High-intensity fire experiments to manage shrub encroachment: lessons learned in South Africa and the United States

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Abstract

Human alteration of fire regimes is a hallmark of the Anthropocene; yet few studies have fully explored the implications of utilizing high-intensity fires in grasslands and savannas to manage shrub encroachment. Decades of fire research in South Africa inspired a unique convergence of high-intensity fire experiments in the USA. In the Great Plains of North America, high-intensity fire trials were designed to remove traditional investigator constraints that minimised variability in fire intensity and to explore woody mortality thresholds across a broader suite of experimental conditions. At the same time, studies in the Kruger National Park, South Africa, similarly investigated high-intensity fires to examine previously unstudied relationships between high-intensity fires and woody encroachment. These scientific pursuits have contributed to theoretical advances in our understanding of fire-vegetation dynamics. In this paper, we synthesise these high-intensity fire experiments, the empirical evidence emerging from them and their importance for managing grassland and savanna ecosystems, and the lessons learned and challenges ahead to maintaining critical ranges of variation in fire regimes during the Anthropocene.

Keywords: fire regime; grassland; Great Plains; Kruger National Park; savanna

Introduction

For centuries, humans have coexisted with and perpetuated fires that maintained rangeland systems across the globe (Pyne 2001; Bowman et al. 2011; Twidwell et al. 2021). Savanna and grassland ecosystems are the most spatially extensive terrestrial ecosystems in the world covering nearly half of Africa, South America, and Australia (Scholes and Walker 1993; Werner 2009). Fires, together with herbivores, are key drivers in maintaining a dynamic equilibrium between the continuous graminoid plant cover and sporadically dispersed woody vegetation. However, global fire activity is in decline (Doerr and Santín 2016) and can be linked to anthropogenic land conversion (Andela et al. 2017) along with negative social perceptions of fires (Weir et al. 2019; Smit et al. 2021), resulting in large-scale fire suppression policies (Nyongesa and Vacik 2018; Starns et al. 2020). Furthermore, local government policy and management practices have contributed to altering fire regimes by limiting or not considering factors, such as fire frequency, seasonality and intensity. Alteration in multiple components of fire regimes can tip the balance between woody plant and grass dominance, with potential implications for ecosystem service delivery. The implications of fire regime alteration are not fully understood in some of the globe's most pyric systems, grasslands and savannas (Twidwell et al. 2021).

Grasslands and savanna areas are among the most severely threatened ecosystems worldwide (Bestelmeyer et al. 2018). In addition to land conversion tied to urban expansion and agricultural intensification, intact grasslands and savannas are globally experiencing large-scale transitions, as a result of woodland encroachment (Archer et al. 2017). Woodland expansion in grassland-dominated areas has been ascribed to the removal of fires and/or browsing by ungulates (Trollope 1980) or simplification of historical fire regimes (Engle et al. 2008) together with poor grazing management and confounding factors, such as increasing atmospheric $CO2$ (Buitenwerf et al. 2012). These transitions have led to declines in ecosystem services, including decreased grazing potential (Anadón et al. 2014), shifting water table characteristics, and losses in grassland and savanna native biodiversity (Ratajczak et al. 2012; Twidwell et al. 2013b). The conversion from a grassland to woody state has often been considered 'irreversible', because low-intensity fires that once helped maintain grassland systems has failed to reverse encroached areas back to a grassland or savanna state. In addition, increased woody cover often reduces herbaceous fuel loads, resulting in lower fire frequency and intensity, and favouring further proliferation of woody vegetation (a reinforcing feedback loop). Recent studies shed light on the importance of manipulating fire characteristics in order to overcome 'irreversible' thresholds created by woody encroachment (Ratajczak et al. 2016; Bielski et al. 2021; Collins et al. 2021). Accordingly, there is a requirement for fire research to explore greater ranges in fire regime variability in order to control additional large-scale grassland and savanna transitions.

Experimental manipulation of fires originally focused on fire presence or absence, without considering variability in fire regime characteristics (McGranahan and Wonkka 2018). The most commonly studied fire characteristics with respect to combating shrub encroachment in savannas and grassland systems generally include types of fire (head- or backfires), return interval, season, severity, intensity, structural heterogeneity, and burned area (Trollope and Potgieter 1985; Keeley 2008; Twidwell et al. 2021). Savanna and grassland studies that have investigated variation in fire regime characteristics have largely focused on fire frequency (e.g. Scholtz et al. 2016), which has in some cases been largely ineffective at reversing woody transitions or controlling additional woodland expansion (Case and Staver 2017; Collins et al. 2021; Scholtz et al. 2021). In other cases, frequently burned areas were shown to have lower woody cover than less frequently burned and unburned areas (Smit et al. 2010). However, frequent fires are not always practically possible, due to lack of sufficient fuel, or because areas critical for grazing cannot be burnt frequently. As a result, these frequent fire treatments, sometimes regarded as 'unsuccessful' or not practical for controlling woodland expansion, have led to the promotion of management alternatives to fires that are more economically costly, and less ecologically beneficial, for example, mechanical removal and herbicide application (Bezuidenhout et al. 2015; Scholtz et al. 2021).

