.00	0.01	-	-	0.01	-
	<i>Eragrostis spectabilis</i>	0.49	0.35	0.02	0.06	0.03	0.17	0.13	0.31
	<i>Muhlenbergia cuspidata</i>	0.11	-	0.00	0.01	0.09	0.03	0.00	0.01
	<i>Panicum virgatum</i>	2.22	6.09	0.77	0.53	1.27	2.20	2.70	3.61
	<i>Schizachyrium scoparium</i>	14.37	14.85	1.90	9.32	11.34	24.92	13.81	29.04
	<i>Sorghastrum nutans</i>	13.49	14.20	5.79	6.92	6.90	6.50	11.75	5.48
	<i>Sporobolus compositus</i>	3.22	0.43	2.15	2.73	1.58	0.69	2.10	1.33
	<i>Sporobolus heterolepis</i>	1.66	0.13	1.57	1.36	1.68	1.37	0.80	0.99
	Total	70.44	79.79	40.54	55.51	57.65	65.49	59.44	68.30
Cool-season Graminoids									
	<i>Agrostis hyemalis</i>	0.00	-	-	-	0.01	-	0.00	-
	<i>Carex austrina</i>	-	-	-	0.05	-	-	-	-
	<i>Carex brevior</i>	0.10	0.02	0.14	0.14	0.34	0.03	0.87	0.02
	<i>Carex gravida</i>	0.00	-	0.08	0.01	0.04	-	0.08	0.01
	<i>Carex inops</i>	0.27	0.43	0.43	12.06	0.19	10.18	0.24	9.27
	<i>Carex meadii</i>	0.09	0.17	0.46	1.24	1.36	0.56	0.51	0.37
	<i>Carex spp.</i>	2.30	-	3.63	-	3.03	-	3.63	-
	<i>Dichanthelium oligosanthes</i>	2.64	0.44	2.46	1.55	2.30	0.94	3.91	1.79
	<i>Dichanthelium ovale</i>	0.08	0.01	0.01	0.05	0.31	0.10	-	-
	<i>Elymus canadensis</i>	0.02	-	0.02	0.00	0.01	-	0.04	-
	<i>Hesperostipa spartea</i>	-	-	-	0.04	-	-	-	-
	<i>Hordeum pusillum</i>	0.00	-	-	-	-	-	-	-
	<i>Koeleria macrantha</i>	0.52	0.01	0.45	1.68	4.31	2.61	1.88	2.66
	<i>Sphenopholis obtusata</i>	-	-	-	-	0.01	-	-	-
	<i>Vulpia octoflora</i>	-	-	-	0.05	-	-	-	-
	Total	6.02	1.09	7.68	16.87	11.90	14.42	11.16	14.11
Non-Legume Forbs									
	<i>Achillea millefolium</i>	0.16	0.01	0.33	0.10	0.28	0.03	0.39	0.06
	<i>Agalinis aspera</i>	-	-	-	0.00	-	-	-	-
	<i>Ambrosia psilostachya</i>	0.99	1.38	0.48	0.13	1.68	2.50	2.56	1.39
	<i>Androsace occidentalis</i>	-	-	-	0.00	-	-	-	-
	<i>Antennaria neglecta</i>	0.05	-	0.07	0.05	0.02	0.09	0.05	0.10
	<i>Artemisia ludoviciana</i>	0.36	0.01	2.62	2.86	0.92	0.91	2.34	0.35
	<i>Asclepias lanuginosa</i>	-	-	-	-	-	0.01	-	0.01
	<i>Asclepias stenophylla</i>	0.03	0.05	0.03	0.05	0.11	0.05	0.18	0.11
	<i>Asclepias syriaca</i>	-	-	0.02	-	0.00	-	-	-
	<i>Asclepias tuberosa</i>	-	-	-	-	-	-	0.08	0.01
	<i>Asclepias verticillata</i>	0.16	1.40	0.02	0.03	0.16	0.08	0.35	0.12
	<i>Asclepias viridiflora</i>	0.16	0.09	0.09	0.04	0.13	0.08	0.06	0.03
	<i>Asclenias viridis</i>	0.33	0.17	0.35	0.11	0.22	0.12	0.45	0.11

<i>Brickellia eupatorioides</i>	1.57	0.15	0.27	0.63	0.69	0.15	1.18	0.18
<i>Callirhoe involucrata</i>	-	-	0.03	0.03	-	-	0.03	-
<i>Cirsium altissimum</i>	0.00	-	0.03	0.02	0.02	-	0.00	-
<i>Cirsium undulatum</i>	0.03	0.03	0.10	0.23	0.15	0.01	0.01	0.04
<i>Comandra umbellata</i>	0.12	0.25	-	-	-	-	-	-
<i>Conyza canadensis</i>	-	-	0.00	0.01	-	-	-	-
<i>Croton monanthogynus</i>	-	-	0.00	-	0.00	-	-	-
<i>Cuscuta glomerata</i>	-	0.00	-	-	-	-	-	-
<i>Delphinium carolinianum</i>	0.00	-	0.01	0.03	0.00	-	-	-
<i>Descurainia pinnata</i>	-	-	-	0.00	-	-	-	-
<i>Draba cuneifolia</i>	-	-	-	0.00	-	-	-	-
<i>Draba reptans</i>	-	-	0.00	0.00	-	-	-	-
<i>Echinacea angustifolia</i>	0.02	0.01	0.01	0.06	0.01	0.01	0.01	0.01
<i>Erigeron strigosus</i>	0.10	0.03	0.00	0.22	0.02	0.00	0.04	0.02
<i>Eupatorium altissimum</i>	-	-	0.07	-	-	-	0.02	-
<i>Euphorbia glyptosperma</i>	0.01	0.03	-	-	0.00	-	0.00	-
<i>Euphorbia marginata</i>	0.00	-	0.02	0.00	0.01	-	0.01	0.00
<i>Euphorbia nutans</i>	-	-	-	-	-	-	0.00	-
<i>Euphorbia serpens</i>	0.04	-	0.00	-	0.00	-	0.00	-
<i>Euphorbia spathulata</i>	-	-	0.06	0.04	0.00	-	0.00	-
<i>Geranium carolinianum</i>	-	-	-	-	0.00	-	-	-
<i>Hedeoma hispida</i>	-	-	0.00	0.01	0.00	-	-	-
<i>Hieracium longipilum</i>	-	-	0.01	0.01	0.04	-	0.01	-
<i>Hybanthus verticillatus</i>	0.06	0.05	-	-	-	-	-	-
<i>Hymenopappus scabiosaeus</i>	-	-	0.06	0.01	-	-	-	-
<i>Liatris punctata</i>	0.01	-	-	0.06	-	-	-	-
<i>Linum sulcatum</i>	0.10	-	0.10	0.25	0.08	0.05	0.11	0.06
<i>Lithospermum incisum</i>	0.00	-	0.04	0.06	0.01	0.01	0.01	0.01
<i>Lomatium foeniculaceum</i>	0.60	0.00	0.29	0.17	0.46	0.12	0.02	-
<i>Mirabilis albida</i>	0.02	0.02	-	0.00	0.01	0.01	-	0.00
<i>Mirabilis linearis</i>	-	-	0.00	-	-	-	-	-
<i>Nothocalais cuspidata</i>	-	-	-	-	0.01	-	-	-
<i>Oenothera curtiflora</i>	-	-	0.01	-	-	-	-	-
<i>Oenothera macrocarpa</i>	-	-	0.01	-	-	-	-	-
<i>Oenothera serrulata</i>	-	-	-	0.01	-	0.01	-	-
<i>Oenothera speciosa</i>	-	-	0.02	0.01	-	-	-	-
<i>Oxalis dillenii</i>	-	-	-	0.03	-	-	-	0.00
<i>Oxalis stricta</i>	0.07	-	0.04	-	0.06	-	0.01	-
<i>Oxalis violacea</i>	-	-	0.00	-	-	-	-	-
<i>Packera plattensis</i>	0.03	-	0.03	0.11	0.08	0.03	0.00	0.00
<i>Penstemon cobaea</i>	0.00	0.00	0.00	0.04	-	-	-	-
<i>Physalis heterophylla</i>	-	0.00	-	-	-	-	0.00	-
<i>Physalis pumila</i>	0.55	0.17	1.72	0.31	0.64	0.13	0.73	0.05
<i>Physalis virginiana</i>	-	0.24	-	0.22	-	0.08	-	0.05
<i>Plantago rhodosperma</i>	0.00	-	-	-	-	-	-	-
<i>Plantago virginica</i>	-	-	-	0.02	-	-	-	-
<i>Ratibida columnifera</i>	0.00	0.00	0.02	0.09	0.09	-	0.09	0.06
<i>Ruellia humilis</i>	0.43	0.41	0.57	0.30	0.45	0.25	0.39	0.23
<i>Salvia azurea</i>	4.75	0.73	1.49	1.39	3.35	1.37	3.93	1.30
<i>Silene antirrhina</i>	-	-	0.08	0.11	0.00	-	0.00	-
<i>Sisyrinchium campestre</i>	0.05	0.00	0.06	0.13	0.14	0.13	0.19	0.15
<i>Solanum carolinense</i>	-	-	0.00	0.00	-	-	-	-
<i>Solidago altissima</i>	-	-	0.04	0.01	-	-	0.02	-
<i>Solidago missouriensis</i>	1.02	0.75	1.28	2.19	0.61	0.21	1.56	0.51
<i>Solidago mollis</i>	-	-	-	0.01	-	-	-	-
<i>Solidago rigida</i>	-	0.01	-	0.02	0.01	0.04	0.01	0.00

