DISTRIBUTION OF RESPROUTING WOODY PLANTS AND THE EFFECT OF FIRE ON VEGETATION TYPES IN THE SOUTHERN GREAT PLAINS

By

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IN THE SOUTHERN GREAT PLAINS

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Abstract: The effects of soil, topography, and fire on woody plant distribution and extent has been studied over numerous systems; however, most literature has focused individually on these influencing variables at single sites. In this study, we evaluated the effects of soil texture, slope, aspect, and fire measured across 39 ecological sites and four different locations in Oklahoma, USA, from 2018–2019. We used an information-theoretic model building approach to develop models describing the effects of these predictor variables on two different estimates of woody plant cover as well as woody plant density across sites. Top models for all three woody plant metrics indicated that both woody plant cover and density were primarily influenced by percent sand, aspect direction, and the number of times burned. Metrics of woody plant cover and density declined in areas with finer soil textures, east-facing aspects, and areas that were burned more frequently across sites. Of these predictor variables, topoedaphic variables appeared overall to have a greater influence than fire. This suggests that managing woody plants with fire is partly limited by underlying soil and topographic conditions. Summary statistics at the site level mostly indicated relationships similar to cross-site analysis among woody plant metrics and predictor variables, however, there were also differences among sites. In addition to examining broad-scale patterns, we also investigated site-level relationships. Specifically, we examined the post-fire effects on woody plant vegetation type at three of the four sites. Our research suggests that these vegetation types of the Southern Great Plains recover quickly from fire and can be burned every 2-3 years to promote heterogeneity, limit the invasion of non-resprouting woody plants, and potentially benefit native wildlife. Following fire, vegetation cover and structure recovered to pre-burn conditions within 2 years post-fire at all three sites. Our research emphasizes the importance of broad-scale and site-level examination of woody plant distribution to better understand the factors influencing woody plant cover and densities to provide insightful management strategies for these landscapes.

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CHAPTER I

EFFECTS OF FIRE ON VEGETATION COVER AND STRUCTURE ACROSS WILDLIFE MANAGEMENT AREAS IN THE SOUTHERN GREAT PLAINS

ABSTRACT

Prescribed fire is often recommended as a management tool across the Great Plains. Fire has been identified as a disturbance regime that can create greater structural and compositional variation in plant communities across the landscape. This can result in a diversity of habitat types, facilitating heterogeneity and supporting biodiversity. Many wildlife species benefit from this phenomenon, as well as the post-fire effects on food availability and quality. Using three grassland sites primarily managed for wildlife, we sought to describe how the dominant vegetation types of each site responded to prescribed fire treatments. Additionally, wildlife usage of prescribed fire treatments was monitored at each site using cellular game cameras. Our results support that these vegetation types can be burned every 2-3 years to promote heterogeneity, limit the invasion of non-resprouting woody plants, and that wildlife native to these systems coexist well with fire. Following fire, vegetation cover and structure recovered to pre-burn conditions within 2 years post-fire at all three sites. Time since fire was the most significant factor influencing vegetation cover and structure. Vegetation responses among seasonal fire treatments were not analyzed because it was difficult to disentangle the effects of season of burn from time since fire due to a limited sampling design. Wildlife use of fire treatments was not different from unburned treatments. Overall, this research suggests that across unique vegetation types, fire can be used to enhance heterogeneity over short periods without negatively affecting wildlife.

INTRODUCTION

Most plant species native to the Great Plains can persist under disturbance regimes such as fire. The morphological traits (e.g., belowground meristems and large carbohydrate root reserves) of these plants allow them to resprout following a fire event (Bond and Midgely 2001). There have been many studies conducted on the fire responses of different plant communities across the Great Plains. Previous research suggests that most of these plant communities achieve post-fire recovery to vegetation states similar to pre-fire within two to three years. For example, shinnery oak (*Quercus havardii* Rydb.) communities returned to pre-burn conditions within two years following a fire event (Boyd and Bidwell 2002). Similarly, sand sagebrush (*Artemisia filifolia* Torr.) communities have exhibited effects from fire lasting less than three years post-fire (Winter et al. 2012). These studies indicate that vegetation types in the Great Plains recover relatively quickly from fire.

Though past studies suggest that many vegetation types respond similarly to time since fire, there is little empirical evidence comparing the post-fire recovery of different plant communities. Aside from morphological adaptations of the plants themselves, there is evidence that local climate factors may also influence the rate of plant community recovery (Stuart-Haëntjens et al. 2018). More research is needed to better understand how plant responses to fire vary across different ecoregions. This information would contribute to management strategies at both local and regional scales in regard to using prescribed fire as a management tool.

Similar to the plant communities of the Great Plains, the native wildlife of this region historically existed with frequent fires on the landscape (Guyette et al. 2012). It has been observed across a wide variety of taxa that wildlife may alter their diets, foraging behaviors, and movements in response to fire (Pausas and Parr 2018). Raptors (e.g. hawks and kites) have been observed congregating over active fires to feed on exposed prey (Hovick et al. 2017). Large herbivores such as white-tailed deer (*Odocoileus virginianus* Zimmermann) and bison (*Bison bison* L.) prefer burned areas due to the increase in palatability and nutritional quality of resprouting vegetation (Wood 1988; Allred et al. 2011). Even invertebrates have shown increases in abundance within recently burned areas, which further creates a potential food-rich environment for many insectivores (Engle et al. 2008). To avoid predation, white-tailed deer and wild turkey (*Meleagris gallopavo* L.) use recently burned areas due to reduced visual obstruction (Main and Richardson 2002). Though wildlife often have positive relationships with fire, wildlife can also have negative responses to fire. For example, female white-tailed deer with fawns avoid areas that have been recently burned and prefer areas with more cover to mitigate predation (Cherry et al. 2017). Likewise, greater prairie-chickens (*Tympanuchus cupido* L.) require dense, unburned herbaceous vegetation to increase the chances of nesting success (McNew et al. 2015). To compensate for the mixed responses of wildlife to fire, it has been suggested to burn in shifting mosaic patterns to provide the maximum range of habitat types to accommodate a greater diversity of wildlife species (Fuhlendorf et al. 2009).

In this study, we compared plant communities under differing prescribed fire seasons and unburned controls. We hypothesized that these plant communities would recover similarly across sites despite differences in vegetation types, mean annual precipitation, and growing degree days. Specifically, we predicted that these plant communities would respond similarly to time since fire. Our objectives for the vegetation portion of this project were to characterize functional group (grass, forb, woody, litter, and bare ground) responses to time since fire and to determine how quickly vegetation types recovered from fire at each site. We also monitored wildlife use of prescribed fire treatments during this study. We hypothesized that wildlife use would be greater in recently burned areas than in unburned areas. Our objectives for the wildlife portion of this study were to determine the amount of wildlife use on prescribed fire treatments at each site and characterize any relationships between wildlife use and burned/unburned treatments.

METHODS

Study Areas

We conducted this study on Beaver River, Packsaddle, and Cross Timbers Wildlife Management Mreas (WMAs) in Oklahoma that are owned and managed by the Oklahoma Department of Wildlife Conservation (ODWC 2020). Each site is classified within a different Major Land Resource Area (MLRA; Figure 1). MLRAs are a form of land classification developed by the United States Department of Agriculture (USDA-NRCS 2020). A unique vegetation type represented each MLRA (Figure 2).

Beaver River WMA is 7,162 hectares of Southern High Plains MLRA and is located in the Panhandle of the state. Common soils on this site consist mostly of Tivoli Fine Sands and Vona-Tivoli complex series consisting of a sandy texture. Slope is 5-30 % and average elevation is 650 m. Average annual rainfall is 558 mm and the average growing season is 190 days. Average winter temperature is -0.56 º C and average summer temperature is 26.9 º C. This site is characterized by sandy soils that support dune shrubland with margins of shortgrass prairie. Dominant plant species include sand sagebrush (*Artemisia filifolia* Torr.), aromatic sumac (*Rhus aromatica* Aiton), plains sunflower (*Helianthus petiolaris* Nutt.), sand lily (*Mentzelia nuda* [Pursh] Torr. & A. Gray), spectacle pod (*Dimorphocarpa wislizeni* [Engelm.] Rollins), sand bluestem (*Andropogon gerardii* ssp. *hallii* [Hack.] Wipff), giant sandreed (*Calamovilfa gigantea* [Nutt.] Scribn. & Merr.), and buffalograss (*Bouteloua dactyloides* [Nutt.] Columbus).

Packsaddle WMA is located in the Central Rolling Red Plains MLRA and encompasses 7,955 hectares in the far west-central part of the state. Soils consist of Nobscot Delwin complex ranging from loamy to sandy textures. Slope is 3-20% and average elevation is 590 m. This region receives an average annual rainfall of 660 mm and has an average growing season of 195 days. Average winter temperature is 0.28 º C and average summer temperature is 26.6 º C. This site is characterized by its large rolling hills dominated by shinnery oak (*Quercus havardii* Rydb.) shrubland. Other dominant plant species include Oklahoma plum (*Prunus gracilis* Engelm. & A. Gray), sand plum (*Prunus angustifolia* Marshall), Engelmann’s daisy (*Engelmannia peristenia* [Raf.]

Goodman & C.A. Lawson), white prickly poppy (*Argemone albiflora* Hornem.), queen's delight (*Stillingia sylvatica* L.), little bluestem (*Schizachyrium scoparium* [Michx.] Nash), blue grama (*Bouteloua gracilis* [Kunth] Lag. ex Griffiths), and sand dropseed (*Sporobolus cryptandrus* [Torr.] A. Gray).

Cross Timbers WMA is located in the West Cross Timbers MLRA and encompasses 4,168 hectares in the south-central part of the state. Soils are composed of Dougherty and Konsil soil complexes, ranging from loamy sand to sandy textures. Slope is 0-8% and average elevation is 220 m. Average annual rainfall is 1,016 mm and the average growing season is 241 days. Average winter temperature is 6.9 º C and average summer temperature is 28 º C. This site is characterized by patches of oak forest, oak savannah, and tallgrass prairie. Dominant plant species include post oak (*Quercus stellata* Wangenh.), blackjack oak (*Quercus marilandica* Münchh.), winged sumac (*Rhus copallinum* L.), rough-leaf dogwood (*Cornus drummondii* C.A. Mey.), cedar elm (*Ulmus crassifolia* Nutt.), western ragweed (*Ambrosia psilostachya* DC.), partridge pea (*Chamaecrista fasciculata* [Michx.] Greene), lemon beebalm (*Monarda citriodora* Cerv. ex Lag.), big bluestem (*Andropogon gerardii* Vitman), switchgrass (*Panicum virgatum* L.), and Canada wildrye (*Elymus canadensis* L.).

Study Design and Data Collection

Packsaddle WMA had 12 treatment plots that Boyd & Bidwell (2001) established in a previous study. Using a similar design, we established 9 treatment plots at both Cross Timbers WMA and Beaver River WMA. All fire plots had not been burned for at least seven years, reducing the potential of any residual fire effects. All treatment plots were 0.4 hectares in size and within the same general proximity from each other at each site. At each site, there were three treatments: control (no burn), dormant season burn, and growing season burn. Cross Timbers WMA and Beaver River WMA had three replicates for each treatment, whereas Packsaddle WMA had four. We sampled plots annually from 2018-2020 during the late growing season. Pre-burn data were collected in 2018, while post-burn data were collected in 2019 and 2020. Dormant season burns were conducted between late February and early April, whereas growing season burns were conducted from mid-June to late July. Fire treatment replicates were burned on the same day at each site; however, fire treatment burn dates varied across sites (Table 1). Two vegetation sampling arrays were randomly assigned to each treatment plot. Arrays were $\geq$ 50 m apart and $\geq$ 30 m from the treatment plot boundary. At the center of each array, four 10-m tapes radiated in each cardinal direction. At the end of each transect, percent basal and canopy cover and maximum height (or depth for litter) of functional groups (grass, forb, woody, litter, and bare ground) were recorded within a 0.25 m^2 (50 cm X 50 cm) modified Daubenmire frame (n = 240). Percent cover was classified using the Daubenmire midpoint cover class index (Daubenmire 1968). Only woody plants were classified by species. Time since fire (months) and season of burn (dormant or growing season) were recorded for each array. We measured vegetation variables at 3-, 6-, 15-, & 18-months post-fire. A timeline illustration of the vegetation portion of this study is provided in Figure 3.

We monitored wildlife use by deploying cellular game cameras on treatment plots. SpyPoint® cameras were placed on one randomly selected replicate of each treatment at all three sites (n = 12) at the end of the first growing season after fire treatments were implemented. These cameras had a detection range of $\leq$ 24.4 meters and were equipped with infrared flash to capture detections at night. Cameras were set to have a latency time between photos of 5 minutes. Photos were transmitted daily and accessed through a software program provided by SpyPoint®. Unlimited photo transmission plans were purchased for each camera individually (SpyPoint 2020). Cameras were mounted to t-posts 80cm above the ground and placed 0.5 m inside plots so that the entire viewshed of each camera trap only included one treatment. These cameras were installed in November 2019 and operated continuously until November 2020 (Figure 3). Date, time, temperature, plot treatment (burned and unburned), wildlife type, and the number of individuals captured were recorded for each camera trap detection (n = 560). To approximate wildlife use, we divided the number of days within each month that wildlife were detected by the number of days respectively for each month. We then converted this to a percentage of monthly wildlife detection days. This gave us a proportion of monthly wildlife detection days for treatments at each site.

We collected on-site prescribed burn conditions for each fire treatment using a handheld weather meter. Temperature (°C), relative humidity (%), wind speed (km h^{-1}), and wind direction were recorded immediately before and after each burn (n = 40). The first three variables listed are primary weather parameters that influence fire behavior. Duration of burn (minutes) was recorded for each replicate as well (Engle et al. 1989; Platt et al. 2015). Soil moisture was derived by sourcing data from the Oklahoma Mesonet System and calculating the Fractional Water Index (FWI) at a 60 cm depth. We also used Oklahoma Mesonet data to estimate growing degree days on each site (based on warm-season herbaceous plants) and estimate the number of days without a precipitation event before and after the prescribed burns (Oklahoma Mesonet System 2020). Fine dead fuel moisture was estimated by dividing recorded relative humidity values by five (NWCG 2021). One-hour fuel loads were collected by using a simple random sampling approach. Samples were collected from locations 20 m outside of the plots for both fire treatments at each site in 2019. We did not sample within the treatment plots so that WMA managers could burn treatments without being postponed by the logistical obstacle of technicians sampling within plots before burning. Each sample was 10 m apart and randomly selected using compass degree directions (0-360º). One-hour fuels were defined as any fine fuel with a diameter ≤ 6.35 mm. At each sample point, all one-hour fuels within a 0.09m^2 metal ring were clipped and gathered into a bag to be oven-dried for two weeks (Cruz et al. 2018). For each fire treatment, samples were used to estimate kilograms per hectare of fine fuel load.

Data Analysis

To evaluate main and interaction effects for each vegetation functional group variable, two-way ANOVAs were used with time since fire (5 levels: Unburned, 3 months, 6 months, 15 months, 18 months) and site (3 levels: each WMA) as independent variables. Mean and standard error values were calculated for functional group variables at each level of time since fire. After further evaluation, we did not analyze or report comparisons of functional groups among seasonal fire treatments and unburned controls due to the potential for erroneous conclusions resulting from a limited sampling design.

To evaluate main and interaction effects for wildlife use, two-way ANOVAs were used with plot treatment (2 levels: burned and unburned) and site (3 levels: each WMA) as independent variables. As a summary analysis of wildlife use across sites, monthly wildlife detection days for burned and unburned treatments were compared. Additional summary analyses included the percent of total detections by wildlife type and the number of wildlife species detected across sites. All statistical analyses were conducted using RStudio version 1.3.1056 (RStudio Team 2020).