Decades of fire research in South Africa have inspired the experimental exploration of the range of variability in fire intensity in both the United States Great Plains and South Africa's

Kruger National Park (KNP; Figure 1). Although the idea of explicitly manipulating fire intensity in order to reduce shrub encroachment in semi-arid grassland and savanna systems is generally quite rare in fire experiments, this foundational research has helped shed light on the potential for hysteretic responses associated with woodland encroachment (Bielski et al. 2021) and set the stage for unravelling how fire intensity shapes grassland and savanna ecosystems.

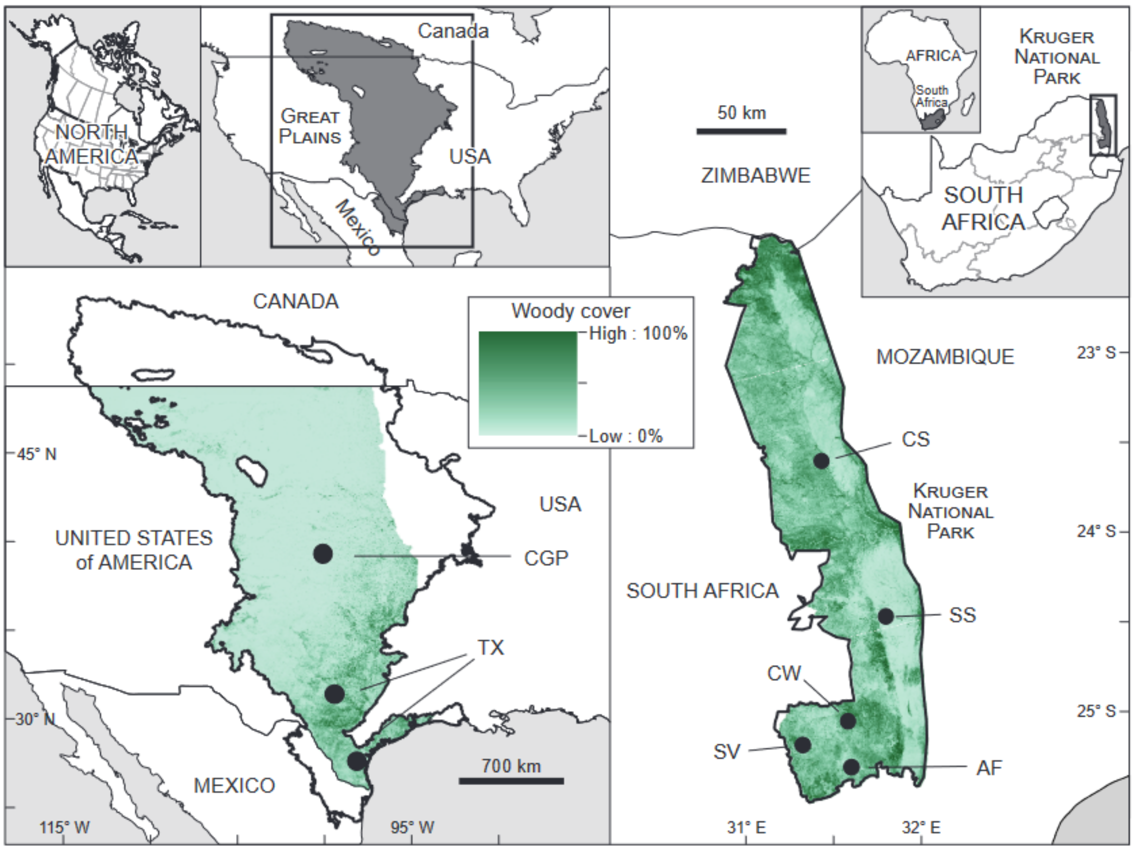

Figure 1: Woody vegetation cover in the United States Great Plains and South Africa's Kruger National Park

Inspiration, communication, and collaboration between researchers in South Africa's KNP and the United States Great Plains has spurred multiple fire experiments to assess the role of high fire intensity in controlling woodland species expansion and restoring or maintaining graminoid dominance in encroached grasslands and savannas. Manipulating fire intensity can be achieved through numerous approaches, such as selecting weather conditions conducive for high-intensity fires (e.g. hot and dry; Twidwell et al. 2016) or targeting high fuel loads (Govender et al. 2006). Altering fire seasonality (e.g. growing season versus dormant season fires) can influence the intensity through prevailing weather conditions and fuel moisture levels (Govender et al. 2006), but can also influence vegetation responses because of phenological shifts in plant ecophysiology (Miller et al. 2019). Accordingly, there is a necessity to summarise and contrast the varying approaches and outcomes of these unique high-intensity fire experiments in order to promote a more thorough understanding of fire intensity outcomes in grasslands and savannas for further experimentation and application globally to improve vegetation management and assess biodiversity outcomes.

In this paper, we assess the outcomes of high-intensity fire trials implemented to reduce shrub encroachment in KNP in South Africa and the US Great Plains, including methodologies and key experimental findings. We then highlight what has been learned across trials and identify remaining knowledge gaps. Finally, we discuss future directions and potential hurdles that still have to be overcome to advance high-intensity fire experiments and application in grasslands and savanna systems.

Kruger High-Intensity Fire Experiments

The KNP is a large conservation area (~2 million ha) located in the north-eastern region of South Africa within the savanna biome, underlain by two dominant geologies, granites in the west and basalts in the east. The climate is characterised by hot and wet summers with an average daily maximum of 34 °C, and dry winters with average daily maximum temperatures of 27 °C and mean annual precipitation of approximately 542 mm (MacFadyen et al. 2019; Strydom et al. 2019). The landscape varies from typical wooded savanna dominated by species, such as *Combretum apiculatum*, *Terminalia sericea* and *Dichrostachys cinerea* in the higher rainfall, granitic regions of the park to more grass-dominated savanna with scattered trees, such as *Sclerocarya birrea* and *Senegalia nigrescens* in the central basaltic regions. The north of the park is dominated by *Colophospermum mopane*.