<i>Solidago speciosa</i>	-	-	0.00	0.01	-	-	-	0.00
<i>Spermolepis inermis</i>	-	-	0.07	0.09	-	-	0.00	-
<i>Spiranthes vernalis</i>	-	-	-	-	-	0.00	-	0.00
<i>Stenaria nigricans</i>	0.08	0.00	-	-	-	-	-	-
<i>Symphyotrichum ericoides</i>	1.94	1.71	8.25	3.57	6.34	2.50	6.08	4.40
<i>Symphyotrichum oblongifolium</i>	1.83	3.56	1.58	2.41	5.95	3.58	4.44	4.09
<i>Symphyotrichum sericeum</i>	0.13	0.03	0.47	0.11	0.62	0.09	0.29	0.07
<i>Teucrium canadense</i>	-	-	0.00	0.01	-	-	-	-
<i>Tragia betonicifolia</i>	0.62	0.47	0.76	0.13	0.43	0.31	0.13	0.07
<i>Tragia ramosa</i>	-	0.05	-	0.08	-	0.02	-	0.01
<i>Triodanis leptocarpa</i>	-	-	-	0.01	-	-	-	-
<i>Triodanis perfoliata</i>	0.00	-	0.01	0.01	0.00	-	-	-
<i>Verbena stricta</i>	-	-	0.00	-	0.00	-	0.00	-
<i>Vernonia baldwinii</i>	0.27	0.27	0.68	0.25	0.33	0.21	0.40	0.22
<i>Viola bicolor</i>	-	-	0.01	0.00	-	-	-	-
<i>Viola nephrophylla</i>	-	-	0.03	-	-	-	-	-
<i>Viola pedatifida</i>	0.06	0.00	0.01	0.01	0.00	0.00	-	-
Total	16.76	12.09	22.40	16.91	24.14	13.19	26.18	13.84
Legumes								
<i>Amorpha canescens</i>	2.98	1.90	2.29	2.83	2.45	2.73	0.51	0.53
<i>Astragalus crassicaupus</i>	0.01	-	0.08	0.34	0.02	0.05	0.36	0.47
<i>Baptisia australis</i>	0.44	0.43	0.11	0.13	0.12	0.27	0.08	0.07
<i>Baptisia bracteata</i>	-	-	0.58	0.62	0.33	0.61	0.41	0.52
<i>Dalea candida</i>	0.09	0.14	0.06	0.07	0.07	0.07	0.12	0.15
<i>Dalea multiflora</i>	0.11	-	0.04	-	0.04	-	0.03	-
<i>Dalea purpurea</i>	0.80	0.29	0.34	0.24	0.34	0.30	0.33	0.17
<i>Desmodium illinoense</i>	0.01	0.01	0.04	0.03	0.04	0.03	-	0.02
<i>Desmodium sessilifolium</i>	0.01	-	-	0.01	-	-	-	-
<i>Lespedeza capitata</i>	0.06	0.17	0.24	0.97	0.09	0.55	0.21	0.36
<i>Lespedeza violacea</i>	0.00	0.14	0.02	1.67	-	0.09	-	0.05
<i>Mimosa quadrivalvis</i>	0.96	1.82	0.42	0.59	0.55	1.19	0.39	1.10
<i>Pedimelum esculentum</i>	0.03	0.00	0.08	0.10	0.03	0.02	0.01	0.02
<i>Pedimelum tenuiflorum</i>	0.33	0.18	0.05	0.12	0.46	0.86	0.00	0.03
<i>Strophostyles leiosperma</i>	-	-	-	-	-	-	0.00	-
Total	5.82	5.07	4.36	7.70	4.54	6.77	2.44	3.48
Introduced								
<i>Bromus arvensis</i>	-	-	-	0.00	-	-	-	-
<i>Bromus inermis</i>	0.00	-	0.24	0.12	-	-	-	-
<i>Lactuca serriola</i>	-	-	-	-	0.00	-	0.00	-
<i>Lepidium densiflorum</i>	0.00	-	0.15	0.05	0.17	-	0.00	-
<i>Melilotus officinalis</i>	-	-	0.00	-	-	-	-	-
<i>Poa pratensis</i>	0.46	-	11.96	1.08	1.43	0.01	0.43	0.02
<i>Securigera varia</i>	-	-	-	0.44	-	-	-	-
<i>Tragopogon dubius</i>	-	-	0.00	0.01	-	-	-	-
Table	0.46	0.00	12.35	1.71	1.61	0.01	0.44	0.02
Woody								
<i>Ceanothus herbaceus</i>	0.45	0.47	0.79	1.17	0.15	0.12	0.18	0.25
<i>Cornus drummondii</i>	-	-	0.05	0.05	-	-	-	-
<i>Rhus glabra</i>	0.05	1.48	11.41	0.05	-	-	0.15	0.00
<i>Rosa arkansana</i>	-	-	0.02	0.01	0.00	0.01	-	-
<i>Rubus pensilvanicus</i>	-	-	-	-	-	-	0.01	-
<i>Symphoricarpos orbiculatus</i>	-	-	0.41	0.02	-	-	-	-
Table	0.49	1.96	12.67	1.30	0.15	0.13	0.35	0.25
Richness	84	63	103	110	85	66	84	68

Table A.8. PERMANOVA results showing the effects of burn season, topographic position, and their interactions on community composition based on Bray-Curtis Dissimilarity. Results are provided for the full study period (1994-2024).

NMDS Adonis2					
	Df	Sum Sq	R ²	F value	Pr(>F)
Burn Season (BS)	3	4.53	0.26	132.05	<0.001
Topography (T)	1	7.13	0.41	623.66	<0.001
Year (Y)	1	1.11	0.06	97.26	<0.001
BS * T	3	1.07	0.06	31.35	<0.001
BS * Y	3	0.50	0.03	14.51	<0.001
T * Y	1	0.24	0.01	20.63	<0.001
BS * T * Y	3	0.12	0.01	3.58	<0.001
Residuals	232	2.65	0.15		
Total	247	17.34	1.00		

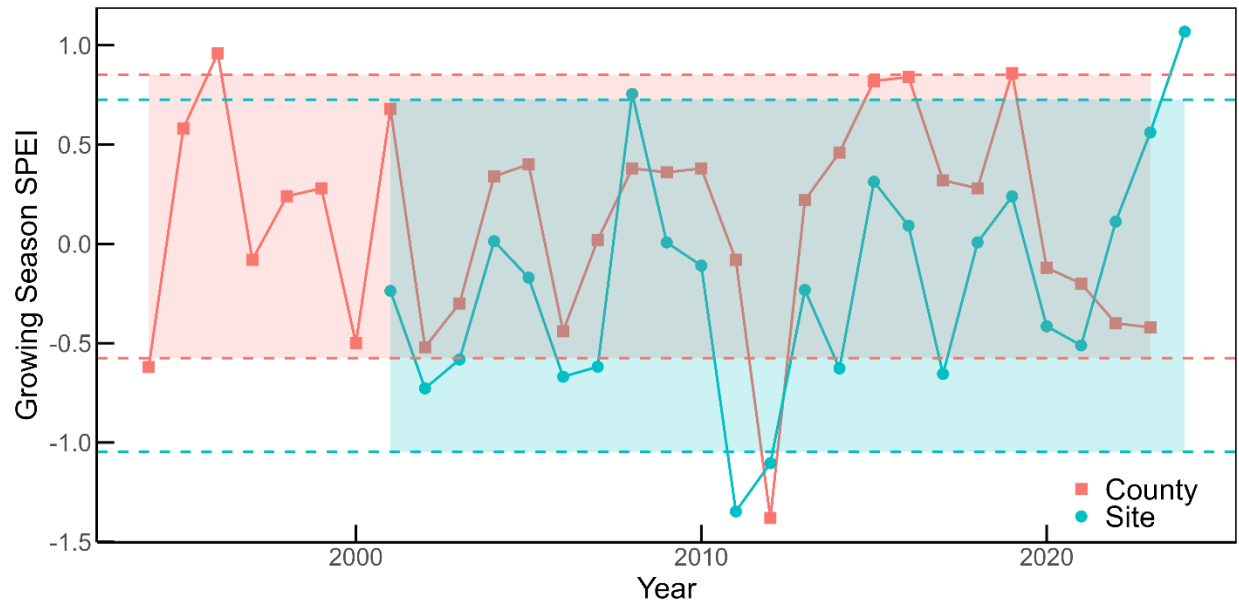


Figure A.1: Changes in one-month Standardized Precipitation-Evapotranspiration Index (SPEI). Site data represents SPEI values calculated from Environmental Data Initiative (Nippert, 2025; Moore, 2025) records at KPBS (2001-2024), while county data represent SPEI values obtained from the Climate Data Guide (1994-2023) (Schneider et al., 2013). Each point represents the annual mean during the growing season (May - September). Dashed lines indicate the 5th and 95th percentiles for each dataset.