RESULTS

As our sites were different in dominant vegetation, it is not surprising that most of the analyses had significant interactions between site and time since fire (Table 2). We found that most functional groups exhibited different responses to time since fire at each site with only forb and litter cover variables exhibiting uniform responses across the three study sites. Although most functional group responses were dependent on site, a general pattern of post-fire recovery was observed. By 1.5 years post-fire, functional groups within all study sites had returned to a state similar to unburned conditions. All of these vegetation sites recover rapidly from prescribed fire.

The initial post-fire response for grass cover and height differed among sites. Grass cover and height within fire treatments at Beaver River WMA exhibited greater amounts than the unburned treatments 6 months post-fire, while grass cover and height was greater in unburned treatments than in fire treatments at Packsaddle and Cross Timbers WMAs (Table 3). However, both grass cover and height recovered to levels similar to unburned treatments within a year. Forb cover within fire treatments across sites decreased immediately following fire but increased to amounts greater than unburned treatments by 6 months post-fire. Forb cover within fire treatments peaked at 15 months post-fire and remained greater than unburned treatments for the remainder of the study (Figure 4). Forb height within fire treatments decreased immediately after fire at all three sites but recovered to levels similar to unburned treatments within 6 months post-fire. Within fire treatments, Packsaddle WMA exhibited an increase in forb height compared to unburned treatments at 1-year post-fire and for the remainder of the study (Table 3). Woody plant cover within fire treatments decreased immediately after fire at each site and remained at lower levels than unburned treatments until 18 months post-fire when it returned to levels similar to unburned treatments (Figure 5). Woody plant height within fire treatments decreased immediately after fire at each site but recovered at different rates. Woody plant height at Cross Timbers WMA returned to levels similar to unburned treatments at 6 months post-fire, whereas it took Beaver River WMA an entire year to recover. After fire, Packsaddle WMA woody plant height within fire treatments was less than unburned treatments for the rest of the study (Table 3). Litter cover within fire treatments across sites decreased immediately following fire and remained at levels lower than unburned treatments until 18 months post-fire. By the end of the study, litter cover within fire treatments across sites had returned to levels similar to unburned treatments (Figure 4). Litter depth within fire treatments at each site declined dramatically immediately following fire. At Cross Timbers WMA, litter depth returned to levels similar to unburned treatments by 6 months post-fire. However, litter depth within fire treatments at Packsaddle and Beaver River WMAs did not return to pre-burned conditions until 1-year post-fire (Table 3). Bare ground cover within fire treatments at each site increased immediately following fire and remained at greater levels than unburned treatments throughout the remainder of the study (Table 3).

We detected a total of 26 wildlife species on treatment plots across all sites from 2019-2020 (Figure 6). Twelve wildlife species were detected at Cross Timbers WMA, 7 species at Packsaddle WMA, and 20 species at Beaver River WMA. Deer (*Odocoileus* sp.) composed 72% of total wildlife detections across sites. Songbirds (*Passeriformes* L.) contributed 10% of total detections, whereas gamebirds (*Phasianidae* L. and *Odontiphoridae* Gould) and coyotes (*Canis latrans* Say) both composed 5% of total detections. Bobcat (*Lynx rufus* Schreber), raptors (*Accipitridae* Vieillot), rabbits (*Lepus* sp. L.), and pigs (*Sus scrofa* L.) individually made up <5% of total detections (Figure 7).

We found that wildlife exhibited different responses to plot treatment (burned or unburned) at the site level (Table 2). Beaver River and Packsaddle WMAs had little difference ($P \geq 0.05$) in wildlife detections between burned and unburned treatments, but Cross Timbers WMA experienced more wildlife use in unburned treatments ($P = 0.012$) than burned treatments. Total wildlife detection days across sites for burned and unburned treatments by month indicated neither a positive or negative relationship between wildlife use and prescribed fire (Figure 7).

Weather conditions for the dormant and growing season burns are presented in Table 1. Temperatures were lower during dormant season burns and higher during growing season burns. Wind speeds and directions varied regardless of season. Relative humidity and fine dead fuel moisture were lower during dormant season burns and higher during growing season burns at Cross Timbers and Packsaddle WMA. However, these variables at Beaver River WMA were lower during the growing season burns than during the dormant season due to the dry conditions occurring in the region during late summer of 2019. Similarly, duration of burn (minutes) was shorter during dormant season burns than for growing season burns at Cross Timbers and Packsaddle WMAs, whereas at Beaver River WMA, growing season burn duration was shorter than dormant season. Fine fuel loads (kg/ha) followed along a gradient of decreasing amounts from east to west by site (Table 1).

DISCUSSION

Our study found that these three unique plant communities of the Great Plains recover quickly from fire, despite differences in vegetation type and local climate. This is supported by previous research conducted at single sites across the Great Plains (Boyd and Bidwell 2002; Winter et al. 2012). This study is unique because it compares empirical fire-response data from three different vegetation types. Despite differences in local climate and vegetation, all sites demonstrated rapid recovery indicating that prescribed fires applied every 2-6 years can be used to provide heterogeneity in vegetation cover and structure on these landscapes (Fuhlendorf and Engle 2001; Guyette et al. 2012).

The amount and timing of precipitation and average annual growing degree days at each site is important for the rate of plant community recovery post-fire (Zhou et al. 2009) The most rapid post-fire recovery occurred at Cross Timbers WMA which received the most rainfall and average annual growing degree days of the three sites (Table 3). Conversely, the most delayed post-fire recovery of the three sites occurred at Packsaddle

WMA, which received the least amount of precipitation among sites in 2019 (Table 3). At Beaver River WMA, post-fire recovery of grass cover and height exhibited substantial increases compared to unburned treatments at 6 months time since fire, a trend unique to this site. By the following year, both grass cover and height within fire treatments had returned to amounts similar to unburned treatments. This short-term increase in grass cover and height within fire treatments is likely explained by an increase in giant sandreed (*Calamovilfa gigantea*) that occurred after burning at this site. This plant seemed to respond positively to fire as it rapidly increased and initiated reproduction with peduncles growing well over 1 meter in height. Though no fire response records could be found for this species in the literature, it has been documented that *C. longifolia* (Hook.) Scribn., a congeneric species, increases after fire events (Bragg 1998). Despite the variability of growing season rainfall among sites and years, average annual growing degree days, and species-specific fire responses, each vegetation type that underwent prescribed fire treatments exhibited relatively quick overall recovery, returning to conditions similar to that of unburned treatments in 1.5 years.

The functional grouping of woody plants decreased within fire treatments immediately following fire but returned to conditions similar to unburned treatments within 1.5 years at all sites. However, when dominant woody plant species are considered independently for each site, there were some slight differences in the rate of recovery. Lack of any long-term decreases in woody cover and height were anticipated, as all dominant species recorded in this study are known resprouters (Bond and Midgely 2001). Across sites, this study included 8 dominant woody plant species and 6 dominant woody plant genera within treatment plots. The dominant woody plants at Beaver River WMA included sand sagebrush (*Artemisia filifolia*) and aromatic sumac (*Rhus aromatica*). Past research at other sites located in western Oklahoma support our conclusions that neither of these shrub species exhibit any effect from fire within < 3 years post-fire (Burton et al. 2011; Winter et al. 2012). At Packsaddle WMA, dominant species included shinnery oak (*Quercus havardii*) and Oklahoma plum (*Prunus gracilis*). Previous research determined that following fire, these dominant shrubs return to pre-burn conditions within 2-3 years (Boyd and Bidwell 2002). Among sites, Cross Timbers WMA had the greatest diversity of woody plant species within treatment plots. Dominant species at this site included winged sumac (*Rhus copallinum*), rough-leaf dogwood (*Cornus drummondii*), cedar elm (*Ulmus crassifolia*), and post oak (*Quercus stellata*). Other studies conducted within similar systems reported that these dominant woody species resprout vigorously after fire, showing no long-term decreases in cover or height unless the fire frequency is applied annually for several consecutive years (Peterson et al. 2007; Burton et al. 2011).

This study illustrates how post-fire vegetation effects are largely conditional on what type of vegetation is being burned and what weather conditions are present during a fire. This study lacked woody plants like the invasive eastern redcedar (*Juniperus virginiana* L.), which would greatly modify post-fire woody plant responses because of their inability to resprout. We likely would have observed fire having a greater, long-term decrease on woody plant cover if our treatment plots were experiencing encroachment of eastern red cedar (Bond and Midgely 2001). Managers should be mindful that periodically burning these disturbance-dependent systems is preventing fire-intolerant species, such as eastern red cedar, from invading. Once established, these plants can have negative impacts on both native and agricultural ecosystems (Archer 1994; Twidwell et al. 2013). In addition to preventing cedar encroachment with periodic fires, our prescribed burn condition records during the study provide insight on how environmental variables can greatly influence fire behavior and intensity (Platt et al. 2015). Many studies have identified correlations between season of burn and the resulting fire intensities and behaviors of a respective season (Platt et al. 1988; Sparks et al. 2002). However, our data support that though seasons of burn have generalized fire intensity and behavior patterns, these fire parameters are ultimately influenced by weather and environmental conditions at the time of burn (Glitzenstein et al. 1995; Bradstock et al. 2009). For example, Packsaddle and Cross Timbers WMAs exhibited traditional season of burn conditions, having higher relative humidity and longer burn durations during growing season burns than in dormant season burns (Platt et al. 1988). However, Beaver River WMA exhibited lower relative humidity and shorter burn duration for growing season burns (Table 1). This was likely caused by a lack of rainfall, resulting in drier weather conditions and presumably increased fire intensity (Oklahoma Mesonet System 2020).

In this study, season of burn was largely confounded by time since fire. Our sampling methods were somewhat limiting (once annually) and did not record both dormant and growing season burns at the same increments of time since fire to better capture seasonal fire effects. Time since fire, season of burn, and fire intensity are three commonly used metrics for examining fire effects, however, the interconnectedness of these variables is not acknowledged nearly enough within study designs (Figure 3). We felt it was appropriate to note that this study is just one example of why fire research should always acknowledge confounding variables within a given study. (Glitzenstein et al. 1995; Ansley et al. 2006).

Our study suggests that wildlife native to the Great Plains are not negatively affected by prescribed fire. Though we didn't find any positive relationships between wildlife use and recently burned areas across sites, our findings show little difference in wildlife use between burned and unburned treatments indicating that wildlife were not deterred by the presence of fire. Previous studies largely echo this conclusion, even indicating positive relationships between wildlife and fire (Main and Richardson 2002). However, other studies have shown wildlife avoiding recently burned areas due to requirements during certain life stages (Cherry et al. 2017). At the site level, our wildlife use data had mixed results between burned and unburned treatments. Both Beaver River and Packsaddle WMAs exhibited more wildlife detections in burned treatments than in unburned treatments whereas Cross Timbers WMA had more wildlife detections in unburned treatments. This inconsistency within the data could potentially be explained by our sampling methods. First, we did not collect any pre-treatment data on wildlife use. Thus, wildlife may have utilized unburned treatment areas more than the nearby fire treatment areas before prescribed fires were conducted (Meek et al. 2015). For example, 71% of total wildlife detections at Cross Timbers WMA were captured within the unburned treatment replicate where a prominent game trail was later identified. Secondly, our sampling design likely missed capturing when wildlife use may have been highest following prescribed burns because of the time-lapse between conducting fires and installing camera traps. Cameras were installed at the beginning of the dormant season (November) after seasonal fire treatments had been applied during the prior dormant and growing season. Because of the post-growing season installation date, the greatest levels of post-fire vegetation responses (e.g., forage quality, forage abundance, and vertical structure) were likely missed. Other studies have provided evidence that these vegetation responses are the factors influencing wildlife to utilize recently burned areas (Fuhlendorf et al. 2009; Pausas and Parr 2018). We recommend that for best potential results, future studies install camera traps before or immediately after fire treatments are burned (Meek et al. 2015).

Cellular camera traps captured a wide array of species, however, the majority (>90%) of species captured were generalists, a potential explanation as to why fires did not have a greater effect on wildlife use. Generalist species have less specific habitat and forage needs, thus they could potentially exhibit less response to fire. Specialist species rely heavily on specific stages of plant succession and forage types and could potentially have stronger relationships with fire. It is possible that we did not detect any specialist species within our fire treatments due to the small scale of the treatments (Pausas and Parr 2018).

CONCLUSIONS

Plant communities in this study returned to pre-burn conditions in less than 2 years after fire, despite differences in vegetation type and local climate. Our study suggests that these systems can be burned every 2-3 years, which could theoretically increase heterogeneity. The implementation of fires are beneficial in preventing fire intolerant species (i.e., eastern red cedar) from encroaching into these grassland systems.

Wildlife exhibited no negative response to prescribed fire treatments. The majority of prior research indicates that many wildlife species, whether generalists or specialists, generally benefit from fire as a disturbance regime. Though this study yielded few conclusive findings on wildlife use of burned areas, our data provide support that wildlife were not deterred from areas experiencing fire as a management tool.

Lastly, this study is one of many examples of fire studies that illustrate how difficult it can be to identify the main effect(s) in fire research. Researchers must acknowledge confounding variables and consider alternative effects before making definitive claims about any particular metric. We must recognize how complex fire studies can be and we must be aware of the confounding nature of fire effect variables.

If you would like to see how the prescribed burns were conducted during this study, what the different vegetation types looked like before and after fire treatments, and would like to browse the entire photo gallery of wildlife we detected on camera, follow this link to our website: https://johndmcquaig.wixsite.com/okwildliferxfire.

ACKNOWLEDGMENTS

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TABLES AND FIGURES

Table 1. Prescribed burn conditions (Mean ± SE) recorded for both dormant and growing season burns in 2019 at Beaver River, Cross Timbers, and Packsaddle WMAs located in Oklahoma, USA. Dormant season burns were conducted from February-March and growing season burns from June-July. The variables listed in this table provide insight on potential explanations for post-fire responses and recovery of functional groups and vegetation types for fire treatments at each site.

	Wildlife Management Area					
	Beaver River		Packsaddle		Cross Timbers	
	DSB	GSB	DSB	GSB	DSB	GSB
Variable	**03/24/2019**	**07/30/2019**	**02/26/2019**	**06/20/2019**	**03/06/2019**	**07/11/2019**
Temperature (°C)	14.80 ± 0.92	37.40 ± 0.53	2.90 ± 0.17	33.20 ± 0.09	8.90 ± 0.25	35.70 ± 0.31
Wind Speed (km h^{-1})	15.30 ± 1.30	15.00 ± 0.80	5.40 ± 0.29	16.90 ± 0.53	12.90 ± 0.72	7.00 ± 0.34
Wind Direction	Northeast	South	North	South	Southeast	Variable
Relative Humidity (%)	53.30 ±3.92	24.30 ± 2.09	38.00 ± 0.19	55.10 ± 1.09	27.70 ± 0.89	53.70 ± 0.92
Fine Dead Fuel Moisture (%)	10.67 ± 0.78	4.87 ± 0.42	7.60 ± 0.04	11.03 ± 0.22	5.40 ± 0.18	10.73 ± 0.18
Soil Moisture (FWI) – 60 cm depth	0.80	0.66	0.68	0.75	0.90	0.87
Fine Fuel Load (kg/ha)	2,510.60 ± 161.79	5,451.20 ± 91.34	6,935.80 ± 157.85	9,149.30 ± 242.21	8,601.50 ± 166.39	10,902.40 ± 225.23
Duration of Burn (minutes)	12.40 ± 1.45	8.00 ± 2.08	8.00 ± 0.58	13.75 ± 1.89	7.33 ± 0.33	10.51 ± 3.38

Table 1 (continued)

	Wildlife Management Area					
	Beaver River		**Packsaddle**		**Cross Timbers**	
	Dormant Season Burn	**Growing Season Burn**	**Dormant Season Burn**	**Growing Season Burn**	**Dormant Season Burn**	**Growing Season Burn**
Variable	**03/24/2019**	**07/30/2019**	**02/26/2019**	**06/20/2019**	**03/06/2019**	**07/11/2019**
Time Since Rainfall (days)	1	9	3	1	2	3
Post-Burn Duration Until Rainfall (days)	8	9	12	1	2	18

Table 2. Results of two-way ANOVAs on vegetation and wildlife responses to fire treatments across sites in 2019-2020, Oklahoma, USA. **A)** Two-way ANOVA results on both cover and structure of each functional group (grass, forb, woody, litter, and bare ground) between time since fire, site, and their interactions. **B)** Two-way ANOVA results on wildlife use between plot treatments (burned vs. unburned), site, and their interaction.