The role of fire as an ecosystem driver, which maintains the codominance of trees and grasses in KNP, has been well established (Eckhardt et al. 2000; Sankaran et al. 2005; Higgins et al. 2007). This is largely as a result of the park's rich and long history of fire management and research. The apparent increase in woodland cover in certain parts of KNP (Eckhardt et al. 2000) has been a management concern for many years, due to uncertainty around the cascading effects that a structural change vegetation would have on altering the fire regime, herbivory dynamics, landscape hydrological patterns and nutrient cycling, as well as the tourism and visitor experience (Gray et al. 2013; Smit and Prins 2015; Case et al. 2020). Although KNP had a number of fire experiments implemented over the years, we will only focus on two high-intensity fire trials, because these fires were explicitly implemented to evaluate fire effects on vegetation over large areas (experiments exceeding 1 000 ha) and they obtained the highest intensities measured in experimental fires in KNP in recent years.

Experimental Burn Plots

The long-term Experimental Burn Plots (EBPs), which were initiated in the early 1950s, aimed at investigating the effect of varying fire frequencies and intensities (through varying seasonality) on savanna vegetation (Biggs et al. 2003; van Wilgen et al. 2007). These EBPs were set up in four of the major vegetation types: the Sourveld (SV, Figure 1) landscape dominated by *T. sericea* and *D. cinerea*, the *C. apiculatum*/*C. zeyheri* woodland (CW, Figure 1), the *S. birrea*/ *S. nigrescens* savanna (SS, Figure 1), and *Colophospermum mopane* shrubveld (CS, Figure 1) (Gertenbach 1983). This experiment allows for comparisons between fire frequencies (i.e. 70 years of fire exclusion, annual, biannual, triannual burning and sites that burned every four and six years), as well as fire intensities (i.e. low fire intensity achieved during the wet or early dry season burns, compared with high fire intensity achieved during late dry season burns). The EBPs have been used to investigate the effect of varying fire regimes on vegetation (Enslin et al. 2000; Kennedy and Potgieter 2003; Higgins et al. 2007), soil nutrients and hydrology (Aranibar et al. 2003; Coetsee et al. 2010; Pellegrini et al. 2018; Strydom et al. 2019), small mammals (Kern 1981), and invertebrates (Davies et al. 2012; Wigley et al. 2019) to name a few (see van Wilgen et al. 2007 for a summary). In terms of woodland vegetation structure, studies on the EBPs have shown that frequent, high-intensity burns are able to suppress woodland shrub dominance, alter their structure by decreasing shrub height, and promote more open landscapes (Enslin et al. 2000; Jacobs and Biggs 2002; Higgins et al. 2007; Smit et al. 2010).

The experimental high-intensity burns have been applied on an annual basis (fuel permitting) since the 1950s during the dry season when grasses have cured, and dry weather conditions are able to support high-intensity fires. These frequent fires were applied on 7 ha plots and had a mean fire intensity of ~2 300 kW m^{-1} (Govender et al. 2006). It is postulated that because these savannas are resilient to fires and most species are adapted to resprout or coppice (a persistence mechanism for many woody plants in fire-prone environments), follow-up burns (generally every one to three years) are required to induce major changes to woodland vegetation structure instead of single high-intensity burn. Such frequent fire applications are highly dependent on rainfall and the ability of the herbaceous layer to recover and produce adequate fuel loads to support follow-up fires.

Afsaal High-Intensity Fire Experiment

In 2010, a large-scale field experiment was initiated to investigate whether several high-intensity fires over a short period of time, applied during the dry dormant season, could be used to reverse woodland encroachment in the KNP (AF, Figure 1). A site in the southern section of the park was selected with extensive stands of woodland vegetation that included targeted encroaching species, such as *D. cinerea*, *T. sericea*, and *C. apiculatum*. This study site is underlain by sandy, granitic soils (Oxisols) and the area receives a mean annual rainfall of 640 mm y−1. Three sites were treated with varying degrees of fire intensity over a four-year period (2010–2013). One site (7 200 ha) was burnt with the first high-intensity fire (~4 000–4 300 kW m^{-1}) in September 2010 and a follow-up high-intensity fire in September 2013 (3 200 kW m^{-1}). Another site (4 100 ha) was burnt with a high-intensity fire in 2010 (~4 000–4 300 kW m^{-1}) and a medium intensity fire (~2 500 kW m^{-1}) in 2013, whereas a third site (2 200 ha) was burnt as low-intensity fires (~1 400–2 100 kW m^{-1}) both in 2010 and 2013 (Table 1).