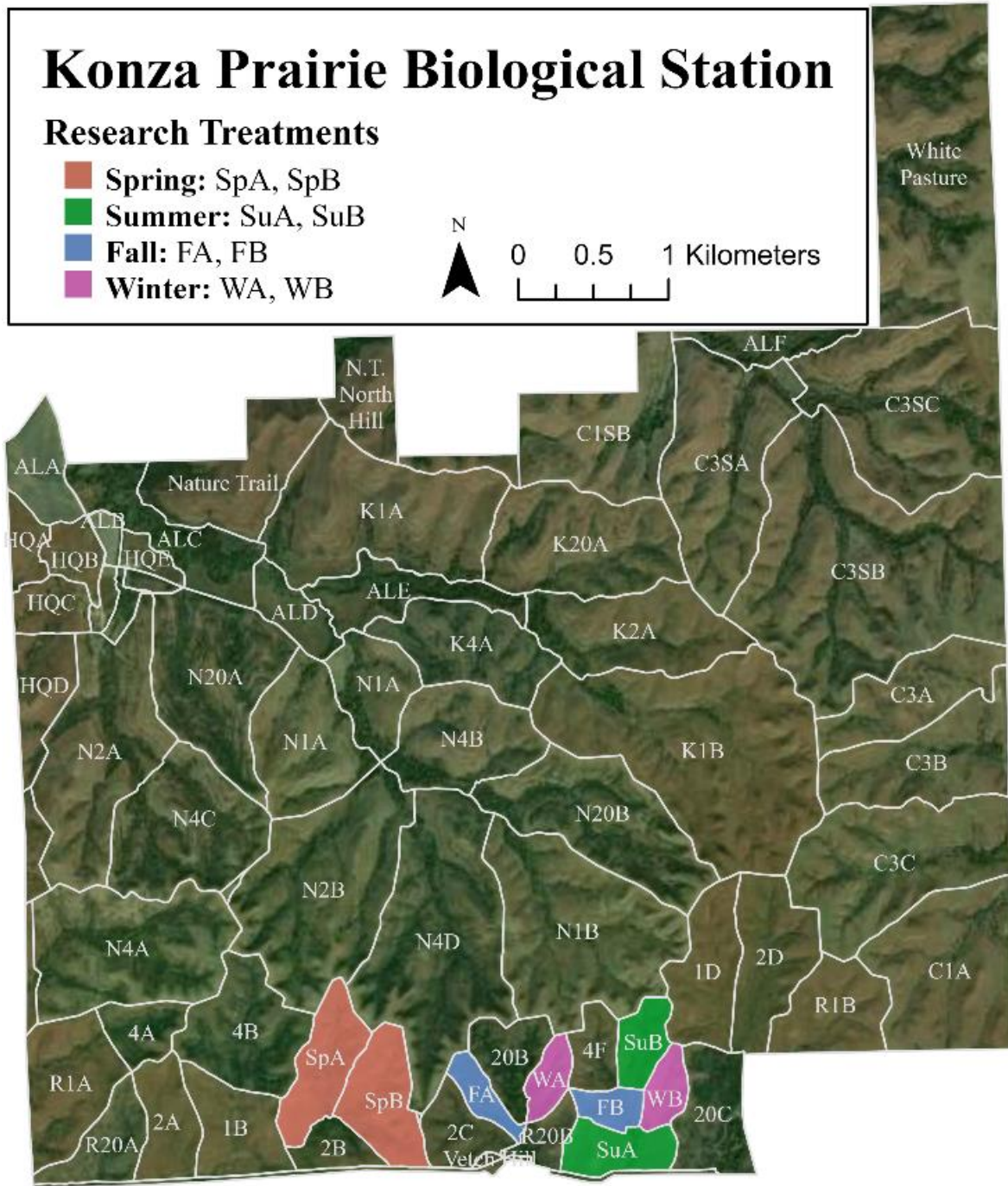


Figure A.2: Site map of the different watersheds, spring, summer, fall, and winter located at Konza Prairie Biological Station.

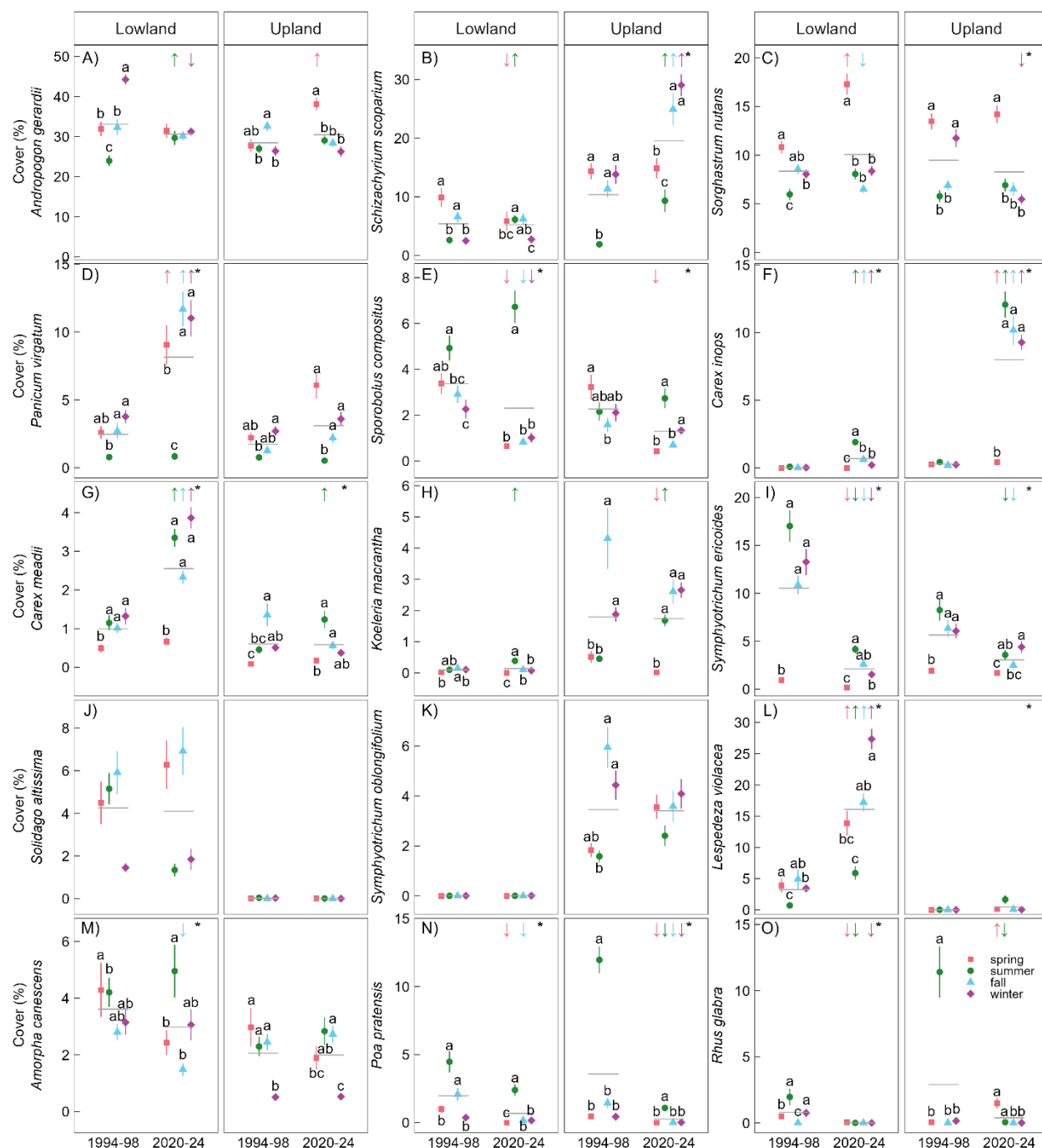


Figure A.3: Five year averages of relative cover for *Andropogon gerardii* (A), *Schizachyrium scoparium* (B), *Sorghastrum nutans* (C), *Panicum virgatum* (D), *Sporobolus compositus* (E), *Carex inops* (F), *Carex meadii* (G), *Koeleria macrantha* (H), *Symphyotrichum ericoides* (I), *Solidago altissima* (J), *Symphyotrichum oblongifolium* (K), *Lespedeza violacea* (L), *Amorpha canescens* (M), *Poa pratensis* (N), *Rhus glabra* (O), in the lowlands and uplands under contrasting burn regimes. Within year differences denoted by different letters, differences over time within burn season are indicated by a directional arrow, and overall difference over time (*). Note differences in scale for cover among different plant species.

REFERENCES

- Moore, T. 2025. *AET01 Konza prairie grass reference evapotranspiration*, ver. 11. Environmental Data Initiative.
<https://doi.org/10.6073/pasta/c60dda305cbfe99e97d71b723ad5842c> (accessed 22 October 2025).
- Nippert, J. 2025. *AWE01 Meteorological data from the Konza prairie headquarters weather station*, ver. 24. Environmental Data Initiative.
<https://doi.org/10.6073/pasta/a267f9b0995f6fa91340ba5886ee2273> (accessed 22 October 2025)
- Schneider, D. P., C. Deser, J. Fasullo, and K. E. Trenberth. 2013: “Climate Data Guide Spurs Discovery and Understanding.” *Eos Trans. AGU* 94: 121–122,
<https://doi.org/10.1002/2013eo130001>.

Appendix B - Chapter 3 supplementary material

Table B.1: Estimated annual trends in aboveground net primary productivity (ANPP) across the 30-year period for each burn season $\times$ topographic position combination. Slope (β) were derived from linear mixed models using *emtrends* and are expressed in $\text{g m}^{-2} \text{y}^{-1}$. Forbs were square-root transformed.

Burn Season	Topographic Position	Functional Group	(β)	95% CI	df	t	p-value
spring	Lowland	Graminoids	1.540	[-0.13, 3.21]	1846	1.808	0.0699
summer	Lowland	Graminoids	3.265	[1.60, 4.93]	1846	3.833	< 0.001
fall	Lowland	Graminoids	3.561	[1.89, 5.23]	1846	4.179	< 0.001
winter	Lowland	Graminoids	4.065	[2.40, 5.73]	1846	4.772	< 0.001
spring	Upland	Graminoids	1.518	[-0.15, 3.18]	1846	1.781	0.0741
summer	Upland	Graminoids	2.111	[0.45, 3.78]	1846	2.478	0.0130
fall	Upland	Graminoids	2.283	[0.62, 3.95]	1846	2.576	0.0073
winter	Upland	Graminoids	2.804	[1.14, 4.47]	1846	3.291	0.0010
spring	Lowland	Forbs	0.090	[0.06, 0.12]	1846	5.452	< 0.001
summer	Lowland	Forbs	-0.038	[-0.07, -0.01]	1846	-3.001	0.0089
fall	Lowland	Forbs	0.082	[0.05, 0.11]	1846	5.837	< 0.001
winter	Lowland	Forbs	0.045	[0.02, 0.07]	1846	3.105	0.0017
spring	Upland	Forbs	-0.005	[-0.03, 0.02]	1846	-0.636	0.7129
summer	Upland	Forbs	-0.016	[-0.04, 0.01]	1846	-1.170	0.2825
fall	Upland	Forbs	-0.058	[-0.09, -0.03]	1846	-2.513	< 0.001
winter	Upland	Forbs	-0.065	[-0.09, -0.04]	1846	-3.250	< 0.001
spring	Lowland	Herbaceous	2.846	[1.16, 4.53]	1846	3.300	< 0.001
summer	Lowland	Herbaceous	2.547	[0.86, 4.23]	1846	2.953	0.0031
fall	Lowland	Herbaceous	4.958	[3.27, 6.64]	1846	5.749	< 0.001
winter	Lowland	Herbaceous	4.809	[3.12, 6.49]	1846	5.576	< 0.001
spring	Upland	Herbaceous	1.365	[-0.32, 3.05]	1846	1.583	0.1122
summer	Upland	Herbaceous	1.831	[0.15, 3.52]	1846	2.123	0.0332
fall	Upland	Herbaceous	1.690	[0.01, 3.38]	1846	1.847	0.0493
winter	Upland	Herbaceous	2.025	[0.34, 3.71]	1846	2.348	0.0185

Table B.2: Summary statistics of ANOVA from linear mixed-effects models evaluating the effects of burn season, topographical position, and growing-season precipitation on graminoids, forbs, and total herbaceous aboveground productivity. All response variables were square-root transformed prior to analysis.