	Variable	Explanatory	F	*P*-value
A.				
	Grass Cover	Time Since Fire	8.63	<0.001
		Site	21.33	<0.001
		Time Since Fire x Site	5.67	<0.001
	Grass Height	Time Since Fire	22.25	<0.001
		Site	18.87	<0.001
		Time Since Fire x Site	8.84	<0.001
	Forb Cover	Time Since Fire	17.53	<0.001
		Site	7.59	<0.001
		Time Since Fire x Site	1.95	0.061
	Forb Height	Time Since Fire	44.34	<0.001
		Site	134.92	<0.001
		Time Since Fire x Site	24.39	<0.001
	Woody Cover	Time Since Fire	29.08	<0.001
		Site	23.91	<0.001
		Time Since Fire x Site	3.23	0.003
	Woody Height	Time Since Fire	20.89	<0.001
		Site	12.27	<0.001
		Time Since Fire x Site	2.38	0.022
	Litter Cover	Time Since Fire	8.76	<0.001
		Site	0.98	0.381
		Time Since Fire x Site	0.97	0.466
	Litter Depth	Time Since Fire	10.77	<0.001
		Site	1.25	0.302
		Time Since Fire x Site	2.51	0.016
	Bare Ground Cover	Time Since Fire	41.29	<0.001
		Site	17.60	<0.001
		Time Since Fire x Site	3.08	0.004
B.				
	Wildlife Detection Days	Plot Treatment	1.36	0.5459
		Site	4.45	0.0081
		Plot Treatment x Site	0.64	0.0022

Table 3. Functional group (grass, forb, woody, litter, and bare ground) response to unburned (CTL), dormant season burns (DSB), and growing season burns (GSB) at each site (Mean ± SE) from 2019-2020, Oklahoma, USA. Additional local climate data was added to provide insight on potential relationships between post-fire functional group recovery and the respective environment.

		Wildlife Management Area								
		Beaver River			**Packsaddle**			**Cross Timbers**		
		CTL	**DSB**	**GSB**	**CTL**	**DSB**	**GSB**	**CTL**	**DSB**	**GSB**
Year	**Variable**	**---**	**03/24/2019**	**07/30/2019**	**---**	**02/26/2019**	**06/20/2019**	**---**	**03/06/2019**	**07/11/2019**
2019										
	Time-Since-Fire (months)	---	6	3	---	6	3	---	6	3
	Growing Season Rainfall (mm)	493.77	493.77	493.77	429.77	429.77	429.77	949.21	949.21	949.21
	Growing Degree Days (GDD)	204	204	204	207	207	207	221	221	221
	Grass Cover (%)	15.58 ± 7.42	55.99 ± 10.08	6.04 ± 5.49	39.72 ± 4.86	29.31 ± 6.49	6.86 ± 7.35	84.10 ± 4.13	64.00 ± 6.36	26.40 ± 8.81
	Bare Ground Cover (%)	28.60 ± 9.93	43.41 ± 8.06	80.25 ± 11.23	0.18 ± 0.12	21.58 ± 3.82	71.18 ± 4.33	2.71 ± 1.83	34.92 ± 4.90	37.58 ± 6.34
	Grass Height (cm)	45.10 ± 2.76	100.09 ± 11.23	5.29 ± 2.19	100.84 ± 5.47	63.47 ± 7.29	25.91 ± 8.26	116.00 ± 10.91	98.92 ± 6.45	41.63 ± 5.22
	Forb Height (cm)	43.52 ± 3.45	49.10 ± 5.23	8.93 ± 3.87	4.06 ± 2.60	8.07 ± 2.75	6.51 ± 3.11	48.50 ± 5.51	88.52 ± 7.18	21.01 ± 2.83

Table 3 (continued)

		Wildlife Management Area								
		Beaver River			Packsaddle			Cross Timbers		
		CTL	DSB	GSB	CTL	DSB	GSB	CTL	DSB	GSB
Year	**Variable**	**---**	**03/24/2019**	**07/30/2019**	**---**	**02/26/2019**	**06/20/2019**	**---**	**03/06/2019**	**07/11/2019**
2019										
	Woody Height (cm)	47.78 ± 4.51	27.25 ± 6.11	3.67 ± 1.66	108.14 ± 5.71	38.31 ± 7.61	23.60 ± 8.63	61.80 ± 32.56	30.84 ± 6.14	13.92 ± 7.65
	Litter Depth (cm)	8.95 ± 1.50	0.68 ± 0.34	0.63 ± 0.21	4.47 ± 0.28	0.75 ± 0.37	0.64 ± 0.41	3.41 ± 2.12	2.79 ± 1.30	0.58 ± 0.39
2020										
	Time-Since-Fire (months)	---	18	15	---	18	15	---	18	15
	Growing Season Rainfall (mm)	209.80	209.80	209.80	247.39	247.39	247.39	752.60	752.60	752.60
	Growing Degree Days (GDD)	206	206	206	209	209	209	232	232	232
	Grass Cover (%)	16.63 ± 6.63	38.31 ± 4.83	34.92 ± 7.31	38.81 ± 8.07	47.06 ± 6.88	40.12 ± 5.22	87.56 ± 7.38	80.32 ± 3.56	70.83 ± 9.14
	Bare Ground Cover (%)	24.96 ± 5.01	27.70 ± 5.21	32.93 ± 6.01	0.16 ± 0.28	6.46 ± 5.99	17.78 ± 4.05	2.80 ± 1.64	6.17 ± 4.38	26.95 ± 5.45
	Grass Height (cm)	47.30 ± 7.45	43.02 ± 5.98	37.67 ± 10.69	106.85 ± 6.51	90.43 ± 11.33	65.28 ± 5.12	120.94 ± 11.89	112.18 ± 14.70	122.30 ± 10.85
	Forb Height (cm)	45.21 ± 8.90	38.75 ± 5.29	50.38 ± 4.88	3.95 ± 2.16	19.91 ± 2.32	45.09 ± 2.91	46.71 ± 6.43	34.31 ± 5.99	44.32 ± 4.54

Table 3 (continued)

		Beaver River			Packsaddle			Cross Timbers		
		CTL	DSB	GSB	CTL	DSB	GSB	CTL	DSB	GSB
Year	**Variable**	---	03/24/2019	07/30/2019	---	02/26/2019	06/20/2019	---	03/06/2019	07/11/2019
2020										
	Woody Height (cm)	49.13 ± 3.58	51.71 ± 3.34	37.46 ± 6.20	113.30 ± 6.87	63.37 ± 7.43	50.45 ± 8.01	65.30 ± 9.43	65.02 ± 14.52	62.76 ± 21.58
	Litter Depth (cm)	9.05 ± 4.89	2.75 ± 2.51	3.00 ± 2.17	5.22 ± 0.39	3.89 ± 0.65	4.47 ± 0.03	3.81 ± 1.71	3.48 ± 2.17	2.89 ± 2.02

Wildlife Management Area (spanning header above Beaver River, Packsaddle, Cross Timbers)

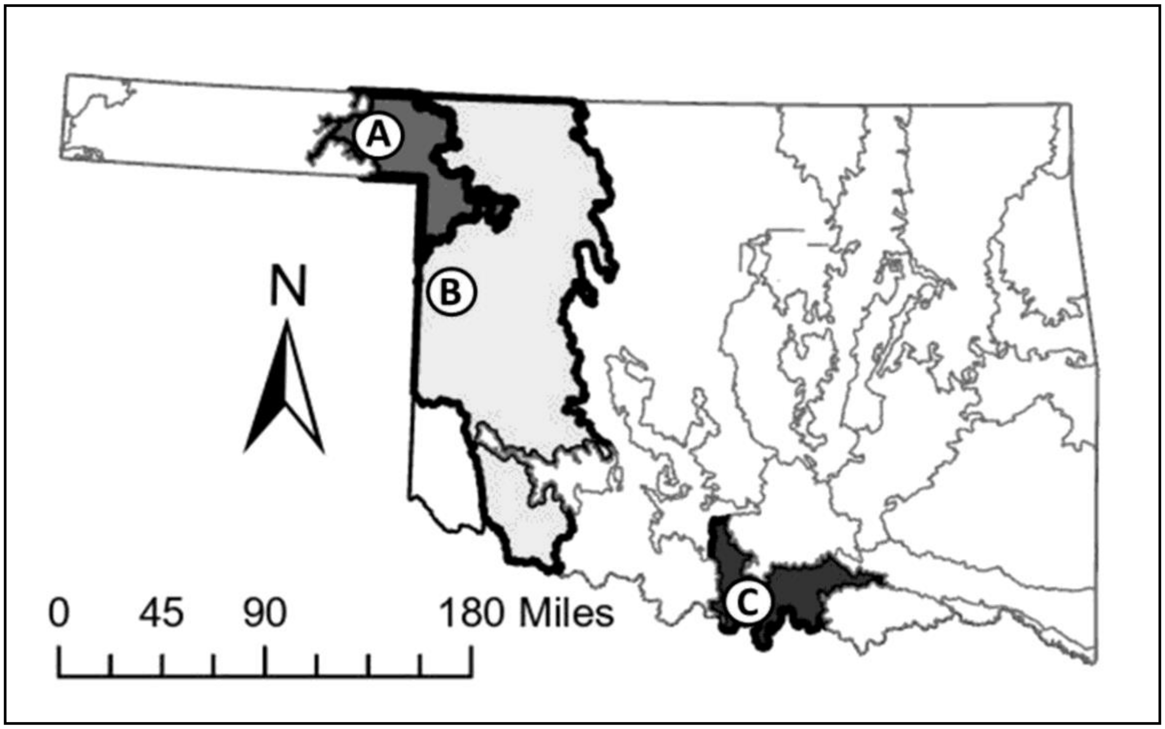

Figure 1. Study site locations of the three wildlife management areas (WMAs) managed by the Oklahoma Department of Wildlife Conservation in Oklahoma, USA. Each of these WMAs represent a different major land resource area (MLRA). From west to east, site names are as follows with their respective MLRAs: **A)** Beaver River WMA – Southern High Plains, **B)** Packsaddle WMA – Central Red Rolling Plains, and **C)** Cross Timbers WMA – West Cross Timbers.

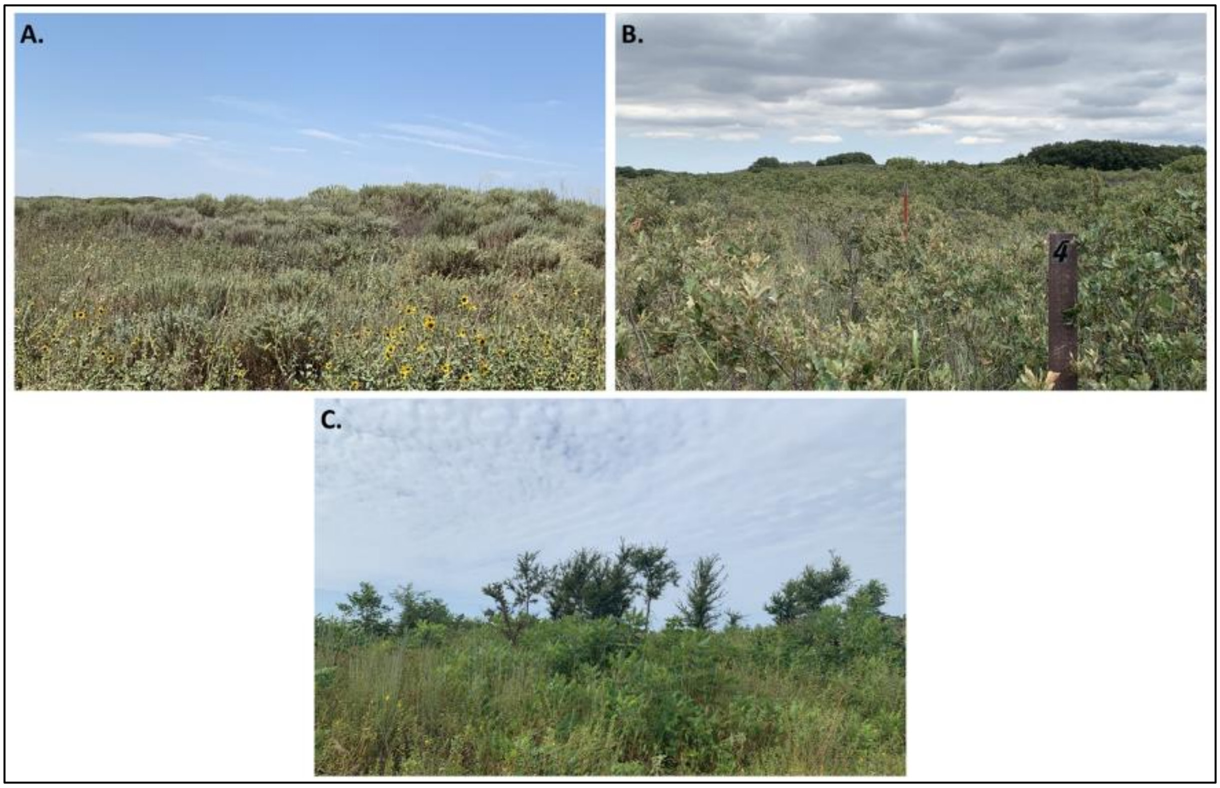

Figure 2. Representative plant communities for each study site located in Oklahoma, USA: **A)** Beaver River Wildlife Management Area (WMA) is dominated by shortgrass species and sand sagebrush (*Artemisia filifolia*), **B)** Packsaddle WMA is dominated by midgrass species and shinnery oak (*Quercus havardii*), and **C)** Cross Timbers WMA is dominated by tallgrass species, oaks (*Quercus* sp.), sumacs (*Rhus* sp.) and elms (*Ulmus* sp.).