Table 1: Fire intensity (2010 and 2013) and LiDAR-derived woody cover estimates for 2010 (pre-fire) and 2014 (post-fire) for the Afsaal High-Intensity Fire Experiment (data obtained from Smit et al. 2016)

Fire treatment	2010 Fire intensity (kW m^{-1})	2013 Fire intensity (kW m^{-1})	% Woody cover pre-fire (2010)	% Woody cover post-fire (2014)	Change in % woody cover (2010–2014)
No fire	N/A	N/A	29.05	43.18	14.13
Low intensity	1 400–2 100	1 400–2 100	23.98	33.05	9.07
High intensity (2010), followed by moderate intensity (2013)	4 000–4 300	2 500	33.91	25.44	−8.47
High intensity (2010 and 2013)	4 000–4 300	3 200	27.61	9.9	−17.71

Several post-fire studies utilised a combination of remote-sensing techniques (i.e. airborne Light Detection and Ranging [LiDAR]), ground surveys, and field observations to determine the effect of these high-intensity burns on the woodland vegetation. Using airborne LiDAR, Smit et al. (2016) found that the high-intensity fires were successful in decreasing woodland cover, compared with low fire intensity and unburnt sites. However, this was predicted to be a short-term effect, confirmed by field survey data collected ten years after the first high-intensity burn conducted in 2010 (Strydom et al., unpubl. data). In areas directly adjacent to the high-intensity fires, low-intensity fires were applied in 2010 and 2013. The low-intensity fire treatments resulted in no short-term reduction in woodland cover, but in fact resulted in an increase in woodland cover between 2010 (pre-fire) and 2014 (one year post the second low-intensity fire). The high-intensity fires were ineffective at decreasing woodland vegetation cover over the long term (Strydom et al., unpubl. data). Although there was a reduction in woodland shrub height and structure, there was no decrease in the number of woodland individuals, due to a lack of mortality during these burns. Therefore, the high-intensity burns were able to decrease vegetation height, however, due to the resilience of the targeted species, *C. apiculatum*, *D. cinerea* and *T. sericea* were able to resprout and coppice vigorously post-fire. The number of stems per individual increased post fire, thereby altering vegetation structure from taller, primarily singlestemmed individuals to shorter, more multistemmed shrubs (Strydom et al., unpubl. data).

US Great Plains High-Intensity Fire Experiments

Southern Great Plains

Savanna ecosystems in the Southern Great Plains, United States are experiencing unparalleled compositional and structural shifts toward woodland plant dominance (Scholes and Archer 1997; Van Auken 2000). This has tremendous ecological significance, as well as socioeconomic consequences that will likely be further exacerbated by changing climate projections (Twidwell et al. 2013b; Wonkka et al. 2019). Traditional management approaches have failed to provide landowners and natural resource stakeholders with a satisfactory means of sustaining the viability of rangeland savanna ecosystems (Kreuter et al. 2008). As historically grass-dominated rangelands became transformed by woodland encroachment from the late 1800s through the Dust Bowl eras of the 1930s and 1950s, land managers began to aggressively pursue 'brush-control' strategies in the 1960s–1970s, using chemical and mechanical treatment of shrubs and trees. Nonetheless, these efforts were fraught by many shortcomings, including being prohibitively expensive, poor assessments of the vast geographical expanses that needed to be treated, and short-lived and/or generally ineffective treatments, due to the high level of resilience in the woodland plant populations. This was particularly true when confronted with resprouting species in a region with average yearly rainfall ranging from 250 to 1 500 mm (Van Liew et al. 2012; Scholtz et al. 2021). In the 1980s, ecologists began to recognise that the prevailing paradigm of steady state, equilibrium dynamics failed to explain why these rangeland ecosystems appeared to have been converted to a semi-permanent woodland plant structural dominance (Westoby et al. 1989). New conceptual ideas associated with non-equilibrium dynamics were developed and the potential for heavily degraded ecosystems to cross ecological thresholds to alternative stable states became recognised (Suding et al. 2004). Indeed, formerly grass-dominated rangeland ecosystems in the Southern Great Plains had become entrenched in a new, stable state that resulted in a reduction of valued herbaceous forage and an increase in highly resilient woodland plant species (Briske et al. 2003, 2005).

This novel appreciation for the nature of these systems and ongoing dissatisfaction with the loss of critical ecosystem goods and services, led landowners, natural resource managers, and associated stakeholders to begin seeking alternative methods to manage rangeland landscapes in the mid-1990s (Taylor 2005). Although the use of prescribed fires was recognised as an effective management tool for maintaining a herbaceous dominated state in the Southern Great Plains, widespread utilisation throughout the region was limited, both because of socio-political constraints and the ineffectiveness of prescribed fires at reversing woodland encroachment, after it had occurred (Twidwell et al. 2013b, 2019; Toledo et al. 2014). Stakeholder groups began to increasingly recognise that high-intensity fires, both prescribed and unintentional, had effects on the density and survival of woodland plant species. Although these anecdotal observations appeared promising, there was little empirical evidence to evaluate the effectiveness of high-intensity prescribed fires at decreasing the density and survival of woodland plants. Moreover, there were no quantitative assessments of the effects of high-intensity fires on herbaceous plant regeneration, vegetation compositional changes (e.g. native versus non-native species responses), physical soil properties like bulk density and hydrophobicity, soil nutrient alterations (particularly carbon and nitrogen), soil biota responses (e.g. bacterial, fungal, and microfauna diversity and abundances), and grazing impacts of livestock and wildlife. Recognising the potential benefits, rigorous experimental assessments of high-intensity fires were developed from the research labs of SD Fuhlendorf at Oklahoma State University and CA Taylor, WE Rogers, and UP Kreuter at Texas A&M University to address these critical knowledge gaps.