Factor	Fun Group	Sum Sq	Mean Sq	DenDF	F value	Pr(>F)
Burn Season (BS)	Graminoids	127.81	42.60	3, 4	7.99	0.0365
Topography (T)	Graminoids	885.86	885.86	1, 52	166.05	< 0.001
Precipitation (P)	Graminoids	4251.32	4251.32	1, 1846	796.89	< 0.001
BS:T	Graminoids	37.75	12.58	3, 52	2.36	0.0822
BS:P	Graminoids	14.80	4.93	3, 1846	0.92	0.4280
T:P	Graminoids	1.40	1.40	1, 1846	0.26	0.6079
BS:T:P	Graminoids	8.56	2.85	3, 1846	0.53	0.6584
Burn Season (BS)	Forbs	97.46	32.49	3, 4	8.23	0.0347
Topography (T)	Forbs	343.10	343.10	1, 52	86.91	< 0.001
Precipitation (P)	Forbs	57.33	57.33	1, 1846	14.52	< 0.001
BS:T	Forbs	7.04	2.35	3, 52	0.59	0.6217
BS:P	Forbs	27.63	9.21	3, 1846	2.33	0.0723
T:P	Forbs	2.30	2.30	1, 1846	0.58	0.4452
BS:T:P	Forbs	17.85	5.95	3, 1846	1.51	0.2107
Burn Season (BS)	Total	53.03	17.68	3, 4	3.75	0.1171
Topography (T)	Total	1188.81	1188.81	1, 52	252.20	< 0.001
Precipitation (P)	Total	4077.65	4077.65	1, 1846	865.05	< 0.001
BS:T	Total	34.13	11.38	3, 52	2.41	0.0771
BS:P	Total	2.02	0.67	3, 1846	0.14	0.9344
T:P	Total	0.79	0.79	1, 1846	0.17	0.6814
BS:T:P	Total	3.10	1.03	3, 1846	0.22	0.8831

Table B.3: Estimated slopes of aboveground net primary productivity (ANPP) in response to growing-season precipitation. Slopes (β) were derived from simple linear models for each combination of burn season and topographic position and are expressed in $\text{g m}^{-2} \text{mm}^{-1}$.

Burn Season	Topographic Position		Slope (β)	95% CI	df	t	r²	p-value
spring	Lowland	Graminoids	0.46	[0.34, 0.58]	238	7.34	0.18	< 0.001
summer	Lowland	Graminoids	0.49	[0.40, 0.58]	238	11.17	0.34	< 0.001
fall	Lowland	Graminoids	0.48	[0.37, 0.59]	238	8.87	0.25	< 0.001
winter	Lowland	Graminoids	0.49	[0.38, 0.61]	238	8.72	0.24	< 0.001
spring	Upland	Graminoids	0.41	[0.34, 0.49]	238	10.77	0.32	< 0.001
summer	Upland	Graminoids	0.38	[0.30, 0.46]	238	9.37	0.27	< 0.001
fall	Upland	Graminoids	0.36	[0.28, 0.45]	236	8.23	0.22	< 0.001
winter	Upland	Graminoids	0.41	[0.33, 0.49]	238	10.25	0.30	< 0.001
spring	Lowland	Forbs	0.03	[-0.02, 0.08]	238	1.27	0.00	0.2063
summer	Lowland	Forbs	-0.01	[-0.05, 0.03]	238	-0.60	0.00	0.5496
fall	Lowland	Forbs	0.05	[0.00, 0.09]	238	2.04	0.01	0.0421
winter	Lowland	Forbs	0.03	[-0.01, 0.07]	238	1.32	0.00	0.1883
spring	Upland	Forbs	0.00	[-0.02, 0.01]	238	-0.10	0.00	0.9237
summer	Upland	Forbs	0.01	[-0.02, 0.03]	238	0.42	0.00	0.6734
fall	Upland	Forbs	0.02	[0.00, 0.04]	236	2.11	0.01	0.0355
winter	Upland	Forbs	0.01	[-0.01, 0.03]	238	1.36	0.00	0.1739
spring	Lowland	Total	0.49	[0.36, 0.62]	238	7.46	0.19	< 0.001
summer	Lowland	Total	0.48	[0.39, 0.56]	238	10.98	0.33	< 0.001
fall	Lowland	Total	0.53	[0.42, 0.64]	238	9.33	0.26	< 0.001
winter	Lowland	Total	0.52	[0.40, 0.64]	238	8.82	0.24	< 0.001
spring	Upland	Total	0.41	[0.34, 0.49]	238	11.21	0.34	< 0.001
summer	Upland	Total	0.39	[0.31, 0.46]	238	9.61	0.28	< 0.001
fall	Upland	Total	0.38	[0.30, 0.47]	236	8.89	0.25	< 0.001
winter	Upland	Total	0.43	[0.35, 0.51]	238	10.75	0.32	< 0.001

Table B.4: Summary statistics of growing and annual precipitation from 1994 to 2024.

Response	Effect	DF	Sum.Sq	Mean.Sq	F value	Pr(>F)
Growing Season Precipitation	Year	1	77	76.7	0.0037	0.9517
	Residuals	29	596423	20566.3		
Annual Precipitation	Year	1	2626	2625.8	0.11	0.7425
	Residuals	29	692020	23862.8		

Table B.5: ANOVA results from linear mixed-effects models for graminoid, forb, and total productivity between years classified as “burned” and “unburned.” Models were fit separately for each burn season to evaluate the effects of burn category (burned vs. unburned), topographic position, and year. Burn classifications are defined by the occurrence of summer fire and applied consistently across all models. Forb productivity was square-root transformed prior to analysis..

SUMMER					
Effect	Fun Group	Sum Sq.	df_n, df_d	F value	Pr(>F)
Burned / Non-burned (BN)	Graminoids	736594.58	1, 461	79.51	< 0.001
Topographic Position (TP)	Graminoids	272543.40	1, 13	29.42	< 0.001
Year (Y)	Graminoids	374374.28	1, 461	40.41	< 0.001
BN x TP	Graminoids	6230.32	1, 461	0.67	0.4126
Burned / Non-burned (BN)	Forbs	0.19	1, 461	0.05	0.8318
Topographic Position (TP)	Forbs	168.19	1, 14	40.21	< 0.001
Year (Y)	Forbs	24.66	1, 461	5.89	0.0156
BN x TP	Forbs	8.00	1, 461	1.91	0.1674
Burned / Non-burned (BN)	Total	706439.96	1, 461	76.21	< 0.001
Topographic Position (TP)	Total	536709.31	1, 13	57.90	< 0.001
Year (Y)	Total	265923.90	1, 461	28.69	< 0.001
BN x TP	Total	1758.12	1, 461	0.19	0.6634
FALL					
Effect	Fun Group	Sum Sq.	df_n, df_d	F value	Pr(>F)
Burned / Non-burned (BN)	Graminoids	28557.46	1, 459	2.14	0.1438
Topographic Position (TP)	Graminoids	673952.24	1, 14	50.61	< 0.001
Year (Y)	Graminoids	279311.37	1, 459	20.97	< 0.001
BN x TP	Graminoids	8719.60	1, 459	0.65	0.4188
Burned / Non-burned (BN)	Forbs	0.0018	1, 459	0.00	0.9809
Topographic Position (TP)	Forbs	82.42	1, 14	26.01	< 0.001
Year (Y)	Forbs	5.45	1, 459	1.72	0.1905
BN x TP	Forbs	5.83	1, 459	1.84	0.1757
Burned / Non-burned (BN)	Total	31299.95	1, 459	2.15	0.1430
Topographic Position (TP)	Total	2019064.18	1, 13	138.90	< 0.001
Year (Y)	Total	364229.61	1, 459	25.06	< 0.001
BN x TP	Total	3113.09	1, 459	0.21	0.6437
WINTER					
Effect	Fun Group	Sum Sq.	df_n, df_d	F value	Pr(>F)
Burned / Non-burned (BN)	Graminoids	392.94	1, 461	0.03	0.8683
Topographic Position (TP)	Graminoids	1751215.46	1, 14	122.71	< 0.001
Year (Y)	Graminoids	420862.22	1, 461	29.49	< 0.001
BN x TP	Graminoids	15902.55	1, 461	1.11	0.2917
Burned / Non-burned (BN)	Forbs	0.03	1, 461	0.01	0.9262
Topographic Position (TP)	Forbs	74.82	1, 14	21.26	< 0.001
Year (Y)	Forbs	3.46	1, 461	0.98	0.3221
BN x TP	Forbs	2.86	1, 461	0.81	0.3680
Burned / Non-burned (BN)	Total	440.72	1, 461	0.03	0.8631

Topographic Position (TP)	Total	1856642.79	1, 14	125.41	< 0.001
Year (Y)	Total	416801.91	1, 461	28.15	< 0.001
BN x TP	Total	11983.76	1, 461	0.81	0.3687
SPRING					
Effect	Fun Group	Sum Sq.	df_n, df_d	F value	Pr(>F)
Burned / Non-burned (BN)	Graminoids	8839.89	1, 461	0.66	0.4174
Topographic Position (TP)	Graminoids	325380.90	1, 14	24.25	< 0.001
Year (Y)	Graminoids	76224.10	1, 461	5.68	0.0175
BN x TP	Graminoids	24386.74	1, 461	1.82	0.1783
Burned / Non-burned (BN)	Forbs	16.97	1, 461	3.48	0.0629
Topographic Position (TP)	Forbs	78.61	1, 14	16.11	0.0015
Year (Y)	Forbs	72.60	1, 461	14.88	< 0.001
BN x TP	Forbs	4.51	1, 461	0.92	0.3371
Burned / Non-burned (BN)	Total	6800.63	1, 461	0.51	0.4740
Topographic Position (TP)	Total	388679.03	1, 14	29.34	< 0.001
Year (Y)	Total	149018.80	1, 461	11.25	< 0.001
BN x TP	Total	41937.47	1, 461	3.17	0.0759

Table B.6: ANOVA results from linear mixed-effects models evaluating the effects of burn season, topographic position, and year on graminoid, forb, and total productivity. Models were analyzed separately for burned and unburned years. Forb biomass was square-root transformed prior to analysis.