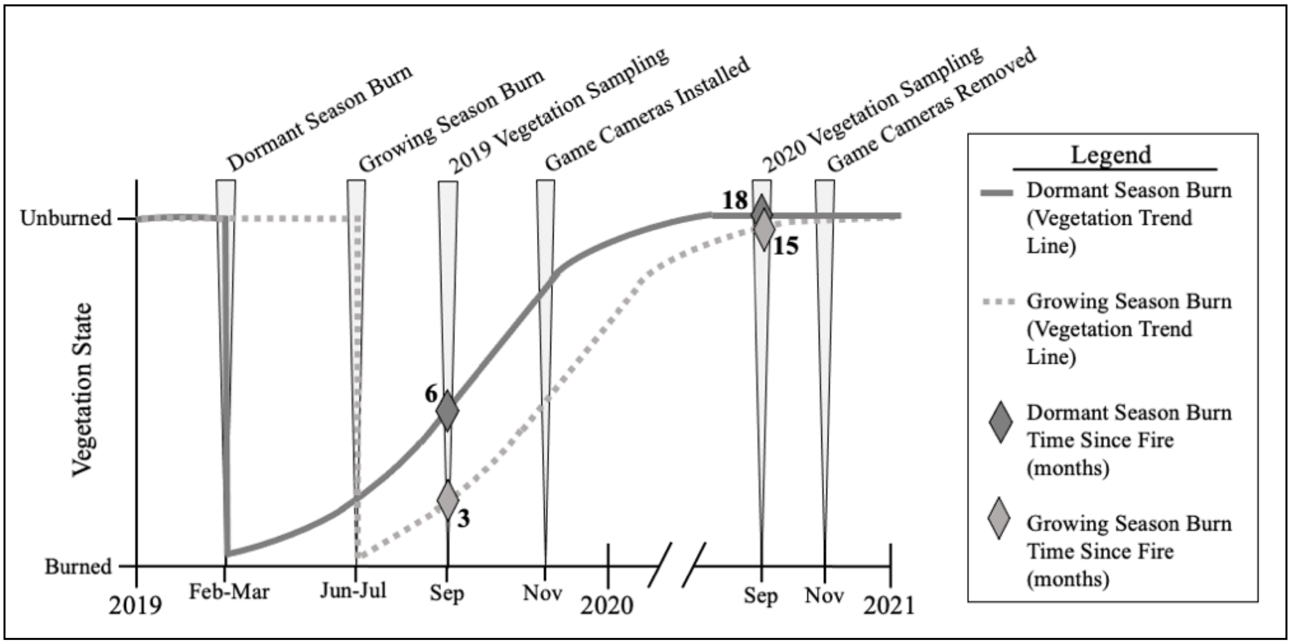

Figure 3. Timeline of this research project illustrating how easily time since fire and season of burn can become confounded with a limited sampling design. The x-axis is the timeline of the study (2019-2021), whereas the y-axis describes vegetation state in relation to being burned or unburned. Solid and dashed trend lines represent estimated vegetation states for plant communities undergoing dormant and growing season burns respectively. Diamonds along trend lines with values represent time since fire (months) sampled for both fire treatments. This timeline illustrates how season of burn can offset increments of time since fire for treatments under a low sampling frequency. It also shows that our game cameras were deployed after the greatest potential fire effect window had already passed. One year post-fire, vegetation states become more similar between fire treatments (15 and 18 months time since fire) as effects from fire begin to fade.

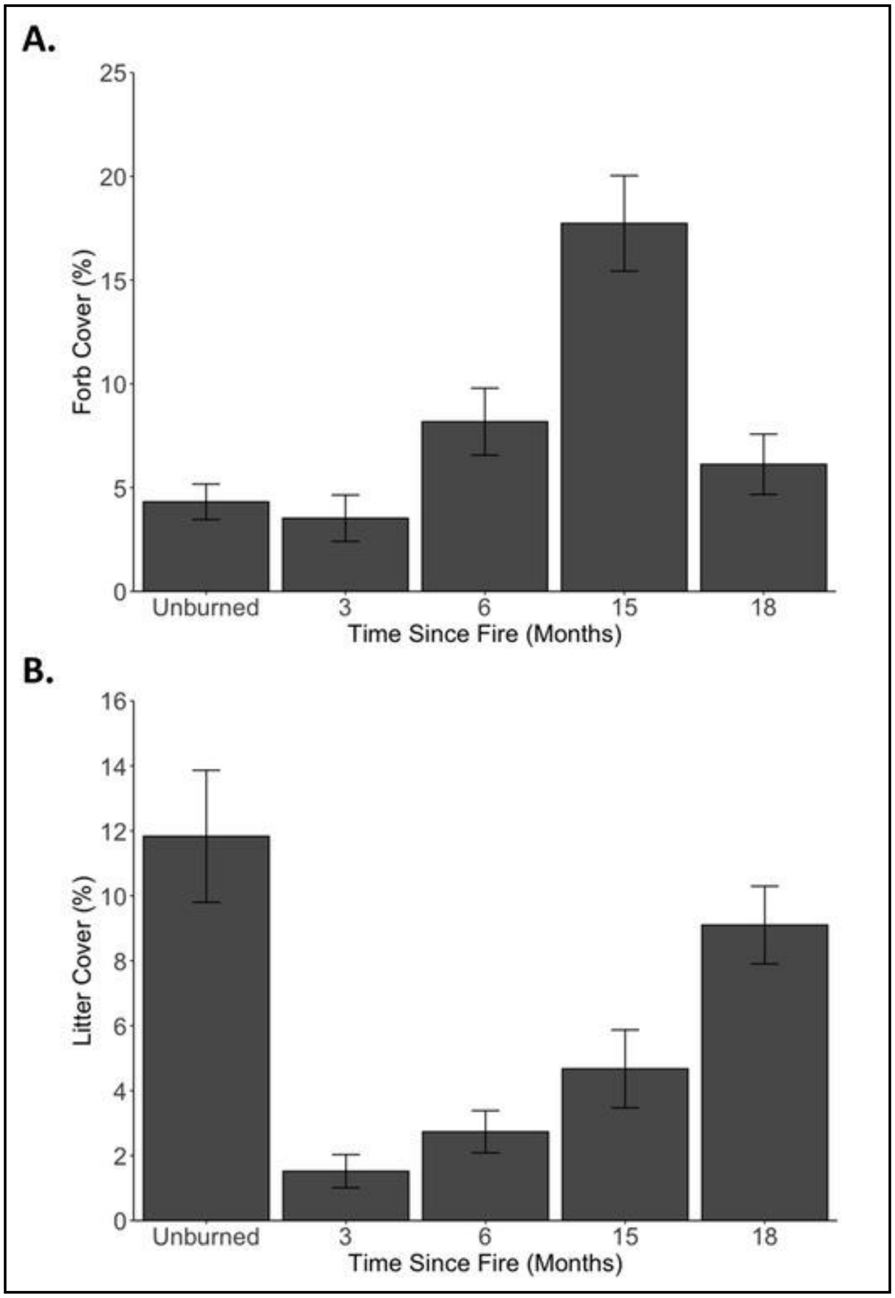

Figure 4. Forb (**A**) and litter (**B**) cover response to time since fire across three sites from 2019-2020 in Oklahoma, USA. Increments of time since fire are compared to the unburned treatment to understand changes in functional groups post-fire.

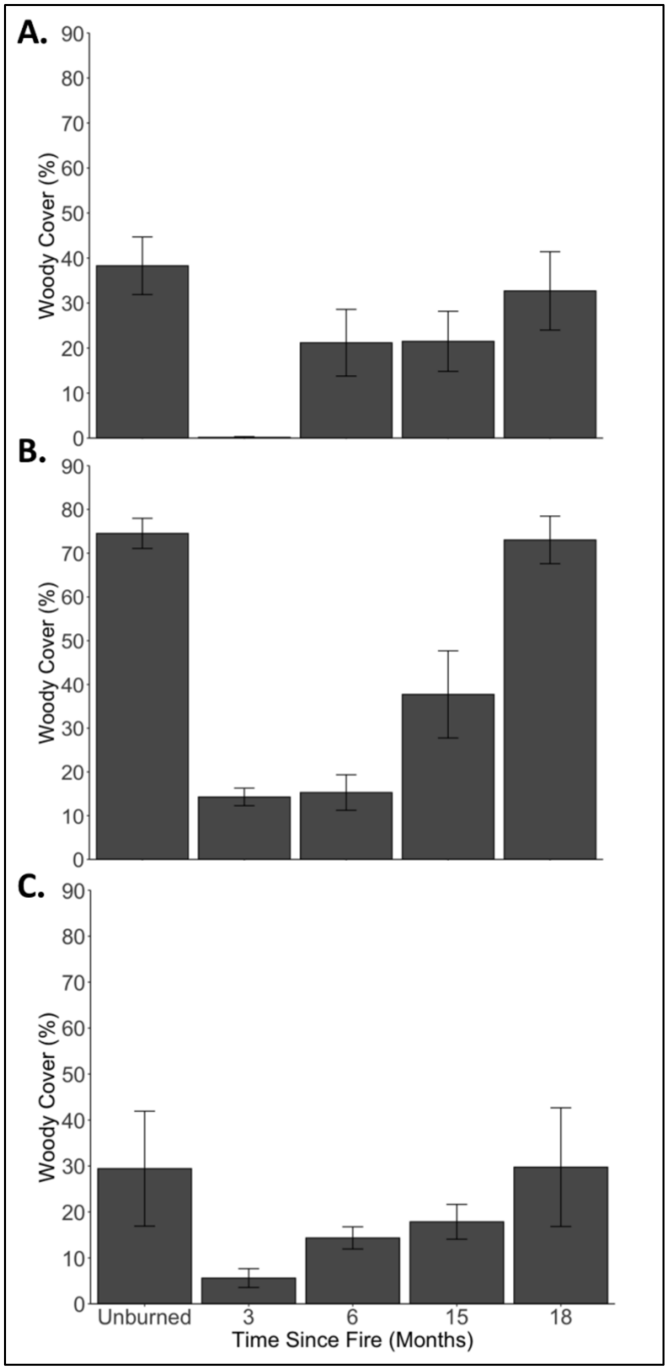

Figure 5. Woody cover response to time since fire at three sites from 2019-2020: **A)** Beaver River Wildlife Management Area (WMA), **B)** Packsaddle WMA, and **C)** Cross Timbers WMA located in Oklahoma, USA. Increments of time since fire are compared to the unburned treatment to understand changes in woody cover post-fire. These sites had different amounts of woody cover and had different dominant woody plant species. As a result there were differences at the site level in response to time since fire. However, all three locations exhibited similar patterns of fire response and recovery rates, returning to levels similar to unburned treatments within 18 months post-fire.

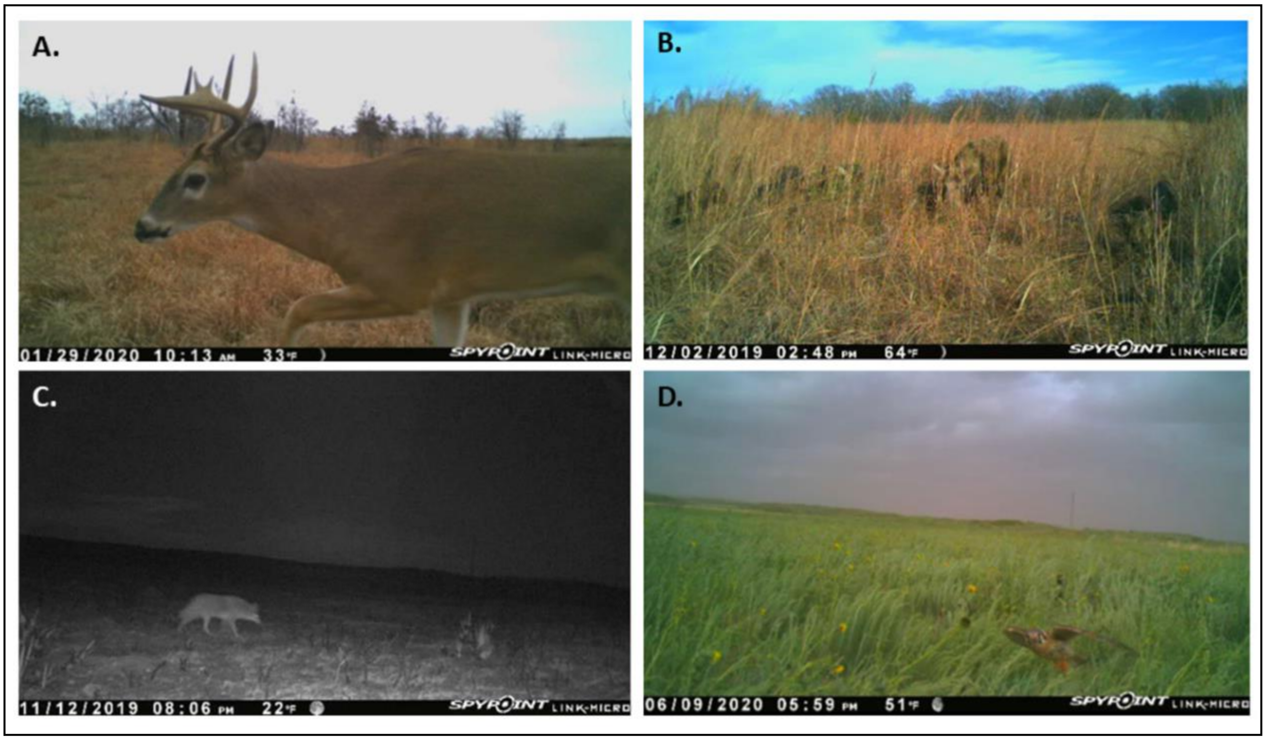

Figure 6. Examples of camera trap wildlife detections across three sites in Oklahoma, USA. A variety of wildlife taxa were detected on prescribed fire treatments using cellular camera traps over the course of a year (2019-2020). A total of 26 species were identified during the study, including: **A)** white-tailed deer (*Odocoileus virginianus*), **B)** feral pig (*Sus scrofa*), **C)** coyote (*Canis latrans*), and **D)** American kestrel (*Falco sparverius*).

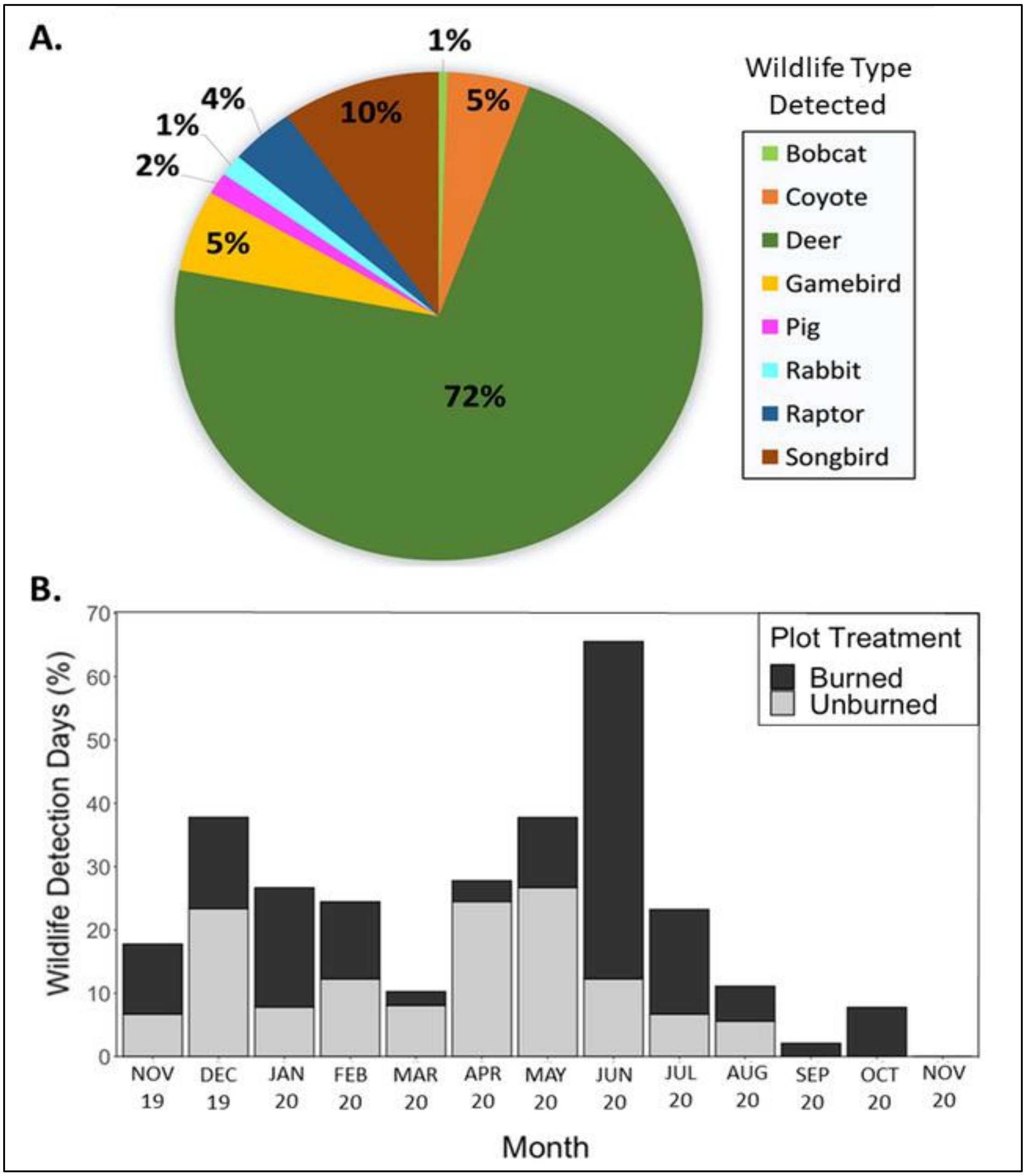

Figure 7. Summary figures of wildlife detections across three sites from 2019-2020 in Oklahoma, USA. **A)** A total of 8 wildlife types were detected over the course of the study, with the top four groups ($\geq$ 5%) respectively: deer, songbird, coyote, and gamebird. **B)** Wildlife detection days by month on burned and unburned plot treatments indicated neither positive nor negative relationships between wildlife use and prescribed fire.