Texas High-Intensity Fire Experiment

The first high-intensity fire study was established at the Texas A&M AgriLife Research Center on the Edward's Plateau in Texas, USA in 2005 (TX, Figure 1). Historically, this site was grassland, with less than 5% woodland cover (Fuhlendorf and Smeins 1997). Total woodland cover at the time of the study was >40%, largely as a result of *Juniperus* encroachment. The study targeted environmental conditions typical during wildfires to determine whether a fire could overcome the resilience of a mature juniper woodland. The study compared the effects of prescribed high-intensity fire with traditional, low-intensity prescribed fires. The prevailing understanding at the time was that fire was ineffective for restoring grass dominance, because at this level of encroachment, *Juniperus* displaced fine fuels, keeping fuel loads too low to cause fires of adequate intensity that could result in *Juniperus* mortality. By targeting low fine fuel moisture during the growing season (i.e. burning during a dry period rather than a wet period within the growing season), Twidwell et al. (2009) were able to achieve >85% mortality, as long as there was adequate fuel to generate a high-intensity fire. They used data from this study, together with a physical fire model to define a threshold of 160 kJ m^{-1} s^{-1} (~2 666 kW m^{-1}) for fire-induced mortality of *Juniperus ashei*, a non-resprouting coniferous shrub. This modelling effort showed that high fire intensity does not require high fine fuel loads, if low fuel moisture is targeted (Twidwell et al. 2013a).

Although these studies established fire-mortality thresholds for non-resprouting *J. ashei,* thresholds for the many resprouting encroaching shrub species in the region were unknown. In 2008, a high-intensity fire trial was established to assess the efficacy for high-intensity prescribed fires to halt or reverse encroachment in resprouting-shrub dominated systems. The study was also conducted at the Texas A&M AgriLife Research Center on the Edwards Plateau with a companion site at the Welder Wildlife Refuge in the Coastal Bend region of Texas. During one of the worst droughts experienced in the region, standing dead trees within 20 × 30 m plots were able to maintain high-intensity prescribed fires in the growing season. Fireline intensities were as high as 8 595 kW m^{-1} at the Coastal Plains site and 68 613 kW m^{-1} in Edwards Plateau (Table 2). They resulted in 35–55% fewer resprouting woodland plants than in control plots with no fire treatments applied. High-intensity fires caused significant mortality and little recruitment, compared with control plots that had greater recruitment than mortality for all three years of the study (Twidwell et al. 2016).

Table 2: Fire intensity (2008, 2009 and 2010), woody mortality (2008 and 2010), and % change in woody density before (2006) and after (2011) fire (data obtained from Twidwell et al. 2016)

Fire treatment	2008 Fire intensity (kW m⁻¹)	2009/2010 Fire intensity (kW m⁻¹)	% Woody mortality (2011)	% Change in woody density (2006–2011)
Coastal Plains Study Site				
High intensity (2008), followed by low intensity (2009)	5 291–8 595	58	16%	−2%
Single high intensity (2008)	5 291–8 595	NA	17%	−8%
Edwards Plateau Study Site				
High intensity (2008), followed by low intensity (2010)	23 879–38 788	627–1 173	23%	−21%
Single high intensity (2008)	23 879–68 613	NA	16%	−12%

One concern associated with using high-intensity prescribed fires is the potential to damage desired grass species, lower native species diversity, and allow disturbance-mediated exotic grass or weed invasion. However, native forb richness increased after the 2008 high-intensity fire trials at the Coastal Bend site; native grass, exotic grass, and exotic forb richness did not differ from controls (Twidwell et al. 2012). Similarly, high-intensity prescribed fires did not result in differences in grass communities at the Edwards Plateau and reduced the prevalence of problematic understory species (Taylor Jr et al. 2012).

Mesquite High-Intensity Fire Experiment

The Texas High-Intensity Fire Experiment showed it was possible to lower densities of resprouting shrubs with high-intensity fires during drought in the growing season (Twidwell et al. 2016). However, the potential for high-intensity fires to similarly reduce resprouting individuals during periods of low plant water stress had not been assessed. In addition, rates of mortality in that study varied within and among species, but the causes of variation were unknown. Furthermore, a common concern regarding the use of high-intensity fires for grassland management is uncertainty regarding native grass persistence. It is well known that high bud production rates and well-protected belowground bud banks allow native grasses to readily persist despite fires (Dalgleish and Hartnett 2008; Russell et al. 2015). Yet, most of these studies were conducted with moderate fire intensities. Grass bud responses to high-intensity fires are largely unknown although data from the Texas High-Intensity Fire Experiment suggest grass community composition is not affected (Hiers et al. 2021). Bud densities and stored reserves, whereas typically sufficient to result in regrowth following low-intensity fires, might fail to regrow following high-intensity fires. The Mesquite High-Intensity Fire Experiment was established in 2018 at the Texas A&M AgriLife Research Center to address these knowledge gaps and to assess resprouting variability within a species more mechanistically, so that universal drivers of resprouter persistence in the face of high-intensity fires during the growing season could be determined.