(Years categorized as “burned”)						
Graminoids						
Factor	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
Burn Season (BS)	102429.36	34143.12	3	4	3.32	0.1384
Topography (T)	1745064.76	1745064.76	1	52	169.61	< 0.001
Year (Y)	1528516.55	1528516.55	1	950	148.56	< 0.001
BS:T	103899.83	34633.28	3	52	3.37	0.0254
BS:Y	79949.33	26649.78	3	950	2.59	0.0516
T:Y	114548.54	114548.54	1	950	11.13	< 0.001
BS:T:Y	4807.58	1602.53	3	950	0.16	0.9260
Forbs						
Burn Season (BS)	97.91	32.64	3	56	9.51	< 0.001
Topography (T)	278.91	278.91	1	56	81.25	< 0.001
Year (Y)	2.25	2.25	1	950	0.66	0.4185
BS:T	6.78	2.26	3	56	0.66	0.5809
BS:Y	38.84	12.95	3	950	3.77	0.0104
T:Y	115.72	115.72	1	950	33.71	< 0.001
BS:T:Y	80.53	26.84	3	950	7.82	< 0.001
Herbaceous						
Burn Season (BS)	38077.75	12692.58	3	4	1.24	0.4067
Topography (T)	2497075.61	2497075.61	1	52	243.11	< 0.001
Year (Y)	1620759.48	1620759.48	1	950	157.80	< 0.001
BS:T	110875.34	36958.45	3	52	3.60	0.0194
BS:Y	39456.85	13152.28	3	950	1.28	0.2798
T:Y	243808.49	243808.49	1	950	23.74	< 0.001
BS:T:Y	10215.15	3405.05	3	950	0.33	0.8026
(Years categorized as “not burned”)						
Graminoids						
Factor	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
Burn Season (BS)	988587.82	329529.27	3	4	21.98	0.0060
Topography (T)	1982115.00	1982115.00	1	52	132.22	< 0.001
Year (Y)	37538.18	37538.18	1	824	2.50	0.1139
BS:T	133134.01	44378.00	3	52	2.96	0.0406
BS:Y	75498.22	25166.07	3	824	1.68	0.1701
T:Y	7619.63	7619.63	1	824	0.51	0.4761
BS:T:Y	20862.00	6954.00	3	824	0.46	0.7076
Forbs						
Burn Season (BS)	69.49	23.16	3	4	5.60	0.0647
Topography (T)	338.94	338.94	1	52	81.94	< 0.001
Year (Y)	1.80	1.80	1	824	0.44	0.5096
BS:T	5.84	1.95	3	52	0.47	0.7043

BS:Y	70.20	23.40	3	824	5.66	< 0.001
T:Y	106.79	106.79	1	824	25.82	< 0.001
BS:T:Y	70.79	23.60	3	824	5.70	< 0.001
Herbaceous						
Burn Season (BS)	524701.72	174900.57	3	4	11.13	0.0207
Topography (T)	3392456.60	3392456.60	1	52	215.86	< 0.001
Year (Y)	47053.93	47053.93	1	824	2.99	0.0840
BS:T	142404.86	47468.29	3	52	3.02	0.0379
BS:Y	81936.08	27312.03	3	824	1.74	0.1577
T:Y	2594.86	2594.86	1	824	0.17	0.6846
BS:T:Y	39061.23	13020.41	3	824	0.83	0.4783

Table B.7: ANOVA results from linear mixed-effects models evaluating the effects burn status (burned versus non-burned), topographical position, and growing season (April – September) precipitation on graminoids, forbs, and total herbaceous aboveground productivity in summer-burned watersheds. Forb productivity was square-root transformed prior to analysis..

Factor	Fun. Group	Sum Sq	Mean Sq	dfn, dfd	F value	Pr(>F)
Burned / Non-burned (BN)	Graminoids	319455.11	319455.11	1, 458	47.07	< 0.001
Topography (T)	Graminoids	201731.76	201731.76	1, 13	29.72	< 0.001
Precipitation (P)	Graminoids	1505182.48	1505182.48	1, 458	221.77	< 0.001
BN:T	Graminoids	2472.07	2472.07	1, 458	0.36	0.5465
BN:P	Graminoids	10436.53	10436.53	1, 458	1.54	0.2156
T:P	Graminoids	25295.32	25295.32	1, 458	3.73	0.0542
BN:T:P	Graminoids	1158.45	1158.45	1, 458	0.17	0.6797
Burned / Non-burned (BN)	Forbs	1.14	1.14	1, 458	0.29	0.5930
Topography (T)	Forbs	155.12	155.12	1, 14	38.96	< 0.001
Precipitation (P)	Forbs	0.91	0.91	1, 458	0.23	0.6337
BN:T	Forbs	5.64	5.64	1, 458	1.42	0.2344
BN:P	Forbs	121.34	121.34	1, 458	30.48	< 0.001
T:P	Forbs	5.05	5.05	1, 458	1.27	0.2606
BN:T:P	Forbs	2.56	2.56	1, 458	0.64	0.4228
Burned / Non-burned (BN)	Total	313076.62	313076.62	1, 458	47.23	< 0.001
Topography (T)	Total	385763.27	385763.27	1, 13	58.20	< 0.001
Precipitation (P)	Total	1472991.28	1472991.28	1, 458	222.23	< 0.001
BN:T	Total	284.17	284.17	1, 458	0.04	0.8361
BN:P	Total	4687.83	4687.83	1, 458	0.71	0.4008
T:P	Total	19163.73	19163.73	1, 458	2.89	0.0897
BN:T:P	Total	1143.06	1143.06	1, 458	0.17	0.6781

Table B.8: Contrasts for estimated slopes of aboveground productivity in response to growing season precipitation within each topographical position in summer watersheds, comparing burned and non-burned years. Estimates represent differences in slopes ($\Delta\beta$; $\text{g m}^{-2} \text{mm}^{-1}$) between burn season pairs. Forb productivity was square-root transformed prior to analysis..

Contrast	Topographic Position	Functional Group	($\Delta\beta$)	SE	df	t	p-value
Burned – Non-burned	Lowland	Graminoids	0.045	0.077	458	0.585	0.5590
Burned – Non-burned	Upland	Graminoids	0.090	0.077	458	1.169	0.2430
Burned – Non-burned	Lowland	Forbs	-0.112	0.032	458	-3.512	< 0.001
Burned – Non-burned	Upland	Forbs	-0.112	0.032	458	-3.522	< 0.001
Burned – Non-burned	Lowland	Herbaceous	-0.067	0.076	458	-0.888	0.3748
Burned – Non-burned	Upland	Herbaceous	-0.023	0.076	458	-0.301	0.7635

Table B.9: ANOVA results for growing-season and annual precipitation based on burn classification (burned versus non-burned) over time.

Response	Effect	DF	Sum. Sq	Mean. Sq	F value	Pr(>F)
Growing Season Precipitation	Year (Y)	1	77	76.7	0.0037	0.9517
	Burned / Non-Burned (BN)	1	18604	18603.7	0.9064	0.3495
	Y:BN	1	23630	23629.8	1.1512	0.2928
	Residuals	27	554189	20525.5		
Annual Precipitation	Year (Y)	1	2626	2626	0.1146	0.7376
	Burned / Non-Burned (BN)	1	28430	28430	1.2403	0.2752
	Y:BN	1	44694	44694	1.9498	0.1740
	Residuals	27	618897	22922		

Table B.10: ANOVA results for soil properties across burn season and topographic positions. Soil variables include pH, base cations (Ca, Mg, Na, K) phosphorus, inorganic nitrogen (ammonium and nitrate), and total carbon and nitrogen (%).

Response	Effect	NumDF	DenDF	Sum.Sq	F value	Pr(>F)
Ca (ppm)	Burn Season (BS)	3	4	315776.51	0.37	0.7783
	Topographic Position (T)	1	52	563850.81	2.00	0.1637
	BS:T	3	52	2225578.04	2.63	0.0601
Mg (ppm)	Burn Season (BS)	3	4	10821.09	1.81	0.2843
	Topographic Position (T)	1	52	137075.81	68.95	< 0.001
	BS:T	3	52	16317.07	2.74	0.0528
K (ppm)	Burn Season (BS)	3	4	5066.04	0.34	0.8014
	Topographic Position (T)	1	52	2836.89	0.56	0.4558
	BS:T	3	52	32050.10	2.13	0.1081
Na (ppm)	Burn Season (BS)	3	4	364.73	2.40	0.2088
	Topographic Position (T)	1	52	76.78	1.51	0.2241
	BS:T	3	52	250.59	1.65	0.1899
pH	Burn Season (BS)	3	4	0.04	0.53	0.6854
	Topographic Position (T)	1	52	0.01	0.42	0.5222
	BS:T	3	52	0.07	0.93	0.4309
C %	Burn Season (BS)	3	4	0.34	0.31	0.8214
	Topographic Position (T)	1	52	0.19	0.50	0.4806
	BS:T	3	52	3.57	3.18	0.0317
N %	Burn Season (BS)	3	4	0.00	0.38	0.7725
	Topographic Position (T)	1	52	0.01	2.59	0.1135
	BS:T	3	52	0.03	3.94	0.0132
NH ₄ (mg/kg)	Burn Season (BS)	3	56	3.40	2.12	0.1077
	Topographic Position (T)	1	56	4.69	8.79	0.0044
	BS:T	3	56	1.78	1.11	0.3519
NO ₃ (mg/kg)	Burn Season (BS)	3	4	8.42	3.08	0.1531
	Topographic Position (T)	1	52	13.59	14.90	< 0.001
	BS:T	3	52	3.10	1.13	0.3445
NO ₃ + NH ₄ (mg/kg)	Burn Season (BS)	3	4	15.33	2.56	0.1925
	Topographic Position (T)	1	52	34.26	17.19	< 0.001
	BS:T	3	52	6.64	1.11	0.3530
PM (ppm)	Burn Season (BS)	3	4	2.94	0.40	0.7609
	Topographic Position (T)	1	52	9.53	3.89	0.0539
	BS:T	3	52	1.61	0.22	0.8824