CHAPTER II

TOPOEDAPHIC FACTORS AND DISTURBANCE REGIMES INFLUENCE THE DISTRIBUTIONS OF RESPROUTING WOODY PLANTS

ABSTRACT

Soils, topography, fire, grazing, and climate have all been described as primary factors contributing to the distribution of woody plants. However, most literature has focused individually on these variables at single sites. In this study, we evaluated the effects of soil texture, slope, aspect, and fire measured across 39 ecological sites and four different locations in Oklahoma, USA, from 2018–2019. All of these sites were located in climatic region. We used an information-theoretic model building approach to develop models describing the effects of these predictor variables on two different estimates of woody plant cover as well as woody plant density across sites. Top models for all three woody plant metrics indicated that both woody plant cover and density were primarily influenced by percent sand, aspect direction, and the number of times burned. Metrics of woody plant cover and density were lower in areas with finer soil textures, east-facing aspects, and areas that were burned more frequently across sites. Of these predictor

variables, topoedaphic variables appeared overall to have a greater influence than fire. This suggests that managing resprouting woody plants with fire is partly limited by underlying soil and topographic conditions. Summary statistics at the site level mostly indicated relationships similar to across-site site analysis among woody plant metrics and predictor variables, however, there were also differences among sites. Our research emphasizes the importance of broad-scale and site-level examination to better understand the distributions and potential management strategies for these landscapes.

INTRODUCTION

Woody plant encroachment is occurring globally across a wide range of ecosystems (Van Auken 2000; Venter et al. 2018). The spread of trees and shrubs into grasslands can cause negative impacts on biological, hydrological, and chemical processes within these invaded systems (Schimel et al. 2001; Huxman et al. 2005; Archer et al. 2017). The magnitude of this issue is so great that it likely receives more attention than almost any other topic in rangeland management. It has taken decades of ecological investigation to gain a better understanding of what is influencing increases in the distribution and extent of woody plants (Scifres 1980; Archer et al. 2011). Climate change is attributed as being a primary driver of woody plant encroachment. Increasing atmospheric CO_2 levels have been found more favorable for woody plant growth (Scheiter and Higgins 2009). Lack of historic disturbances such as fire and herbivory have also been attributed to the increase in woody plants (Fuhlendorf et al. 2009; O'Connor et al. 2020).

Topoedaphic factors such as soil texture, aspect, and slope have been associated with determining the spatial arrangement and locations of various plant taxa (Bailey 2014). Past studies indicate that woody plants are generally more abundant in either sand or clay textured soils (Archer et al. 2017). Woody plants have also been documented to be more or less abundant on various aspect directions. It has been observed that north-facing slopes generally have greater amounts of woody plants than south-facing slopes (Kutiel and Lavee 1999; Sternberg and Shoshany 2001). Degree of slope has been documented to have both negative and positive relationships on vegetation cover, indicating that the underlying determinant is likely soil texture and available water (Wilcox et al. 1988; Wu and Archer 2005). Adaptations to various disturbance regimes can also influence woody plant distribution at local and regional scales. Lack of disturbances such as fire and grazing have been suggested to increase woody plant abundance (Bond et al. 2004). However, other studies have indicated that these disturbances do not always have the effect of increasing woody plant abundance despite repeated applications of fire (Briggs et al. 2002). Woody plant response to disturbance largely depends upon whether a species is capable of resprouting or not. Resprouting woody plants possess morphological traits (e.g., belowground meristems, large root reserves of carbohydrates) that allow them to regrow following fire or herbivory. Non-resprouting woody plants cannot withstand fire and have a lower tolerance for herbivory and are thus killed when they are burned or consumed (Bond and Midgely 2001). Fire effect on woody plants can vary by site, as it is largely dependent on the disturbance adaptations local woody plant taxa possess.

Though understanding distribution and invasion patterns among woody plants is often focused on developing better methods of preventing and controlling these species, it must be noted that these plants are not inherently bad. Many species provide both cover and food value to a variety of wildlife species. For example, northern bobwhite (*Colinus virginianus* L.) utilize woody plants to avoid predation and thermoregulate during temperature extremes (Guthery et al. 2005; Hernández and Guthery 2012). Both native and domestic ungulates rely on woody plants for food and cover, especially during periods when other types of forages are limited (Everitt and Drawe 1974; Welch 1989). Thus, there is a needed balance between preventing the continued conversion of grasslands to forest systems and maintaining adequate amounts of woody plants to fulfill habitat requirements of many wildlife species (Archer 2010). Evaluating this balance is commonplace when managing landscapes for wildlife. The abundance and arrangement of woody plants within a given area often determine the type and quality of wildlife habitat (George and Zack 2001).

The sites within this study are primarily managed for wildlife. Our study region is located within the Southern Great Plains, a landform that is currently experiencing the impacts of woody plant encroachment (Twidwell et al. 2013). To better understand influential factors on woody plant distributions at the regional and local scale, we collected data across four different sites that had unique soils, fire regimes, and dominant vegetation types. A wide variety of woody plant taxa were recorded in this study; ranging from robust tree species to low-statured shrubs. Gaining insight on broad patterns, as well as site-level relationships, will offer a better understanding of how woody plants are distributed and respond to environmental influences at different scales. Site-level results provide managers with a greater knowledge base on what management practices best suit their specific locality. In this study, we evaluated how soil, topography, and fire regimes influence woody plant cover and density. We hypothesized that soil texture and topography would be the primary drivers of woody plant distribution and abundance. Specifically, we predicted that across sites, woody plant cover and density would respond positively to coarse soil textures and respond negatively to south-facing slopes. We speculated that woody cover and density would not be greatly influenced by the number of times burned given that our sites are dominated by resprouting woody plants. Our objectives were to characterize the influence of soil texture, aspect, slope, and the number of times burned on woody plant cover and woody plant density across four vegetation types. Additionally, we recorded relationships between woody plant metrics and environmental variables at the site level to evaluate these associations at a smaller scale. Lastly, we used findings for individual vegetation types to suggest site-specific management recommendations.

METHODS

Study sites

We conducted this study on four wildlife management areas (WMAs) in Oklahoma. These sites are owned and managed by the Oklahoma Department of Wildlife Conservation (Figure 1; ODWC 2020). Each WMA represented a different major land resource area (MLRA) as well as a unique vegetation type (Figure 2; Table 1).

Beaver River WMA is 7,162 hectares of Southern High Plains MLRA and is located in the State's Panhandle. This site is characterized by eolian sand deposits, created by winds depositing sand during the Quaternary period (Holliday 2001). These sandy soils primarily support dune shrubland, dominated by sand sagebrush (*Artemisia filifolia* Torr.). Our northwesternmost site, Beaver River WMA has the shortest growing season and is the most arid of our study sites (Figure 2; Table 1). This site is primarily managed for northern bobwhite, white-tailed deer (*Odocoileus virginianus* Zimmermann), and mule deer (*Odocoileus hemionus* Rafinesque). Vegetation management has included disc strips and occasionally prescribed fires. This site often has wildfires occur across portions of the WMA. Aerial herbicide applications have been applied to expansive stands of salt cedar (*Tamarix chinensis* Lour.), a non-native invasive, in riparian areas.

Packsaddle WMA is located in the Central Rolling Red Plains (eastern part) MLRA and encompasses 7,955 hectares in the far west-central part of the state. Similar to Beaver River WMA, this site is also comprised of Quaternary eolian sand deposits. At this site, shinnery oak (*Quercus havardii* Rydb.) is the dominant species comprising this shrubland (Figure 2; Table 1). This site is managed primarily for northern bobwhite, white-tailed deer, and wild turkey (*Meleagris gallopavo* L.). Vegetation management includes disc strips and juniper mastication in bottomland areas. This site is managed under a rigorous prescribed fire program which ensures a 6-year fire-return interval over the majority of the property.

Sandy Sanders WMA is 12,046 hectares of Central Rolling Red Plains (western part) MLRA and is located in the southwest corner of the state. This site is characterized by gypsiferous, clayey soils with saline components. These harsh, exposed soils primarily support savannas and forests of honey mesquite (*Prosopis glandulosa* Torr.) and redberry juniper (*Juniperus pinchotii* Sudw.). Sandy Sanders WMA is the largest of our sites, while also having the roughest terrain (Figure 2; Table 1). This site is primarily managed for northern bobwhite and white-tailed deer. Vegetation management includes mastication of redberry juniper within selected portions of the WMA as well as targeted herbicide applications on honey mesquite. Prescribed fire is rarely implemented at this site.

Cross Timbers WMA is located in the West Cross Timbers MLRA and encompasses 4,168 hectares in the south-central part of the state. The loamy soils found at this site support savannas and forests of post oak (*Quercus stellata* Wangenh.) and blackjack oak (*Quercus marilandica* Münchh.). Our southeasternmost site, Cross Timbers WMA is the smallest of our sites while having the longest growing season and greatest average annual rainfall (Figure 2; Table 1). This site is primarily managed for white-tailed deer, wild turkey, and northern bobwhite. Vegetation management includes targeted herbicide applications on sericea lespedeza (*Lespedeza cuneate* G. Don), a non-native invasive legume. This site is managed with a rigorous prescribed fire program which ensures a 4-year fire-return interval over the majority of the property.

Data collection

Initially, locations for sampling vegetation were randomly generated across each site using ArcGIS Pro 2.4.0 (ESRI 2020). Further, we placed 300 m buffers around each sampling point to reduce overlap of our sampling points. Following the selection of our sampling points, we used a handheld GPS unit to locate each sampling point in the field using assigned coordinates. These points were sampled once during the study and sampling took place from 2018-2019.

Woody vegetation data were collected using two different cover estimation methods and one density estimation method at each point. Modified Daubenmire frames were placed 10 m from a sampling point in each cardinal direction (n = 3,780). Within each frame, we used the Daubenmire midpoint cover class index to visually estimate percent canopy cover of woody vegetation within each 0.5m x 0.5 m modified Daubenmire frame (Daubenmire 1959; Floyd and Anderson 1987). Additionally, we recorded visual estimates of woody plant cover in a 50 m radius from the center of each sampling point. Estimation at a broader scale was conducted by visually estimating canopy cover of woody plants within a 50 m radius centered on the sampling point using cover categories (0-5%, 5-25%, 25-50%, and $\geq$ 50%). A laser rangefinder was used to determine the perimeter of the 50 m radius. Estimations were made using the same methods by one individual observer throughout the study to minimize potential bias (Kennedy and Addison 1987; Kercher et al. 2003).

To better understand the proximity and spatial arrangement of woody plants, we calculated the absolute density of woody vegetation at each array using the point-centered quarter method. In each quarter, we measured the distance to the nearest woody plant from the sample point using a laser rangefinder, truncated to 100 m (Cottam and Curtis 1956; Mitchell 2015). Our study sites are managed primarily for wildlife, causing relevancy for considering woody plant measurements as metrics of wildlife habitat. We measured both woody plant cover and density in this study because they are often used to determine occupancy thresholds for various wildlife species. Woody plant cover is often used to determine the amount of a particular habitat type within a given area. Woody plant density is a better metric for understanding the spatial arrangement and vegetation architecture of a particular habitat, which is equally important to wildlife species (Hays et al. 1981; Morrison et al. 2006).

Topography, soil, and fire data associated with each sampling point were obtained from various online and digital sources and assigned to points using ArcGISPro (ESRI 2020). Slope and aspect data were calculated from digital elevation models (National Elevation Dataset; 10 m resolution) obtained through the GeoSpatial Data Gateway (USDA 2020). Slope was notated by a percentage (increments of 10%) while aspect was categorized by cardinal directions. Boundary data for soil types, ecological sites, and major land resource areas (MLRAs) were obtained from the Gridded Soil Survey Geographic (gSSURGO; 30 m resolution). Soil texture data were obtained from Web Soil Survey using the online tool provided for calculating texture class estimates (USDA 2021). Percent sand, percent silt, and percent clay were estimated for each sampling point at a soil depth range of 0-3 m by a weighted average. We chose this depth range based on previous work that suggests the woody plant taxa in our study have an average root depth of 3 m (Schenk and Jackson 2002).

Fire data for prescribed burns and wildfires were provided by wildlife biologists at each site. Across sites, we were able to assess an 8-year fire history. Given the fire-prone nature of these systems, we determined that 8 years of fire history was sufficient to capture potential post-fire effects (Boyd and Bidwell 2002; Guyette et al. 2012). Using ArcGIS Pro, we were able to calculate the number of times each sampling point had experienced fire from 2012-2019 (ESRI 2020). We chose the number of times burned as our primary fire metric because previous studies indicate that fire frequency can have greater effects on woody vegetation than time since fire at broad temporal scales (Morrison et al. 1995; Robertson and Hmielowski 2014).

Data analysis

We used linear mixed-effects models (LME) with the site as a random effect in all of our models to examine the broad-scale influence of soils, topography, and fire on both woody plant cover and density across sites. We developed a two-step model building approach for both metrics of woody plant cover as well as woody plant density. We used previous biological knowledge to develop parsimonious models (Burnham and Anderson 2004). For our initial step, we considered soil texture variables (percent sand, percent silt, and percent clay) as predictors for each woody plant metric because prior biological knowledge supports that soil texture is a significant factor influencing woody plant distribution (Archer 1994, Morrison et al. 1995). Our base model for each woody plant metric was developed by selecting the soil texture variable that occurred within the top model using Akaike's Information Criterion corrected for sample size (AIC_c; Burnham and Anderson 1998). In the second and final step of the model building process, we compared separate models that contained topographic (slope and aspect) and fire (number of times burned) variables in addition to the top-ranked base model of each woody plant metric. We considered each topography and fire variable supportive if they improved model fit by >2 AIC_c over the respective base model (Symonds and Moussalli 2011). For both steps of the model building process, we evaluated Pearson's correlation coefficient among candidate predictor variables before including them in any model sets. If predictor variables had a correlation coefficient of $|r| \geq 0.7$, the variable that exhibited the highest ranking (ΔAIC_c) was retained for the model development and selection process. Identifying correlated predictor variables is important when developing model sets, as highly correlated variables can lead to erroneous model selection (Yamashita et al. 2007; Freckleton 2011). Once the second step was completed in the model building process, the top-ranking model of each model set was considered to be the best model describing each respective woody plant metric (Burnham and Anderson 1998). In cases where there were multiple competitive models (<2 AIC_c) within a model set, we did not perform model averaging as this procedure can lead to spurious parameter estimates (Grueber et al. 2011). Beta coefficients and summary statistics were calculated for predictor variables within top models for each woody plant metric (Nakagawa and Cuthill 2007). Additionally, we evaluated Pearson's correlation between each continuous predictor variable and the woody plant metric being examined within top models (Hedges and Olkin 1985; Rogers and Nicewander 1988). These summary analyses were conducted to provide further support of individual relationships between influential variables and woody plant cover and density respectively. Additional summary statistics were conducted to describe and compare site-level relationships among predictor variables and woody plant metrics. All statistical analyses were conducted using RStudio version 1.3.1056 (RStudio 2020).