This experiment (Hiers et al. 2021; Starns et al. 2022) comprised 10 × 10 m plots centered on a focal mesquite tree that either received a traditional prescribed fire treatment, burned with hay additions to normalise fuel loads across treatments, a high-intensity prescribed fire treatment with cut and dried juniper added below the focal mesquite, or no fire treatment. The amount of juniper fuel added to the high-intensity fire plots was determined via a series of trials to find a fuel addition that approximated the flame lengths observed in the Texas High-Intensity Fire Experiment. Because resprouting theory predicts that resprouter persistence is related to both number and protection of buds, as well as the protection of transport channels for mobilizing resources to resprouting tissue, the bases of some of the mesquite were exposed to assess the importance of basal meristematic tissue protection relative to resource availability and remobilisation. Some epicormic and basal buds were protected from typical and high-intensity fires and top-killed mesquites were able to remobilise nutrients and water. However, epicormic meristematic tissue was damaged in most of the high-intensity fire focal mesquites. High-intensity fire focal mesquites also had lower survival rates and almost complete loss of apical dominance. In those that did resprout, resprout numbers were lower than those of focal mesquite exposed to typical fires, which may have additional implications for long-term survival (Starns et al. 2022). These high-intensity fires resulted in even higher mesquite mortality than the Texas High-Intensity Fire Experiment: ~29% mesquite mortality, compared with ~16% found by Twidwell et al. (2016). Bud banks of two dominant grass species differing in photosynthetic pathway and growth form were also assessed, *Nassella leucotricha* (C3, caespitose) and *Hilaria belangeri* (C4, stoloniferous). The phenology and growth form resulted in different bud loss and recovery; *N. leucotricha* recovered all buds killed by high-intensity fires within eight weeks and *H. belangeri* did not, suggesting it is more sensitive to high-intensity fires, because its buds are shallowly located and active during the time of burning. However, the percentage mortality of buds following fires for both was small for typical and high-intensity fires (Hiers et al. 2021). In addition, there was no change in soil microbes or fungi after high-intensity fires (Culpepper 2020), grass biomass, or loss of biomass to subsequent herbivory (Preiss 2021).

Central Great Plains

Although not as severely encroached as the Southern Great Plains, the Central Great Plains, USA is also experiencing regime shifts from grass-dominated to woodland states, as a result of fire suppression and tree plantings (Donovan et al. 2018; Morford et al. 2021). This is largely driven by a single species, *Juniperus virginiana* (eastern red cedar), which, akin to *Juniperus ashei*, is a non-resprouting, fire sensitive species. Similar to *J. ashei*, *J. virginiana* woodlands cannot be restored to grass-dominance by reinstating traditional low-intensity prescribed fires (Engle and Stritzke 1995; Ortmann et al. 2012; Twidwell et al. 2013a). Seeing losses in forage production from eastern red cedar, a group of ranchers in the Loess Canyon of south-central Nebraska, USA (CGP, Figure 1) formed a prescribed burn association, the Loess Canyon Rangeland Alliance (LCRA), to pool resources to control *J. virginiana* using high-intensity prescribed fires applied near the end of the dormant season (early spring). They take advantage of woodland plant removal cost-shares provided by the United States federal government to cut *J. virginiana* from fire breaks around pastures and use them to add highly flammable ladder fuel that can sufficiently increase fire intensity and residence time to overcome the juniper-fire mortality threshold. The LCRA collaborated with the research laboratory of D. Twidwell at University of Nebraska to study their 15-year management approach, forming the Loess Canyon Experimental Landscape to assess the impacts of high-intensity prescribed fires at an ecoregion-level.

High-intensity fires reduced juniper cover by ~85%, thereby shifting most closed-canopy juniper woodlands back to a grass dominated landscape. Among juniper woodlands that experienced 100% juniper mortality, herbaceous biomass recovered to levels similar to open grassland within a year of high-intensity fires treatments and was maintained at this level for at least 15 years (Bielski et al. 2021). In addition to restoring forage productivity in the region, high-intensity fires has benefited other ecosystem services including increases in grassland bird richness in the Loess Canyons (Roberts et al. 2022).

As of 2020, the LCRA has burned approximately 34 000 ha. The average prescribed fire size was 283 ha from 2002 to 2016, with the LCRA applying several fires per year.

The annual prescribed fire footprint has steadily increased since 2005. In 2016, 4% of Loess Canyons was burned (Roberts et al. 2022). Although woodland encroachment across Nebraska increased by >200 000 ha from 2000 to 2017, trends of encroachment were stabilised in the Loess Canyon after 2011, suggesting the effectiveness of high-intensity fires for halting the trajectory of the woodland regime shift (Fogarty et al. 2020). Because the region is primarily private land, the social network in the Loess Canyons is a critical driver of the success of high-intensity fires. Burn association members own a majority of the ecoregion, collaborate across property lines, work closely with agencies and scientists, and are actively involved in the state Prescribed Fire Council and broader efforts to address woodland encroachment (e.g. providing information during a legislative hearing on eastern red cedar and engaging with the broader Great Plains fire community).

An additional study examined re-encroachment following woodland collapse with high-intensity fires (Fogarty et al. 2021). Juniper seedlings re-established within 1–2 years after fires and quickly recovered to densities greater than or equal to unburned woodlands within 4–11 years. Rapid re-encroachment was largely attributed to high levels of seed availability that allowed nearly instantaneous re-establishment of this non-resprouting species; although, the relative contributions of nearby seed sources versus soil seed banks remains unknown. There is some indication that rates of re-encroachment in this area exceed initial rates of encroachment (DT Fogarty, unpubl. data). Nevertheless, research from the Loess Canyons suggests that frequent, low-intensity follow-up fires would be sufficient to sustain grasslands initially restored with high-intensity fires. Accordingly, high-intensity fire played a special initial role in the long-term maintenance of grassland landscapes prone to woodland encroachment historically by restoring woodland encroached areas that can subsequently be maintained by restarting the grass-fire feedback via frequent low-intensity fires.