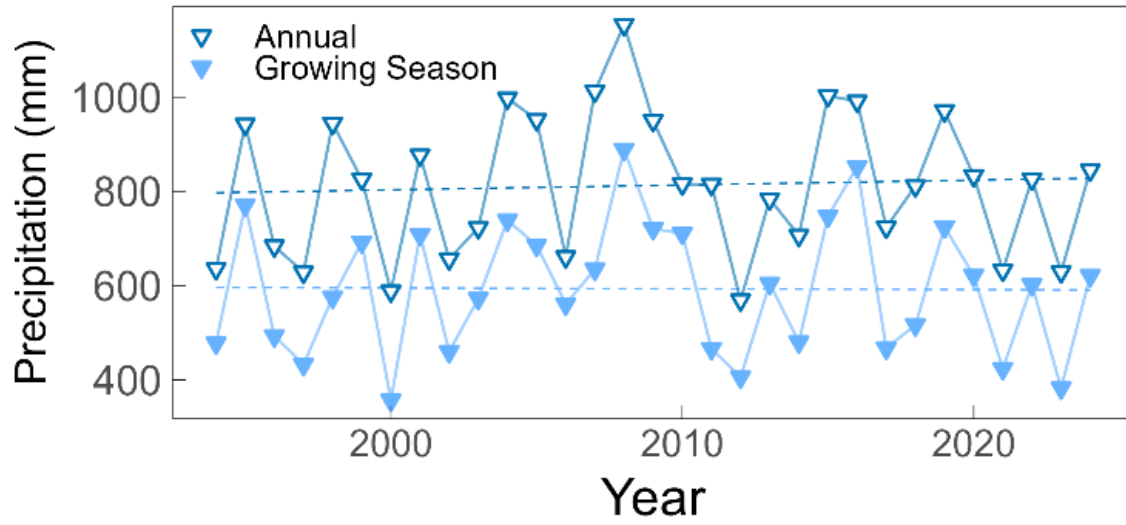


Figure B.1: Growing-season (April – September; filled symbols) and annual (open symbols) precipitation over time. Temporal trends in precipitation were evaluated using separate linear regression models for annual and growing-season precipitation with year as a continuous predictor. Lines indicate linear regression fits; dashed lines denote non-significant trends.

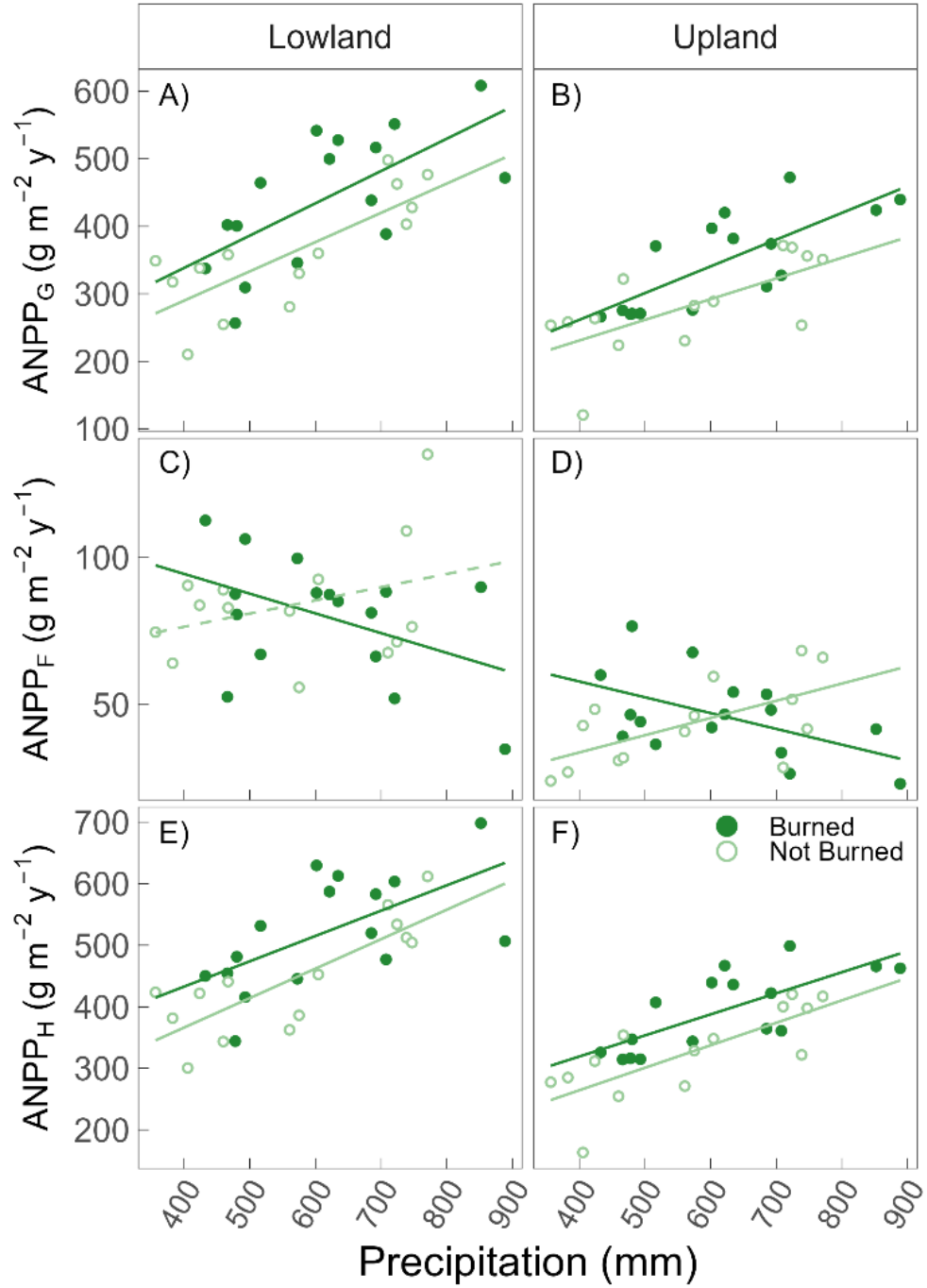


Figure B.2: Regression fit for graminoid, forb, and total herbaceous productivity in summer watersheds separated by whether it was in a burned year versus non burned year, against growing season (Apr – Sep) productivity.

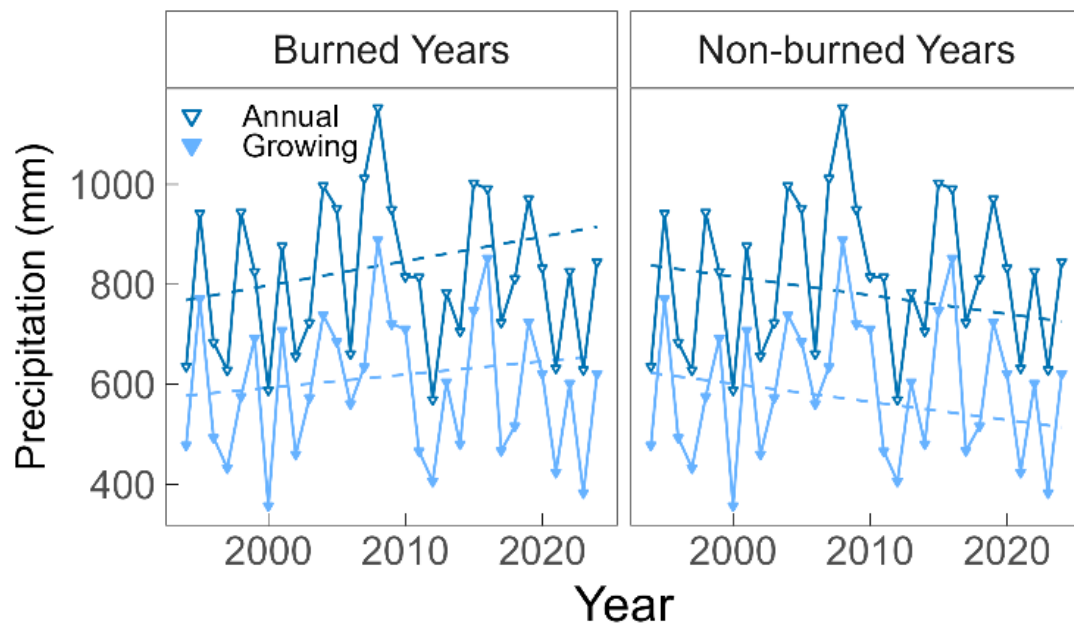


Figure B.3: Growing-season (April – September; filled symbols) and annual (open symbols) precipitation over time in burned and non-burned years. Lines indicate linear regression fits; dashed lines denote non-significant trends.

Appendix C - Chapter 4 supplementary material

Table C.1: Burn history data by year. Prescribed burns planned to burn that year (PP). Wildfire on the watershed planned to be burned that year (WP).