RESULTS

Broad-Scale Relationships

Across sites, we sampled 39 of the 53 ecological sites (ESDs) present within WMA boundaries. We sampled $\geq$60 % of total ESDs present at each site. Only 13 % of

ESDs sampled occurred at multiple sites (Table 2). Across sites, the average Daubenmire woody cover was 26.6% whereas the radius woody cover estimate was higher at 44.2%. The average woody density was 327.7 plants/ha across sites (Table 3).

During the initial step of the two-part model development process, AIC_c indicated that among the three soil texture categories, percent sand had the strongest effect on both estimates of woody cover as well as woody density (Table 4). The best model for woody cover estimated by using modified Daubenmire frames included percent sand, aspect, and number of times burned (Table 5). Woody cover had a positive relationship with percent sand (β = 0.79, 95% CI = 0.65-0.95). The number of times the vegetation was burned exhibited a slightly stronger influence, leading to lower woody cover (β = -1.14, 95% CI = -3.97-1.69). Aspect directions appeared to have the greatest effect on woody cover. North- (β = 5.20), south- (β = 5.09), and west-facing aspects (β = 6.22) exhibited positive relationships with woody cover. No aspect (β = -2.55) and east-facing aspects had negative influences on woody cover, with east-facing slopes having the greatest impact (-22.38, 95% CI = -39.88-4.88) on woody cover within the model set (Table 6). A model lacking the number of times burned as a predictor variable was competitive (ΔAIC_c = 1.18), but indicated similar relationships among remaining predictor variables (Table 5). Pearson's correlation further supported a positive relationship with woody cover and percent sand (r = 0.34; Figure 3). Summary statistics further indicated the number of times burned having a negative influence on woody cover (Figure 4). Relationships between woody cover and various aspect directions support similar relationships as suggested by beta coefficients (Figure 5).

The best model for woody cover using 50 m radius estimate included percent sand, aspect, slope, and number of times burned (Table 5). Woody cover had a positive relationship with percent sand ($\beta = 0.81$, 95% CI = 0.59-1.47). The number of times the vegetation was burned exhibited a slightly stronger influence, having lower levels of woody cover ($\beta = -1.88$, 95% CI = -3.97-1.69). Percent slope had little effect on radius woody cover ($\beta = 0.12$, 95% CI = 0.04-0.20) when compared to other predictor variables in the model set. Aspect directions appeared to have the greatest effect on radius woody cover. North- ($\beta = 5.62$), south- ($\beta = 4.33$), and west-facing aspects exhibited positive relationships with radius woody cover, with west-facing aspects having the greatest impact ($\beta = 6.34$, 95% CI = -5.47-8.16) on radius woody cover within the model set. East-facing aspects ($\beta = -2.95$) and no aspect ($\beta = -4.43$) had negative influences on radius woody cover (Table 6). A model without the predictor variable of slope was competitive ($\Delta AIC_c = 1.83$), but indicated similar relationships among the remaining predictor variables (Table 5). Pearson's correlation further supported woody cover having positive relationships with percent sand ($r = 0.27$) while little relationship with slope ($r = 0.06$). Summary statistics further indicated the number of times burned having a negative influence on woody cover (Figure 4). Relationships between radius woody cover and various aspect directions support similar relationships as suggested by beta coefficients (Figure 5).

The best model for woody density (plants/ha) included percent sand, aspect, slope, and number of times burned (Table 5). Woody density had a positive relationship with percent sand ($\beta = 7.09$; 95% CI = 1.54-12.58). Number of times the vegetation was burned exhibited a stronger influence, with lower woody densities ($\beta = -63.49$, 95% CI =

-69.62-186.60). Percent slope had little effect on woody density (β = 0.63, 95% CI = -3.42-4.68) when compared to other predictor variables in the model set. Aspect directions appeared to have the greatest effect on woody density. North- (β = 240.72), south- (β = 234.88), and west-facing aspects (β = 328.53) exhibited positive relationships with woody density. No aspect (β = -294.18) and east-facing aspects had negative influences on woody density, with east-facing slopes having the greatest impact (-372.38, 95% CI = -814.86-70.10) on woody density within the model set (Table 6). A model lacking slope as a predictor variable was competitive ($\Delta AIC_c = 1.07$) but indicated similar relationships among the remaining predictor variables (Table 5). Pearson's correlation further supported a positive relationship with woody density and percent sand (r = 0.25; Figure 3), while indicating woody density having little relationship with slope (r = -0.01). Summary statistics further indicated that overall, the number of times burned had a negative influence on woody density. However, woody density was greater in vegetation that had been burned once or twice within 8 years than unburned vegetation. Vegetation burned 3 times within 8 years had less woody density than unburned vegetation (Figure 4). Relationships between woody density and various aspect directions support similar relationships as suggested by beta coefficients (Figure 5).

Site-Level Relationships

Among the four study sites, Packsaddle WMA exhibited the highest averages for woody cover and density, followed by Beaver River and Cross Timbers WMAs. Sandy Sanders WMA exhibited the lowest averages for woody cover and density (Table 3). Across sites, percent sand was the most dominant soil texture. Beaver River, Cross Timbers, and Packsaddle WMAs had mean percent sand contents $\geq$ 50%; the first two sites having $\geq$ 70% percent sand. Conversely, Sandy Sanders WMA had low average percent sand, but had the highest levels of percent clay and silt among sites (Table 3). The average slope across sites was 21.9% and appeared steepest at Sandy Sanders WMA (Table 3). On average, sample points across sites experienced fire once in the past 8 years. Sampling points at Packsaddle and Cross Timbers WMAs experienced fire almost twice on average, with over 75% of points exposed to fire within 8 years. Beaver River and Sandy Sanders WMA had an average fire exposure of less than once, with less than 10% of sample points experiencing fire during the same period (Table 3).

Examining vegetation types at the site level, woody cover and density had mostly similar relationships with predictor variables as indicated by across-site analyses. Beaver River, Packsaddle, and Cross Timbers WMAs exhibited greater levels of woody cover and woody density in sandy soils than clayey soils (Table 7). However, Sandy Sanders WMA exhibited the converse of this relationship, having higher levels of woody cover and woody density in clayey soils (Table 7). Beaver River, Packsaddle, and Cross Timbers WMAs exhibited similar patterns among aspect directions as suggested by beta coefficients for woody cover and woody density (Table 7). Unlike other sites, Sandy Sanders WMA had the greatest levels of woody cover and density on north-facing aspects rather than west-facing (Table 7). Beaver River WMA exhibited lower levels of woody cover and woody density in vegetation that was burned once in 8 years than vegetation that was unburned. At Cross Timbers and Packsaddle WMA, vegetation that had been burned 3 times within 8 years exhibited lower woody cover and woody densities than unburned vegetation. However, vegetation at these sites that had been burned only once or twice within 8 years had greater levels of woody cover and density than unburned vegetation. Sandy Sanders WMA had higher levels of woody cover and density in vegetation that was burned once than vegetation that was unburned within 8 years (Table 7).

DISCUSSION

Our research supports previous studies which documented woody plant distributions influenced by topoedaphic factors (Bailey 2014; Archer et al. 2017). Additionally, we found that fire also played a role in woody plant distributions, though past research on resprouting species have reported both supportive and contrary findings (Briggs et al. 2002; Bond et al. 2004). Predictor variables influencing woody plant distributions at individual sites generally followed similar trends as broad-scale findings, however, some variables exhibited substantially different relationships among sites. The results of this study imply an overarching concept that examining multiple scales of an ecological question can sometimes provide differing results at different scales (Levin 1992). Realizing these differences between broad regions and specific sites can be critical for management efforts.

Broad-Scale Relationships

We found that across sites, percent sand had the greatest effect on woody plant cover and density when compared to other soil particle sizes that influence soil texture (i.e., clay and silt). Sand is the largest soil particle (ø = 0.05-2.00 mm), while silt (ø = 0.002-0.05 mm) and clay are smaller (ø = $\leq$ 0.002 mm; Shepard 1954). Research supports that woody plants tend to be more abundant in areas with larger soil aggregates at both regional and global scales (Dodd et al. 2002; Bailey 2014). These deep, coarse soils increase rates of rainfall infiltration and nutrient leaching which allow woody plant species to utilize resources at depths that herbaceous plants cannot access as easily (Archer 1994). Coarse soil textures promote deeper wetting depths regardless of the degree of rainfall intensity, furthering the ability of woody plants to outcompete herbaceous species for water resources (Fravolini et al. 2005). Soils containing greater amounts of sand have been documented to advance fine root biomass production in woody plants, enabling these species to accrue a larger amount of available resources and facilitate increased woody plant density and rate of encroachment (Zhou et al. 2017; Archer et al. 2017). It must be recognized that soil texture data used in this study was not the same resolution as our scales of woody plant cover and density estimates and that this soil dataset is estimated by interpolating sample data, creating the potential for soil boundary errors (USDA-NRCS 2020). However, we feel that these data are adequate for the intent of this study.

We found that the number of times vegetation had been burned within the past 8 years had a negative effect on both woody plant cover and density. The effect of this variable appeared slightly greater than soil texture within top-ranked models. Points that had been burned three times within the past 8 years showed a lower abundance of woody plants when compared to points that had been burned once, twice, or were unburned. It is not surprising that fire had a relatively small effect on woody plant cover and density as the woody plant species measured in this study were fire-tolerant (Bond and Midgely 2001). Previous studies support that post-fire effects on these plants are only apparent for 1 – 3 years depending on the level of fire intensity and available resources present during regrowth (Briggs et al. 2002; Boyd and Bidwell 2002; Winter et al. 2012; Stuart-Haëntjens et al. 2018).

Our results indicated that within our model sets, aspect direction played the largest role in determining woody plant cover and density across sites. This however could be a result of interactions between other predictor variables and aspect direction (Li and Wu 2004). For both estimates of woody cover, areas with no aspect (i.e., flat) and east-facing aspects had negative relationships with the amount of woody cover. East-facing aspect consistently had the strongest effect of all aspect directions. North, south, and west-facing aspects had positive relationships with all three metrics of woody cover, with north and west-facing aspects having the highest levels of woody cover. Woody plant density exhibited similar relationships among aspect directions except that it had a positive relationship with areas lacking aspect direction. Prior research has documented less woody plant abundance on south-facing aspects due to more xeric conditions across the Northern Hemisphere (Gong et al. 2008; Bailey 2014). Though our findings indicate a positive relationship with woody plant cover on south-facing aspects, our results consistently indicate north-facing aspects having greater levels of woody cover and density than that of south-facing aspects. Past studies have indicated that more mesic microclimates often occur on north-facing slopes, being more suitable for woody plant growth (Sternberg and Shoshany 2001; Desta et al. 2004; Gong et al. 2008).

Differences in woody plant cover and density between west and east-facing aspects are also likely explained by historic geological processes. These processes have been attributed to the differences in soil type and texture among aspect directions, resulting in different vegetation types (Kutiel and Lavee 1999; Yimer et al. 2006). Across the Great Plains during the early Quaternary period (~ 2 million years ago), prevailing westerly winds began depositing eolian sands that eventually became crescentic dunes (Kocurek and Dott 1981; Holliday 2001). These dunes are often found on the north side of river systems, particularly describing our two western-most sites (i.e., Beaver River and Packsaddle WMAs). Due to the wind direction that developed these formations, larger volumes of sand can be found on west-facing aspects, thus being more suitable for woody plants (Holliday 2001; Archer et al. 2017).

Slope showed little effect in top-ranking models and was only in the best models for radius woody cover and woody plant density. Past research has suggested that steeper slopes usually have more rock and exposed soil, thus reducing fuel continuity and providing some woody plant species a refuge from fire (Bragg and Hulbert 1976). However, other research has indicated that due to advanced runoff resulting in decreased water availability on steep slopes, less woody plant cover can occur (Wu and Archer 2005). Broader conclusions due to these equivocal findings at local and regional scales suggest that soil texture and available water resources are greater influences on slope vegetation cover (Wilcox et al. 1988).

Site-Level Relationships and Management Implications

The relationships identified among woody plants and environmental variables across sites remained mostly similar for dominant woody vegetation types at the site level, with some notable exceptions. Sites in this study are dominated by shrubland and savanna systems, however, each site has unique dominant woody vegetation (Duck and Fletcher 1945). These various plant taxa mostly require similar forms of management methods, however, strategies to achieve similar objectives vary by each site. These site-specific relationships provide better insight to guide management towards effective strategies using a targeted approach (Twidwell et al. 2013). Provided is a summary of individual site management objectives geared towards enhancing heterogeneity and biodiversity at these locations (Table 7). These management approaches benefit focal wildlife species (i.e., quail, turkey, and deer) as well as a suite of other game and non-game species (Pickett et al. 2012).

Beaver River WMA is dominated by sand sagebrush and has relatively high levels of woody cover and woody densities when compared to other sites. However, past research indicates that this vegetation type can fully recover from fire within 3 years and rarely exhibits mortality from fire (Winter et al. 2012). This study suggests that managers could use fire frequency as a tool to reduce woody cover and density at this site (Thacker et al. 2013). Areas at this site with coarse, sandy soils still require periodic fire to manage for biodiversity, but less effort should be directed towards shrub management where woody plants currently persist under optimal environmental conditions.

Packsaddle WMA is dominated by shinnery oak and has the highest levels of woody cover and density when compared to other sites. Shinnery oak is most often found on deep, sandy soils (Small 1975). Past studies support that this vegetation type can fully recover from fire within 2 years and vigorously resprouts following single fire events (Boyd and Bidwell 2002). Fire events would likely reduce woody cover for relatively short periods, requiring fire to be applied regularly at frequent intervals for maintaining heterogeneity (Fuhlendorf and Engle 2001). Managers would likely see more reduction in woody cover than woody density using fire as a management tool at this site because of the increased stem-densities associated with post-fire resprouting (Boyd and Bidwell 2002). Fire application efforts should be allocated similar to Beaver River WMA, as shinnery oak persists strongly in areas with optimal environmental conditions. Livestock have been known to utilize this plant, enabling targeted browsing (i.e., goats) as an additional management tool for reducing levels of shinnery oak in areas where this clonal species forms large monotypic stands (Villena and Pfister 1990; O'Connor et al. 2020).

Sandy Sanders WMA has the lowest levels of woody cover and density when compared to other sites. Dominant woody vegetation consists of honey mesquite and redberry juniper. Unlike dominant woody vegetation at other sites, these species favor shallow, clayey soils (Virginia and Jarrell 1983; Ansley et al. 1995). The two species that make up this site's woody vegetation type (honey mesquite and redberry juniper) are both resprouting species but they have differing fire responses. Redberry juniper appears to be more sensitive to intense fires, with saplings susceptible to mortality during fire events (Ansley et al. 1995), whereas honey mesquite exhibits aggressive resprouting after fire in all life stages and can increase in density (Wright et al. 1976). Managers could expect increased levels of mesquite as a product of burning, however redberry juniper could potentially be reduced. Though costly, herbicide applications could prove more effective at reducing mesquite. However, these treatments rarely last more than 20 years (Ansley et al. 2004).