Summary and future directions

Experimental studies across continents suggest that high-intensity fires have the potential to control or halt shrub encroachment in semi-arid grassland and savanna systems under certain conditions. Assessments of non-resprouting species in the Great Plains indicate the potential for high-intensity fires to return encroached areas back to grasslands (Bielski et al. 2021). Such fires were also shown to reduce woodland cover of resprouting species in the KNP (but only in the short term Smit et al. 2016; Strydom et al., unpubl. data) (but only in the short term, Smit, et al. 2016; Strydom et al., unpubl. data) and in the southern Great Plains (Twidwell et al. 2016). High-intensity prescribed fires targeting resprouting species in the southern Great Plains resulted in high levels of mortality across resprouting shrub species, whereas in the KNP, mortality was low (Strydom et al., unpubl. data). Resprouting plants typically allocate resources to root reserves during the dormant season and top growth during the growing season (Kays and Canham 1991; Pelc et al. 2011). Top kill in the dormant season has been shown to result in higher resprouting growth rates than top kill during the growing season, because root reserves necessary for resprouting are typically drawn down by early growing season aboveground growth (Buell 1940; Clark and Liming 1953; Wenger 1953; Trapnell 1959; Geldenhuys 1977; Robertson and Hmielowski 2014).

Differing results between high-intensity burn experiments in the KNP (dormant season) and the southern Great Plains (growing season) suggest that the interaction between fire intensity and fire season (and its influence on soil moisture for example) is a key component of fire effectiveness for reducing shrub encroachment in semi-arid systems. Therefore, fire intensity and season are likely to have differing (whether dependent or independent of one another) effects on plant communities, because high fire intensities can be achieved during various seasons. Another potential explanation for these different results is that substantially higher fire intensities were achieved in the Great Plains, compared with the KNP. Accordingly, the application of growing season fires of similar intensities to Great Plains experiments in the KNP might result in higher shrub mortality rates. Whether high-intensity fires in the KNP during the growing season are achievable remains unknown. It will be important to test whether the results from the growing season fires from the Great Plains also apply to other systems, like the KNP, under what conditions such fire intensities are achievable in the growing season, and also what the unintended consequences of such fires may be to other aspects of biodiversity (e.g. loss of tall trees, grass composition).

A number of different methods for achieving high-intensity fires have been used across the reviewed experiments e.g. weather conditions, which may play a role in differential outcomes. Other factors, such as fuel additions, could result in different fire behaviour and attendant effects on woodland plants than low-moisture ambient fuels. In addition, there are a number of experimental design manipulations related to high-intensity fire treatments that are still untested. For example, combinations of fire intensity and frequency manipulations might affect woodland plants differently than a single application of either low- or high-intensity fires. As such, the effects of repeated high-intensity fires and multiple subsequent low-intensity fires at varying frequencies on woodland plant density, reinvasion, and mortality have not been thoroughly assessed. Furthermore, the impacts of ignition patterns (e.g. ring fire versus head fire) as a mechanism to influence fire intensity and hence affect woodland responses are also largely unknown. Fire behaviour and woodland vegetation exposure to high-intensity fires will vary among ignition types. High-intensity fire trials tied to resprouting species in the Great Plains were primarily conducted using ring fires, which can drive higher fire intensities and increase plant exposure to heat. In contrast, successive head fires were used in the 2013 follow up high-intensity fire at the Afsaal site. This was specifically chosen in order to create safe zones for animals to move away from the fire and not be trapped in ring fires. Differences in the impacts of variables like heterogeneity in fuel structure and moisture in relation to ignition type are also unknown and require more direct comparisons.

It is worth noting that the Texas High-Intensity Fire Experiment was conducted during the worst drought on record since the 1950s in that region, and plants were substantially water stressed. Woodland plant mortality in unburned control plots was assumed to be driven in part by drought. In Texas, drought events occur every few years; however, the potential for taking advantage of major drought for applying a high-intensity fires might be less likely in other regions that experience drought less frequently or have large populations of native herbivores that remove fine fuel during droughts. Experiments in Texas used standing-dead fuel to carry surface fires during drought; however, areas where herbivory is high might lack sufficient fuel in the grassland layer during droughts to carry fires. It may also be challenging to convince land managers with grazing animals or conservation managers in National Parks to burn the remaining grass in these drought years, because this would further reduce already limited forage resources. This represents a trade off between short-term losses of immediate grazing during drought years versus potential longer-term forage losses, if woodland plants continue to proliferate. Alternative options, such as supplemental fuel loading, could be considered in such instances to support woodland mortality, as had been shown to be effective in the Central Great Plains and Mesquite High-Intensity Fire Experiments, although this approach may not be feasible at large scales.