Year	Catchment (subcatchment)	Hectares Burned	Date of fire	Type
1986	N4C	4	3/17	WP
1986	N4C	77.8	4/22	PP
1990	N4C	77.8	4/7	PP
1994	N4C	77.8	3/31	WP
1998	N4C	77.8	4/10	PP
2002	N4C	77.8	4/3	PP
2006	N4C	77.8	4/20	PP
2010	N4C	77.8	4/8	PP
2014	N4C	77.8	3/10	PP
2018	N4C	77.8	3/13	PP
2022	N4C	77.8	3/1	PP
2023	N4C (summer)	42	9/25	PP
2024	N4C (spring)	34	3/12	PP
2024	N4C (summer)	42	9/26	PP
2025	N4C (spring)	34	4/15	PP

Table C.2: ANOVA results for cover, richness, diversity from species composition plots:

Effect	Response	Sum Sq.	Mean Sq.	df	F value	Pr(>F)
Burn Season (BS)	Warm-season grasses	0.019	0.019	1,12	1.629	0.2260
Topography (TP)	Warm-season grasses	0.107	0.107	1,12	9.084	0.0108
Year (YR)	Warm-season grasses	0.369	0.185	2,24	15.607	< 0.001
BS × TP	Warm-season grasses	0.000	0.000	1,12	0.014	0.9074
BS x YR	Warm-season grasses	0.057	0.028	2,24	2.390	0.1131
TP x YR	Warm-season grasses	0.126	0.063	2,24	5.340	0.0121
BS x TP x YR	Warm-season grasses	0.019	0.010	2,24	0.822	0.4517
Burn Season (BS)	Cool-season graminoids	0.123	0.123	1,12	1.457	0.2507
Topography (TP)	Cool-season graminoids	1.171	1.171	1,12	13.868	0.0029
Year (YR)	Cool-season graminoids	1.708	0.854	2,24	10.113	< 0.001
BS × TP	Cool-season graminoids	0.014	0.014	1,12	0.166	0.6912
BS x YR	Cool-season graminoids	0.138	0.069	2,24	0.816	0.4542
TP x YR	Cool-season graminoids	1.840	0.920	2,24	10.895	< 0.001
BS x TP x YR	Cool-season graminoids	0.524	0.262	2,24	3.100	0.0634
Burn Season (BS)	Forbs	1.065	1.065	1,12	0.077	0.7866
Topography (TP)	Forbs	95.081	95.081	1,12	6.845	0.0225
Year (YR)	Forbs	536.418	268.209	2,24	19.309	< 0.001
BS × TP	Forbs	25.576	25.576	1,12	1.841	0.1998
BS x YR	Forbs	41.330	20.665	2,24	1.488	0.2460
TP x YR	Forbs	182.741	91.371	2,24	6.578	0.0053
BS x TP x YR	Forbs	28.272	14.136	2,24	1.018	0.3765
Burn Season (BS)	Woody	0.074	0.074	1,12	0.014	0.9083
Topography (TP)	Woody	20.909	20.909	1,12	3.926	0.0709
Year (YR)	Woody	54.645	27.322	2,24	5.131	0.0140
BS × TP	Woody	0.001	0.001	1,12	0.000	0.9917
BS x YR	Woody	38.542	19.271	2,24	3.619	0.0423
TP x YR	Woody	1.988	0.994	2,24	0.187	0.8309
BS x TP x YR	Woody	34.468	17.234	2,24	3.236	0.0570
Burn Season (BS)	Native species richness	22.458	22.458	1,12	1.697	0.2172
Topography (TP)	Native species richness	81.925	81.925	1,12	6.189	0.0285
Year (YR)	Native species richness	3915.233	1957.617	2,152	147.887	< 0.001
BS × TP	Native species richness	10.606	10.606	1,12	0.801	0.3883
BS x YR	Native species richness	246.433	123.217	2,152	9.308	< 0.001
TP x YR	Native species richness	31.233	15.617	2,152	1.180	0.3102
BS x TP x YR	Native species richness	17.033	8.517	2,152	0.643	0.5269
Burn Season (BS)	Shannon-Hill Diversity	3.222	3.222	1,12	0.741	0.4061
Topography (TP)	Shannon-Hill Diversity	56.715	56.715	1,12	13.047	0.0036
Year (YR)	Shannon-Hill Diversity	403.611	201.806	2,152	46.424	< 0.001
BS × TP	Shannon-Hill Diversity	5.885	5.885	1,12	1.354	0.2672
BS x YR	Shannon-Hill Diversity	92.139	46.070	2,152	10.598	< 0.001
TP x YR	Shannon-Hill Diversity	37.762	18.881	2,152	4.343	0.0146
BS x TP x YR	Shannon-Hill Diversity	1.287	0.644	2,152	0.148	0.8625

Table C.3. PERMANOVA results showing the effects of burn season, topographic position, and their interactions on community composition based on Bray-Curtis Dissimilarity. Results are provided for the full study period (2023-2025).

	Df	Sum Sq	R²	F-value	Pr(>F)
Topography (TP)	1	1.344	0.204	12.684	0.001
Year (YR)	1	0.370	0.056	3.492	0.002
Burn Season (BS)	1	0.260	0.039	2.457	0.022
TP x YR	1	0.102	0.015	0.962	0.456
TP x BS	1	0.174	0.026	1.646	0.104
YR x BS	1	0.068	0.010	0.645	0.771
TP x YR x BS	1	0.043	0.007	0.410	0.959
Residual	40	4.238	0.642		
Total	47	6.601	1		

Table C.4: ANOVA results evaluating the effects of burn season, year, and their interactions on shrub area (m²) for dogwood and sumac.

Effect	Species	Sum Sq.	Mean Sq.	NumDF	DenDF	F value	Pr(>F)
Burn Season (BS)	Dogwood	0.029	0.029	1	123	0.981	0.3239
Year (YR)	Dogwood	0.929	0.465	2	245	15.818	< 0.001
BS × YR	Dogwood	0.475	0.238	2	245	8.090	< 0.001
Burn Season (BS)	Sumac	0.481	0.481	1	300	9.406	0.0024
Year (YR)	Sumac	5.062	2.531	2	493	49.469	< 0.001
BS × YR	Sumac	6.013	3.006	2	493	58.766	< 0.001

Table C.5: ANOVA results evaluating the effects of burn season, year, and their interaction on proportional change in shrub area relative to 2023 for dogwood and sumac.

Effect	Species	Sum Sq.	Mean Sq.	NumDF	DenDF	F value	Pr(>F)
Burn Season (BS)	Dogwood	0.145	0.145	1	123	4.702	0.0321
Year (YR)	Dogwood	0.287	0.287	1	124	9.306	0.0028
BS × YR	Dogwood	0.344	0.344	1	124	11.168	0.0011
Burn Season (BS)	Sumac	0.658	0.658	1	252	13.527	< 0.001
Year (YR)	Sumac	0.846	0.846	1	248	17.397	< 0.001
BS × YR	Sumac	5.335	5.335	1	248	109.663	< 0.001

Table C.6: ANOVA results testing whether initial shrub size influences proportional change in shrub area across burn seasons and years for dogwood and sumac.

Effect	Species	Sum Sq.	Mean Sq.	NumDF	DenDF	F value	Pr(>F)
Initial Size (IS)	Dogwood	0.066	0.066	1	120	2.249	0.1363
Burn Season (BS)	Dogwood	0.034	0.034	1	120	1.167	0.2822
Year (YR)	Dogwood	0.301	0.151	2	241	5.109	0.0067
IS × BR	Dogwood	0.006	0.006	1	120	0.190	0.6634
IS × YR	Dogwood	0.083	0.041	2	241	1.401	0.2483
BR × YR	Dogwood	0.069	0.035	2	241	1.177	0.3099
IS × BR × YR	Dogwood	0.006	0.003	2	241	0.105	0.9006
Initial Size (IS)	Sumac	0.113	0.113	1	243	2.228	0.1368
Burn Season (BS)	Sumac	0.352	0.352	1	243	6.960	0.0089
Year (YR)	Sumac	0.272	0.136	2	489	2.690	0.0689
IS × BR	Sumac	0.060	0.060	1	243	1.188	0.2768
IS × YR	Sumac	0.200	0.100	2	489	1.977	0.1396
BR × YR	Sumac	1.540	0.770	2	489	15.223	< 0.001
IS × BR × YR	Sumac	0.085	0.042	2	489	0.838	0.4332

Table C.7: ANOVA results from linear mixed-effects models testing the effects of burn season, year, and their interaction on shrub irregularity, with shrub area (log-transformed) included as a covariate.

Effect	Species	Sum Sq.	Mean Sq.	NumDF	DenDF	F value	Pr(>F)
Burn Season (BS)	Dogwood	0.006	0.006	1	121	0.289	0.5919
Year (Y)	Dogwood	5.317	2.658	2	247	135.823	< 0.001
Shrub Area	Dogwood	0.410	0.410	1	150	20.954	< 0.001
BS × Y	Dogwood	0.307	0.153	2	246	7.834	< 0.001
Burn Season (BS)	Sumac	0.015	0.015	1	239	2.595	0.1085
Year (Y)	Sumac	0.828	0.414	2	497	71.791	< 0.001
Shrub Area	Sumac	0.009	0.009	1	399	1.481	0.2243
BS × Y	Sumac	0.405	0.203	2	499	35.151	< 0.001

Table C.8: ANOVA results evaluating the effects of burn season, grazing, year, and their interactions on *C. drummondii* stem density (stems m⁻²) and aboveground biomass (grams m⁻²) across shrub island positions (outside, edge, and interior).

Dogwood Stem Density (stems m ⁻²)	Outside			Edge			Interior		
	df _{n, d}	F-value	P-value	df _{n, d}	F-value	P-value	df _{n, d}	F-value	P-value
Burn Season (BS)	1,28	0.938	0.3410	1,28	0.044	0.8347	1,28	1.000	0.3259
Grazed (GR)	1,28	4.734	0.0382	1,28	3.015	0.0935	1,28	0.662	0.4226
Year (YR)	2,184	1.744	0.1778	2,184	18.170	<0.001	2,472	13.922	<0.001
BS * GR	1,28	0.006	0.9376	1,28	0.574	0.4549	1,28	0.028	0.8678
BS * YR	2,184	1.454	0.2363	2,184	0.234	0.7918	2,472	1.328	0.2659
GR * YR	2,184	0.131	0.8771	2,184	6.734	0.0015	2,472	0.374	0.6885
BS * GR * YR	2,184	1.387	0.2524	2,184	0.605	0.5472	2,472	1.422	0.2422

Dogwood Biomass (g m ⁻²)	Outside			Edge			Interior		
	df _{n, d}	F-value	P-value	df _{n, d}	F-value	P-value	df _{n, d}	F-value	P-value
Burn Season (BS)	1,28	0.078	0.7819	1,28	0.984	0.3298	1,28	0.554	0.4630
Grazed (GR)	1,28	2.788	0.1061	1,28	1.060	0.3119	1,28	0.021	0.8865
Year (YR)	2,184	3.848	0.0231	2,184	101.966	<0.001	2,472	17.451	<0.001
BS * GR	1,28	0.027	0.8698	1,28	0.506	0.4826	1,28	0.056	0.8142
BS * YR	2,184	4.028	0.0194	2,184	14.740	<0.001	2,472	5.667	0.0037
GR * YR	2,184	1.321	0.2693	2,184	10.758	<0.001	2,472	2.982	0.0517
BS * GR * YR	2,184	0.405	0.6675	2,184	0.917	0.4014	2,472	1.007	0.3662

Table C.9: ANOVA results from linear mixed-effects models evaluating the effects of burn season, grazing, mowing, year, and their interactions on percent cover of graminoids, forbs, woody vegetation, and bare ground across shrub island positions (outside, edge, and interior).