Cross Timbers WMA is dominated by post oak and winged sumac and has lower levels of woody cover and woody densities when compared to other sites. Post oak, sumac, and most other woody plants in the Cross Timbers ecoregion favor coarse loamy-sandy soils (Collins et al. 1989). The species that make up this site's woody vegetation type are known to recover rapidly from fires implemented as frequently as 1-3 years (Briggs et al. 2002; Burton et al. 2011; Collins et al. 2021). Managers could expect sustained levels of woody cover and density as a product of burning, however, these fires would provide short-term (i.e., 6-12 month) variations in habitat structure (Fuhlendorf et al. 2009). Targeted browsing using livestock such as goats could be used to temporarily reduce woody plant abundance in areas that are so thick that there is inadequate fuel to carry a fire (Lopes and Stuth 1984).

CONCLUSIONS

Topoedaphic variables and disturbance regimes appear to have substantial influence over amounts of woody plant cover and density across these study sites. Identifying relationships among these predictor variables at the site level can provide information useful for tailoring management objectives concerning heterogeneity and focal wildlife species.

Analyzing woody plant distributions at two different scales indicated that management results have the potential to be less equilibrial at specific sites than over broad regions. Future woody plant management of the Southern Great Plains should take this phenomenon into account when making management recommendations in the face of a changing climate (Scheiter and Higgins 2009). Determining where resprouting woody species persist naturally and where current encroachment is occurring could potentially make resources allocated for management more impactful (Wilcox et al. 2018).

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TABLES AND FIGURES

Table 1. Climate, topography, soil, and vegetation characteristics for Beaver River, Cross Timbers, Packsaddle, and Sandy Sanders WMAs, Oklahoma, USA. Local climate data were sourced from the Oklahoma MESONET system. Elevation, dominant soil types, soil textures, dominant plant taxa, and MLRA classification collected from the Ecosystem Dynamics Interpretive Tool (EDIT).

	Wildlife Management Area			
Site Variable	**Beaver River**	**Cross Timbers**	**Packsaddle**	**Sandy Sanders**
Site Area (ha)	7,162	4,168	7,955	12,046
Average Annual Precipitation (mm)	558	1,061	660	736
2018 Annual Precipitation (mm)	675	1,167	694	719
2019 Annual Precipitation (mm)	683	1,151	663	826
Average Growing Season Days	190	241	195	236
2018 Growing Season Days	204	221	207	227
2019 Growing Season Days	206	232	209	237
Temperature Range (º C)	-0.56 – 26.9	6.9 – 28.0	0.28 – 26.6	6.5 – 29.5
Average Elevation (m)	650	220	590	490
Soil Types	Tivoli Fine Sands, Vona-Tivoli complex	Dougherty complexes, Konsil complexes	Nobscot Delwin complexes	Knoco-Cornick-Rock outcrop complexes
Soil Textures	Sandy	Loamy sand – sandy loam	Loamy – sandy	Loamy – clayey; saline component

Table 1 (continued)

Site Variable	**Wildlife Management Area**			
	Beaver River	**Cross Timbers**	**Packsaddle**	**Sandy Sanders**
Grasses	sand bluestem (*Andropogon gerardii* spp. *hallii*), giant sandreed (*Calamovilfa gigantea*), buffalograss (*Bouteloua hirsuta*).	big bluestem (*Andropogon gerardii*), switchgrass (*Panicum virgatum*), Canada wildrye (*Elymus canadensis*)	little bluestem (*Schizachyrium scoparium*), blue grama (*Bouteloua gracilis*), sand dropseed (*Sporobolus cryptandrus*).	little bluestem (*Schizachyrium scoparium*), buffalograss (*Bouteloua dactyloides*), western wheatgrass (*Pascopyrum smithii*)
Forbs	plains sunflower (*Helianthus petiolaris*), sand lily (*Mentzelia nuda*), spectacle pod (*Dimorphocarpa wislizeni*)	western ragweed (*Ambrosia psilostachya*), partridge pea (*Chamaecrista fasciculata*), lemon beebalm (*Monarda citriodora*)	Engelmann’s daisy (*Engelmannia peristenia*), white prickly poppy (*Argemone albiflora*), queen’s delight (*Stillingia sylvatica*)	American basketflower (*Centaurea americana*), woolly paperflower (*Psilostrophe tagentina*), annual broomweed (*Amphiachyris dracunculoides*)
Woody Plants	sand sagebrush (*Artemisia filifolia*), skunkbush sumac (*Rhus aromatica*), sand plum (*Prunus angustifolia*)	post oak (*Quercus stellata*), blackjack oak (*Quercus marilandica*), winged sumac (*Rhus copallinum*), rough-leaf dogwood (*Cornus drummondii*), cedar elm (*Ulmus crassifolia*)	shinnery oak (*Quercus havardii*), sand plum (*Prunus angustifolia*), Oklahoma plum (*Prunus gracilis*) black locust (*Robinia pseudoacacia*)	honey mesquite (*Prosopis glandulosa*), redberry juniper (*Juniperus pinchotii*), fragrant mimosa (*Mimosa borealis*)
Major Land Resource Area (MLRA)	Southern High Plains	West Cross Timbers	Central Rolling Red Plains	Western Red Rolling Plains
Number of Points Sampled (2018-2019)	253	218	231	242

Table 2. Summary of ecological sites sampled at Beaver River, Packsaddle, Sandy Sanders, and Cross Timbers Wildlife Management Areas, Oklahoma, USA, 2018-2019. Provided are the number of points sampled within each ecological site for each WMA, along with the percent area each ecological site composes of its respective WMA. Totals at the bottom provide insight on the percentage of how many ecological sites were sampled of the total located within each WMA.

	Wildlife Management Area							
	Beaver River		Cross Timbers		Packsaddle		Sandy Sanders	
Ecological Sites	**Points Sampled**	**Percent of WMA**	**Points Sampled**	**Percent of WMA**	**Points Sampled**	**Percent of WMA**	**Points Sampled**	**Percent of WMA**
Clay Flat 19-26”	---	---	---	---	---	---	16	4.5%
Clay Loam 19-26”	---	---	---	---	---	---	6	2.1%
Clayey Breaks	---	---	---	---	---	---	21	12.7%
Deep Sand 29-33”	---	---	65	21.8%	---	---	---	---
Deep Sand Shrubland	---	---	---	---	45	17.1%	---	---
Depressional Upland	---	---	---	---	---	---	1	1.1%
Gypsum 19-26”	---	---	---	---	---	---	20	7.0%
Limy Upland 16-24”	9	4.1%	---	---	---	---	---	---
Loamy Bottomland 19-26”	1	0.6%	---	---	---	---	12	2.4%
Loamy Bottomland 29-33”	---	---	12	5.8%	---	---	---	---
Loamy Sand 29-33”	---	---	62	29.9%	---	---	---	---
Loamy Upland	1	0.2%	---	---	---	---	111	45.3%

Table 2 (continued)

Ecological Sites	**Wildlife Management Area**							
	Beaver River		**Cross Timbers**		**Packsaddle**		**Sandy Sanders**	
	Points Sampled	**Percent of WMA**	**Points Sampled**	**Percent of WMA**	**Points Sampled**	**Percent of WMA**	**Points Sampled**	**Percent of WMA**
Loamy Upland 19-26”	---	---	---	---	6	2.4%	---	---
Mixedland Slopes	1	0.7%	---	---	5	2.0%	---	---
Rolling Sands	7	6.2%	---	---	82	41.7%	---	---
Saline Bottomland	---	---	---	---	---	---	14	5.1%
Sand Hills 23-31”	103	37.1%	---	---	3	0.6%	---	---
Sandy 16-22”	56	20.3%	---	---	---	---	---	---
Sandy 16-24”	27	6.2%	---	---	8	3.6%	---	---
Sandy 29-33”	---	---	16	9.2%	---	---	---	---
Sandy Bottomland	39	22.2%	---	---	20	8.2%	---	---
Sandy Bottomland 16-24”	1	0.2%	---	---	---	---	---	---
Sandy Loam 23-31”	---	---	---	---	29	7.0%	---	---
Sandy Loam 29-33”	---	---	61	33.2%	---	---	---	---
Shallow Clay 19-26”	---	---	---	---	---	---	5	1.0%
Shallow Upland	---	---	---	---	33	12.8%	---	---
Subirrigated Bottomland	6	1.5%	---	---	---	---	2	0.07%

Table 2 (continued)

Ecological Sites	Wildlife Management Area							
	Beaver River		Cross Timbers		Packsaddle		Sandy Sanders	
	Points Sampled	Percent of WMA	Points Sampled	Percent of WMA	Points Sampled	Percent of WMA	Points Sampled	Percent of WMA
Tight Sandy Loam 29-33"	---	---	2	0.09%	---	---	---	---
Very Shallow 16-24"	1	0.5%	---	---	---	---	---	---
Very Shallow 19-26"	---	---	---	---	---	---	22	7.8%
Very Shallow Clay 19-26"	---	---	---	---	---	---	12	6.0%
Total ESDs Sampled	12		6		9		12	
Total ESDs in WMA	13		6		14		20	
Percent of WMA ESDs Sampled	92%		100%		64%		60%	

Table 3. Data collected at Beaver River, Packsaddle, Sandy Sanders, and Cross Timbers Wildlife Management Areas, Oklahoma, USA, 2018-2019. Means and ranges provided for both woody cover (%) and woody density (plants/ha) and predictor variables at the site level and across sites. Variables listed were included within the Akaike information criterion (AIC$_c$) model selection process.

	Wildlife Management Area									
	Beaver River		**Cross Timbers**		**Packsaddle**		**Sandy Sanders**		**Across Sites**	
Dependent Variables	**Mean**	**Range**	**Mean**	**Range**	**Mean**	**Range**	**Mean**	**Range**	**Mean**	**Range**
Daubenmire Woody Cover	30.4	0.0-98.0	24.1	0.0-98.0	31.6	0.0-98.0	20.3	0.0-98.0	26.6	0.0-98.0
Radius Estimate Woody Cover	45.3	0.0-98.0	42.7	0.0-98.0	47.7	0.0-98.0	41.3	0.0-98.0	44.2	0.0-98.0
Woody Density	374.4	0.0-1,975.3	355.7	0.0-1,600.0	393.2	0.0-1,975.3	180.6	0.0-1,600.0	327.7	0.0-1,975.3
Independent Variables										
Percent Sand	77.8	34.8-92.2	57.5	48.7-70.6	73.3	41.9-92.2	23.15	14.2-77.8	58.0	14.2-92.2
Percent Silt	12.2	2.0-37.0	18.1	16.3-20.8	15.2	2.0-37.6	33.8	10.7-53.5	19.8	2.0-53.5
Percent Clay	10.0	5.8-28.3	24.5	13.1-30.5	11.5	4.6-20.5	43.1	11.5-50.0	22.2	4.6-50.0
Percent Slope	14.3	0.0-90.0	12.3	0.0-80.0	26.4	0.0-100.0	34.0	0.0-100.0	21.9	0.0-100.0
Number of Times Burned	0.1	0.0-1.0	1.9	0.0-3.0	1.5	0.0-3.0	0.1	0.0-1.0	0.8	0.0-3.0

Table 3 (continued)

Aspect Direction (% direction of samples)	**Beaver River**	**Cross Timbers**	**Packsaddle**	**Sandy Sanders**	**Across Sites**
None	29.2	26.1	14.3	6.6	19.0
North	24.9	27.1	30.3	30.2	27.7
South	22.9	23.3	26.0	34.7	26.7
East	11.8	9.6	15.6	14.5	13.1
West	12.6	14.2	13.4	13.6	13.4

Table 4. Akaike information criterion (AIC_c) for the first step in the two-part model building process. Top-ranked and competitive models show effects of soil texture on two estimation methods for percent woody cover (Daubenmire frame and radius estimate) as well as woody density (plants/ha) across Beaver River, Packsaddle, Sandy Sanders, and Cross Timbers Wildlife Management Areas, Oklahoma, USA, 2018-2019. Additionally, we present the number of parameters (K), model weight within a variable set (w_i), and maximum log-likelihood (LL). Top models within each model set become the base model for the second step of model development.

Metric	**Model**	K	**AIC_c**	**ΔAIC_c**	w_i	**LL**
Daubenmire woody cover						
	percent sand	5	37404.95	0.00	1.00	-18697.46
	percent silt	5	37421.22	16.27	0.00	-18705.60
	percent clay	5	37471.24	66.29	0.00	-18730.61
	null model	4	37495.97	91.02	0.00	-18743.98
Radius estimate woody cover						
	percent sand	4	8975.90	0.00	1.00	-4483.93
	percent silt	4	8999.67	23.77	0.00	-4495.81
	percent clay	4	9038.63	62.74	0.00	-4515.30
	null model	3	9061.33	85.43	0.00	-4527.65
Woody density	percent sand	4	2251.63	0.00	0.91	-1121.67
	percent silt	4	2256.47	4.83	0.08	-1124.09
	percent clay	4	2260.62	8.99	0.01	-1126.17
	null model	3	2264.31	12.68	0.00	-1129.07

Table 5. Akaike information criterion (AIC_c) for the second and final step of the two-part model building process. Top-ranked and competitive models show effects of soil, topography, and fire variables on two estimation methods for percent woody cover (Daubenmire frame and 50 m radius estimate) as well as woody density (plants/ha) across Beaver River, Packsaddle, Sandy Sanders, and Cross Timbers Wildlife Management Areas, Oklahoma, USA, 2018-2019. Additionally, we present the number of parameters (*K*), model weight within a variable set (w_i), and maximum log-likelihood (LL).

Metric	Model	*K*	AIC_c	ΔAIC_c	w_i	LL
Daubenmire woody cover						
	percent sand + aspect + number of times burned	10	37384.61	0.00	0.51	-18682.28
	percent sand + aspect	9	37385.80	1.18	0.28	-18683.87
	percent sand + aspect + slope + number of times burned	11	37387.12	2.50	0.14	-18682.52
	percent sand + aspect + slope	10	37388.16	3.55	0.08	-18684.05
	percent sand + number of times burned	6	37404.22	19.61	0.00	-18696.10
	percent sand + slope + number of times burned	7	37404.90	20.28	0.00	-18695.43
	percent sand	5	37404.95	20.33	0.00	-18697.46
	percent sand + slope	6	37495.56	20.95	0.00	-18696.77
	number of times burned	5	37495.19	110.58	0.00	-18742.59
	null model	4	37495.97	111.35	0.00	-18743.98
Radius estimate woody cover						
	percent sand + aspect + slope + number of times burned	14	8930.86	0.00	0.54	-4451.20
	percent sand + aspect + number of times burned	13	8931.34	1.83	0.22	-4452.48
	percent sand + aspect + slope	13	8933.18	2.23	0.18	-4453.39
	percent sand + aspect	12	8934.01	4.43	0.06	-4454.84
	percent sand + slope + number of times burned	6	8969.03	38.17	0.00	-4478.47
	percent sand + slope	5	8970.37	39.51	0.00	-4480.15
	percent sand + number of times burned	5	8974.35	43.49	0.00	-4482.14
	percent sand	4	8975.90	45.04	0.00	-4483.93
	number of times burned	4	9060.45	129.59	0.00	-4526.20
	null model	3	9061.33	130.47	0.00	-4527.65

Table 5
(continued)

Metric	**Model**	***K***	**AIC$_c$**	**ΔAIC$_c$**	w_i	**LL**
Woody density						
	percent sand + aspect + slope + number of times burned	10	2204.42	0.00	0.62	-1091.40
	percent sand + aspect + number of times burned	9	2205.49	1.07	0.36	-1093.09
	percent sand + aspect + slope	9	2212.99	8.57	0.01	-1096.83
	percent sand + aspect	8	2214.05	9.63	0.01	-1098.50
	percent sand + slope + number of times burned	6	2246.56	42.14	0.00	-1116.98
	percent sand + number of times burned	5	2247.64	43.22	0.00	-1118.61
	percent sand + slope	5	2255.36	50.94	0.00	-1122.47
	percent sand	4	2255.68	51.26	0.00	-1123.70
	number of times burned	4	2256.47	52.05	0.00	-1124.09
	null model	3	2264.31	59.89	0.00	-1129.07

Table 6. Beta coefficients, standard errors, and confidence intervals for two estimation methods of percent woody cover (Daubenmire frame and 50 m radius estimate) as well as woody density (plants/ha) across Beaver River, Packsaddle, Sandy Sanders, and Cross Timbers Wildlife Management Areas, Oklahoma, USA, 2018-2019. Variables listed were included within the top models of each respective model set as determined by Akaike information criterion (AIC_c).