Woodland plant recovery (or reinvasion in the case of the Great Plains) was recorded during a field survey 10 to 20 years post fire for resprouting (Afsaal High-Intensity Fire Experiment) and non-resprouting woodland species (Loess Canyons Experimental Landscape) following dormant season fires. This suggests that repeat fires will be necessary to prevent additional reinvasion or densification (Fogarty et al. 2021; Strydom et al., unpubl. data). In African savannas, however, the role of herbivory by large mammals on woodland cover is just as important as fires on tree/grass coexistence. In a mesic savanna, Staver et al. (2009) found that the interacting effects of fires and browsing herbivores had the greatest impact on suppressing tree density. In the Great Plains, mass extinction of Pleistocene megafauna in combination with the near extirpation of remnant browsing and mixed feeding ungulate species, such as pronghorn (*Antilocapra americana*), elk (*Cervus elphus*), and mule deer (*Odocoilues hemionus*), has left grazing cattle as the primary mammalian herbivore, and thus drastically changed browser-fire interactions (O'Connor et al. 2020). Although browsing deer and the introduction of browsing herbivores, such as goats, may reduce woodland vegetation, the densities and feeding impact of large mammals vary widely between continents and land uses and consequently their effect is context-specific and could be further confounded by natural events, such as droughts.

Conclusion

The information provided in these high-intensity fire experiments provides an ideal baseline for additional investigations into the complex relationships between shrub encroachment and high-intensity fires. There are a number of experimental design manipulations related to high-intensity fire treatments that are still untested. Outstanding questions include more species-specific assessments during high-intensity fire trials, direct assessments of plant physiology during fires, direct comparisons of dormant versus growing season fires within the same landscapes and same species, and manipulations of scale among experimental burn plots. Current evidence suggests that the outcomes of high-intensity fires on reducing shrub encroachment require more context as they relate to various environmental variables. Although evidence from studies in the Great Plains suggest there are no strong negative impacts of high-intensity fires on herbaceous vegetation in grasslands systems, concerns remain regarding the effects of high-intensity fires on non-target vegetation, for example, tall trees in African savanna systems. Smit et al. (2016) and Strydom et al. (unpubl. data) found that there was high mortality of tall trees within high-intensity fires plots burned during the dormant season at the KNP experimental sites. Although this is an undesired outcome for park managers, little is known about how tall trees might respond to growing season prescribed burning although we expect less tree mortality with lower intensity fires as experienced in the growing season in the KNP. Similarly, understanding the impacts of fuel structure (e.g. structural heterogeneity of fuels surrounding tall trees), drought conditions, and wildlife interactions (e.g. elephant damage) is necessary to predict undesired tree mortality from high-intensity fires in African savanna systems. Additional research is also required to understand environmental relationships that may affect re-encroachment following high-intensity fires. For example, the relationship between fire intensity and soil seed bank viability, as well as the spatial relationships between seed sources and re-encroachment of high-intensity burned areas are unclear. Alterations to soil microbial communities by woodland encroachers and high-intensity fires (Talbot et al. 2008) are unknown (but see Culpepper 2020), yet they could promote or impede reinvasion. The relationships between high-intensity fires and woody encroachment will also likely shift in response to rising CO_2, warming temperatures, and changing precipitation patterns resulting from climate change.

Moving forward, negative social perceptions about fires remain a barrier for experimentation and implementation (Toledo et al. 2013; Smit et al. 2021). In many regions in the US Great Plains, policy makers and land managers perceive prescribed fires as risky, which has contributed to more destructive wildfires by encouraging fire suppression and woody plant expansion into rangelands (Briggs et al. 2005; Nyongesa and Vacik 2018; Wilcox et al. 2018; Weir et al. 2019). In the KNP, shifting social perceptions about fires have altered fire management activities over the past century, driving changes in fire regime characteristics over time (Strydom and Midzi 2019). Where private landowners dominate a large portion of land management, as in the United States, fear of liability for escaped fires is extremely high (Kreuter et al. 2019), although liability reform has reduced this barrier to prescribed burning in some states (Wonkka et al. 2015). Additionally, social norms (expressed through perspectives about fires by influential relatives and neighbours) have been found to strongly affect decision making about prescribed fires (Toledo et al. 2013). Furthermore, there is a general lack of knowledge on fire application, equipment, and labour that limits the landowners'current ability to apply fires safely (Taylor 2005; Kreuter et al. 2008). Publicly managed lands face considerations tied to negative tourist and visitor perceptions and subsequent publicity linked to fire outcomes that can limit fire management policies. For example, entrenched disincentives to work with fires in the United States hinder major shifts in
fire management policy 'because of liability and casualty risks and little tolerance for management errors' (North et al. 2015). Therefore, a key strategy for moving forward with studying and applying high-intensity fires to reduce shrub encroachment is addressing social perceptions linked to fires, by highlighting the important role and benefits that these prescribed fires can provide. Citizen knowledge is linked to support for practices like prescribed fires (Loomis et al. 2001). Outreach programs that highlight the role of fires in landscape management can be an effective tool for increasing public support for fire application (Loomis et al. 2001; Toman et al. 2006). In addition, scientists should inform the fire narratives in media that the public, land managers, and policy-makers are exposed to in order to inform them about the inevitability of fires in fire prone landscapes and provide more nuanced perspectives on both the benefits and negative impacts of fires (Smit et al. 2022). On private lands specifically, voluntary prescribed burning associations have the capacity to change social norms regarding fires as land management tools and facilitate its use during times when fire intensity is likely to be higher than expected, but also when burn bans are most frequently enacted (Twidwell et al. 2013b; Toledo et al. 2014; Kreuter et al. 2019; McDaniel et al. 2021). Therefore, future research focusing on high-intensity fires should incorporate a social-ecological systems approach that simultaneously addresses the mufti-facetted interactions of the social and biophysical drivers of fire-woody plant dynamics in grasslands and savannas.

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