Graminoid Cover (%)	Outside			Edge			Interior		
	df _{n, d}	F-value	P-value	df _{n, d}	F-value	P-value	df _{n, d}	F-value	P-value
Burn Season (BS)	1,28	1.069	0.3100	1,28	4.312	0.0471	1,28	12.324	0.0015
Grazed (GR)	1,28	1.441	0.2401	1,28	0.012	0.9130	1,28	0.325	0.5730
Year (YR)	2,56	4.224	0.0196	2,56	1.628	0.2055	2,152	7.088	0.0011
BS * GR	1,28	0.456	0.5049	1,28	1.669	0.2070	1,28	0.610	0.4413
BS * YR	2,56	5.274	0.0080	2,56	1.735	0.1858	2,152	4.492	0.0127
GR * YR	2,56	3.829	0.0276	2,56	3.537	0.0358	2,152	4.980	0.0080
BS * GR * YR	2,56	0.157	0.8550	2,56	2.126	0.1289	2,152	0.166	0.8471

Forb Cover (%)	Outside			Edge			Interior		
	df _{n, d}	F-value	P-value	df _{n, d}	F-value	P-value	df _{n, d}	F-value	P-value
Burn Season (BS)	1,28	2.883	0.1006	1,28	5.532	0.0259	1,28	1.666	0.2073
Grazed (GR)	1,28	0.450	0.5078	1,28	1.956	0.1730	1,28	2.794	0.1058
Year (YR)	2,56	3.733	0.0301	2,56	17.819	<0.001	2,152	34.518	<0.001
BS * GR	1,28	1.034	0.3180	1,28	1.325	0.2594	1,28	0.448	0.5086
BS * YR	2,56	4.920	0.0108	2,56	12.494	<0.001	2,152	26.609	<0.001
GR * YR	2,56	1.999	0.1450	2,56	8.810	<0.001	2,152	1.931	0.1485
BS * GR * YR	2,56	0.095	0.9097	2,56	1.249	0.2946	2,152	3.850	0.0234

Woody Cover (%)	Outside			Edge			Interior		
	df _{n, d}	F-value	P-value	df _{n, d}	F-value	P-value	df _{n, d}	F-value	P-value
Burn Season (BS)	1,28	0.065	0.8005	1,28	2.551	0.1215	1,28	0.101	0.7526
Grazed (GR)	1,28	0.212	0.6489	1,28	2.145	0.1541	1,28	2.509	0.1244
Year (YR)	2,56	3.458	0.0384	2,56	28.869	<0.001	2,152	7.984	<0.001
BS * GR	1,28	0.822	0.3723	1,28	0.136	0.7155	1,28	0.171	0.6827
BS * YR	2,56	2.214	0.1187	2,56	3.281	0.0449	2,152	1.302	0.2751
GR * YR	2,56	6.708	0.0024	2,56	1.512	0.2293	2,152	0.189	0.8282
BS * GR * YR	2,56	3.395	0.0406	2,56	1.617	0.2077	2,152	2.134	0.1219

Bare ground (%)	Outside			Edge			Interior		
	df _{n, d}	F-value	P-value	df _{n, d}	F-value	P-value	df _{n, d}	F-value	P-value
Burn Season (BS)	1,28	2.801	0.1054	1,28	12.419	0.0015	1,28	12.459	0.0015
Grazed (GR)	1,28	0.054	0.8184	1,28	0.772	0.3869	1,28	3.925	0.0575
Year (YR)	2,56	1.381	0.2598	2,56	0.100	0.9049	2,152	38.593	<0.001
BS * GR	1,28	0.002	0.9634	1,28	0.761	0.3905	1,28	0.360	0.5533
BS * YR	2,56	12.956	<0.001	2,56	5.831	0.0050	2,152	2.648	0.0740
GR * YR	2,56	1.497	0.2327	2,56	1.667	0.1980	2,152	1.913	0.1512
BS * GR * YR	2,56	0.023	0.9771	2,56	0.622	0.5404	2,152	2.912	0.0574

Table C.10: ANOVA results from linear mixed-effects models evaluating the effects of burn season, grazing, mowing, year, and their interactions on dogwood recruitment (stems m⁻²). Recruits were defined as ramets < 0.15 m in height.

	Sum Sq	Mean Sq	df_{n, d}	F-value	P-value
Burn Season (BS)	0.171	0.171	1,24	0.709	0.4080
Grazed (GR)	0.972	0.972	1,24	4.038	0.0558
Mowed (MO)	0.368	0.368	1,24	1.528	0.2283
Year (YR)	24.842	12.421	2,48	51.627	<0.001
BS * GR	0.048	0.048	1,24	0.202	0.6575
BS * MO	0.025	0.025	1,24	0.102	0.7518
GR * MO	0.249	0.249	1,24	1.033	0.3196
BS * YR	1.811	0.906	2,48	3.764	0.0303
GR * YR	0.152	0.076	2,48	0.316	0.7305
MO * YR	1.812	0.906	2,48	3.767	0.0302
BS * GR * MO	0.275	0.275	1,24	1.143	0.2956
BS * GR * YR	0.162	0.081	2,48	0.336	0.7160
BS * MO * YR	0.082	0.041	2,48	0.170	0.8441
GR * MO * YR	0.163	0.082	2,48	0.339	0.7141
BS * GR * MO * YR	0.371	0.185	2,48	0.771	0.4682

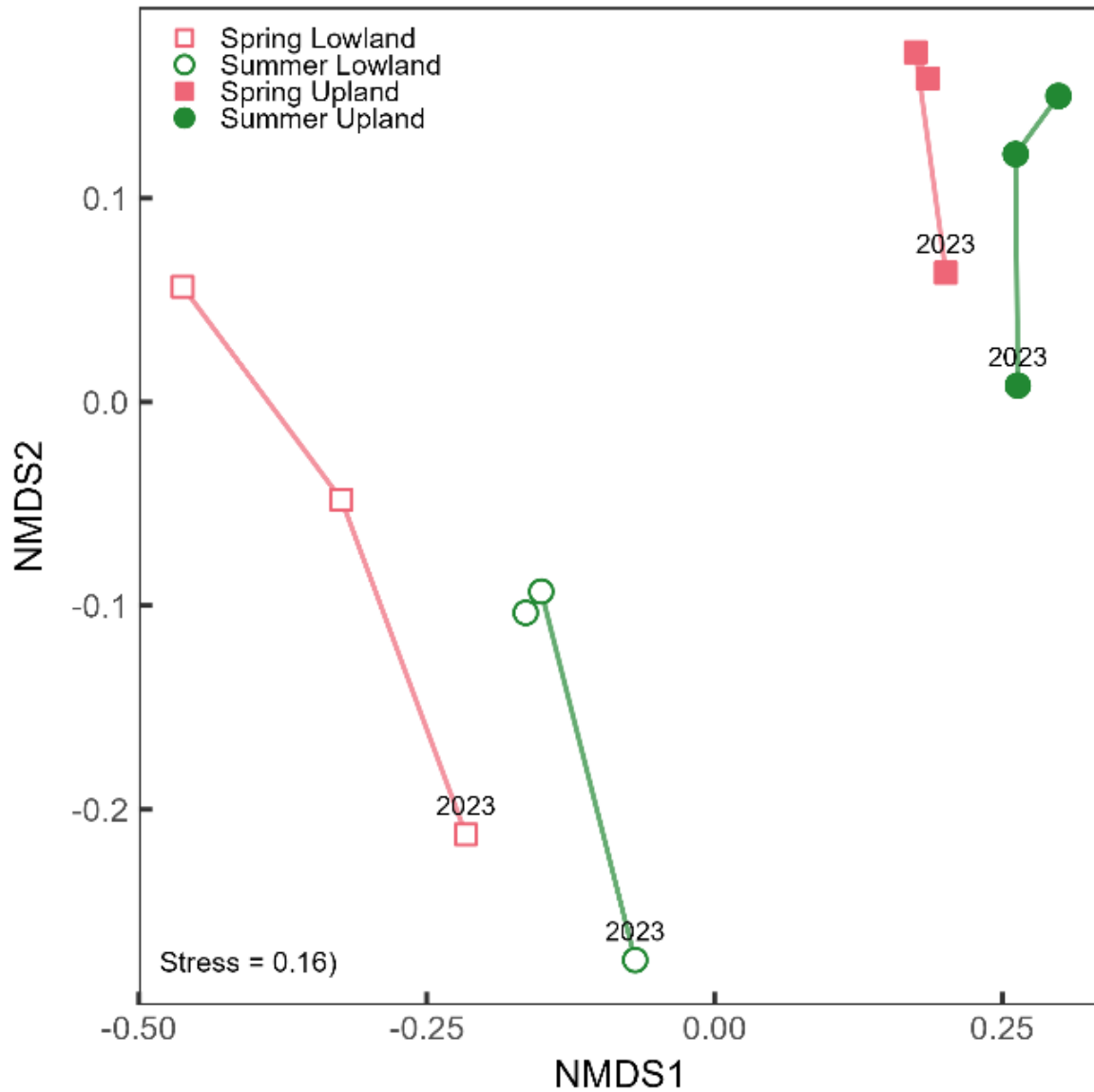


Figure C.1: NMDS of communities composition in spring and summer subcatchments in the uplands and lowlands over time.