				95 % CI	
Metric	**Variable**	**β**	**Std. Error**	**Lower**	**Upper**
Daubenmire woody cover					
	percent sand	0.79	0.08	0.65	0.95
	no aspect	-2.55	3.30	-9.02	3.92
	north aspect	5.20	3.06	-0.79	11.19
	south aspect	5.09	3.03	-0.86	11.04
	east aspect	-22.38	8.93	-39.88	4.88
	west aspect	6.22	3.52	-0.67	13.11
	number of times burned	-1.14	1.45	-3.97	1.69
Radius estimate woody cover	percent sand	0.81	0.11	0.59	1.47
	no aspect	-4.43	3.28	-10.86	2.01
	north aspect	5.62	3.00	0.74	12.51
	south aspect	4.33	3.02	-5.59	6.26
	east aspect	-2.95	10.66	-23.84	17.94
	west aspect	6.34	3.48	-5.47	8.16
	slope	0.12	0.04	0.04	0.20
	number of times burned	-1.88	1.44	-4.70	0.93
Woody density					
	percent sand	7.06	2.86	1.54	12.58
	no aspect	-294.18	158.86	-317.18	65.55
	north aspect	240.72	162.18	-77.14	558.59
	south aspect	234.88	147.05	-53.32	523.09
	east aspect	-372.38	225.76	-814.86	70.10
	west aspect	328.53	174.38	-13.25	670.32
	slope	0.63	2.07	-3.42	4.68
	number of times burned	-63.49	62.81	-69.62	186.60

Table 7. Woody cover (%) and woody density (plants/ha) values at Beaver River, Packsaddle, Sandy Sanders, and Cross Timbers Wildlife Management Areas, Oklahoma, USA, 2018-2019. Mean and range values are provided for both woody plant metrics as they occur within each soil, topography, and fire variable. These variables were all included within the Akaike information criterion (AIC_c) model selection process. Slope was omitted from this table due to its marginal influence on woody plant metrics as indicated by Pearson's correlation and beta coefficients. Soil texture categories (sandy, silty, clayey) were classified using three-way ratios as recommended by Shepard 1954. Due to similar patterns among woody cover estimates, Daubenmire frame woody cover is presented below as a representative metric to describe woody cover relationships.

	Wildlife Management Area											
	Soil Texture			Aspect Direction					Number of Times Burned			
Woody Vegetation	Sand	Silt	Clay	None	North	South	East	West	0	1	2	3
Beaver River WMA												
Woody Cover												
Mean	31.84	---	27.4	25.44	32.6	27.2	24.8	38.3	32.0	11.9	---	---
Range	0.0-98.0	---	20.5-28.9	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0	---	---
Woody Density												
Mean	352.4	---	312.02	185.5	334.9	266.8	156.6	354.6	267.2	231.0	---	---
Range	0.0-1,975.3	---	0.0-1,772.9	0.1-1,975.3	0.87-1,975.3	0.2-1,600.0	0.0-1,772.9	0.2-1,600.0	0.0-1,975.3	0.0-1,975.3	---	---

Table 7 (cont.)

Woody Vegetation	Wildlife Management Area: Soil Texture: Sand	Silt	Clay	Aspect Direction: None	North	South	East	West	Number of Times Burned: 0	1	2	3
Cross Timbers WMA												
Woody Cover												
Mean	21.4	---	20.90	19.4	32.4	22.9	20.6	32.8	33.9	30.5	31.2	25.1
Range	0.0-98.0	---	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0
Woody Density												
Mean	323.7	---	309.3	279.8	344.7	340.0	262.5	347.9	323.6	284.1	362.7	315.3
Range	0.0-1,600.0	---	0.0-1,600.0	0.0-1,600.0	0.0-1,600.0	0.0-1,600.0	0.2-1,600.0	0.0-1,600.0	0.0-1,600.0	0.0-1,600.0	0.0-1,600.0	0.0-1,600.0
Packsaddle WMA												
Woody Cover												
Mean	33.79	---	4.9	26.7	34.1	28.5	26.5	28.2	41.55	28.4	34.9	23.7
Range	0.0-98.0	---	0.0-86.0	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0

Table 7 (cont.)	Wildlife Management Area											
	Soil Texture			Aspect Direction					Number of Times Burned			
Woody Vegetation	**Sandy**	**Silty**	**Clayey**	**None**	**North**	**South**	**East**	**West**	**0**	**1**	**2**	**3**
Packsaddle WMA												
Woody Density												
Mean	378.8	---	294.08	317.7	470.3	372.7	310.8	492.0	751.1	779.5	649.1	569.6
Range	0.0-1,975.3	---	0.0-1,975.3	0.5-1,975.3	0.1-1,975.3	0.0-1,600.0	0.3-1,600.0	0.2-1,600.0	0.2-1,600.0	0.0-1,975.3	0.6-1,600.0	0.1-1,600.0
Sandy Sanders WMA												
Woody Cover												
Mean	8.3	27.65	20.4	21.0	25.9	22.6	21.3	23.8	20.6	21.8	---	---
Range	0.0-63.0	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0	0.0-98.0	---	---
Woody Density												
Mean	109.9	329.7	320.8	149.4	445.3	384.2	148.1	246.6	322.4	330.1	0.0	0.0
Range	0.3-19.8	0.0-1,600.0	0.0-1,600.0	0.1-1,600.0	0.0-1,600.0	0.0-1,600.0	0.7-1,600.0	0.8-1,600.0	0.0-1,600.0	1.2-400.00	0.0	0.0

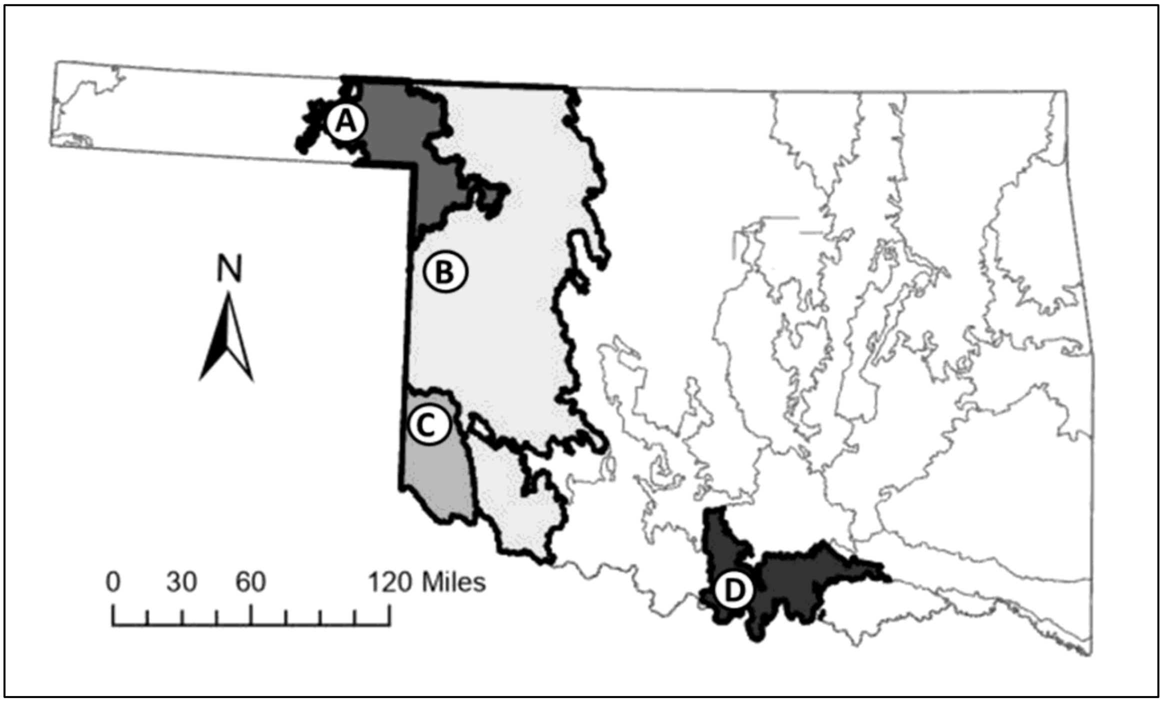

Figure 1. Study site locations of the four wildlife management areas (WMAs) managed by the Oklahoma Department of Wildlife Conservation in Oklahoma, USA. Each of these WMAs represent a different major land resource area (MLRA). From west to east, site names are as follows with their respective MLRAs: **A)** Beaver River WMA – Southern High Plains, **B)** Packsaddle WMA – Central Red Rolling Plains (eastern part), Sandy Sanders WMA – Central Red Rolling Plains (western part), and **C)** Cross Timbers WMA – West Cross Timbers.

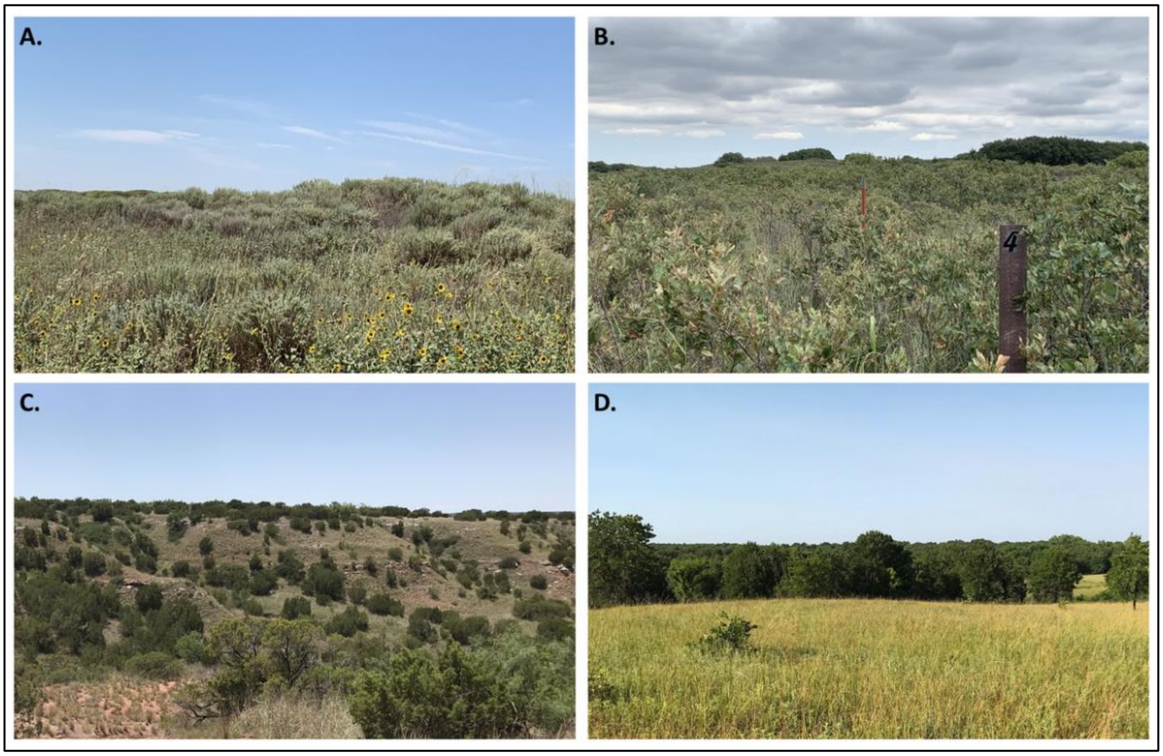

Figure 2. Representative plant communities for each study site located in Oklahoma, USA: **A)** Beaver River Wildlife Management Area (WMA) is dominated by shortgrass species and sand sagebrush (*Artemisia filifolia*), **B)** Packsaddle WMA is dominated by midgrass species and shinnery oak (*Quercus havardii*), **C)** Sandy Sanders WMA is dominated by midgrass species, honey mesquite (*Prosopis glandulosa*), and redberry juniper (*Juniperus pinchotii*), and **D)** Cross Timbers WMA is dominated by tallgrass species, oaks (*Quercus* sp.), sumacs (*Rhus* sp.) and elms (*Ulmus* sp.).

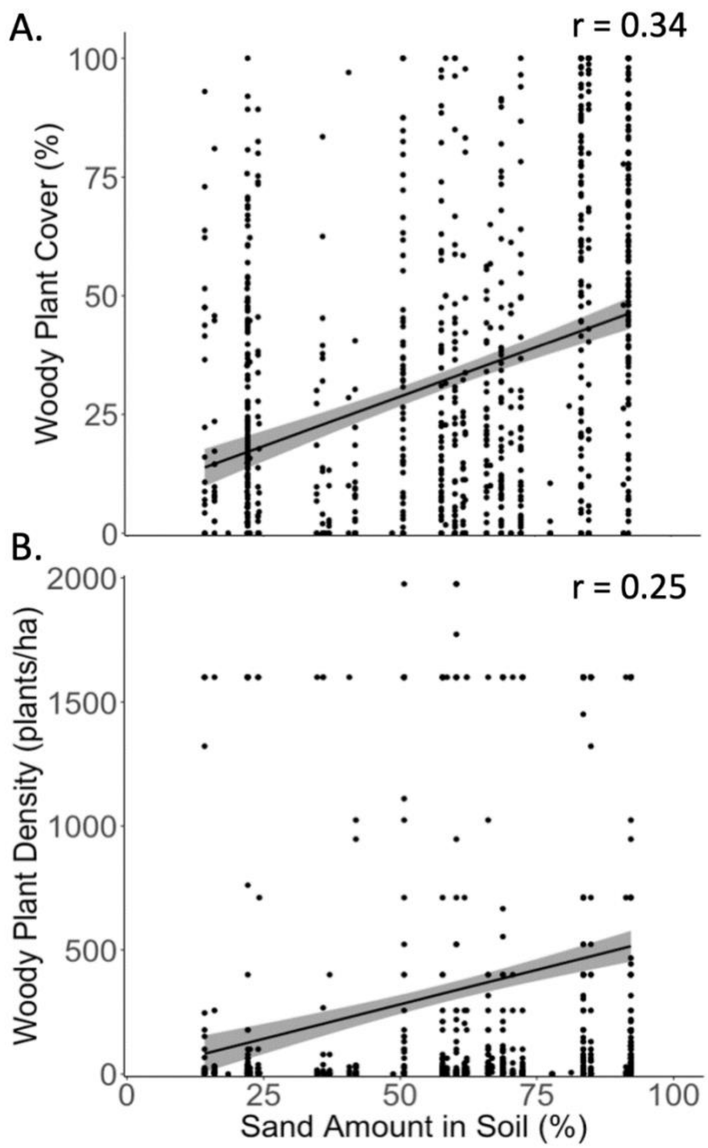

Figure 3. Relationships between **A)** woody cover (%) and percent sand (%) and **B)** woody density (plants/ha) and percent sand (%) across Beaver River, Packsaddle, Sandy Sanders, and Cross Timbers Wildlife Management Areas, Oklahoma, USA, 2018-2019. Percent sand (%) is a weighted average derived from a soil depth of 0-3 m. Gray bands indicate 95% confidence intervals for regression lines and r values are located in the top-right corner of each graph. Because both methods of woody cover estimation yielded similar correlations with percent sand (r ± 0.07), Daubenmire woody cover (**A.**) is shown above as a representative graph to describe this relationship.

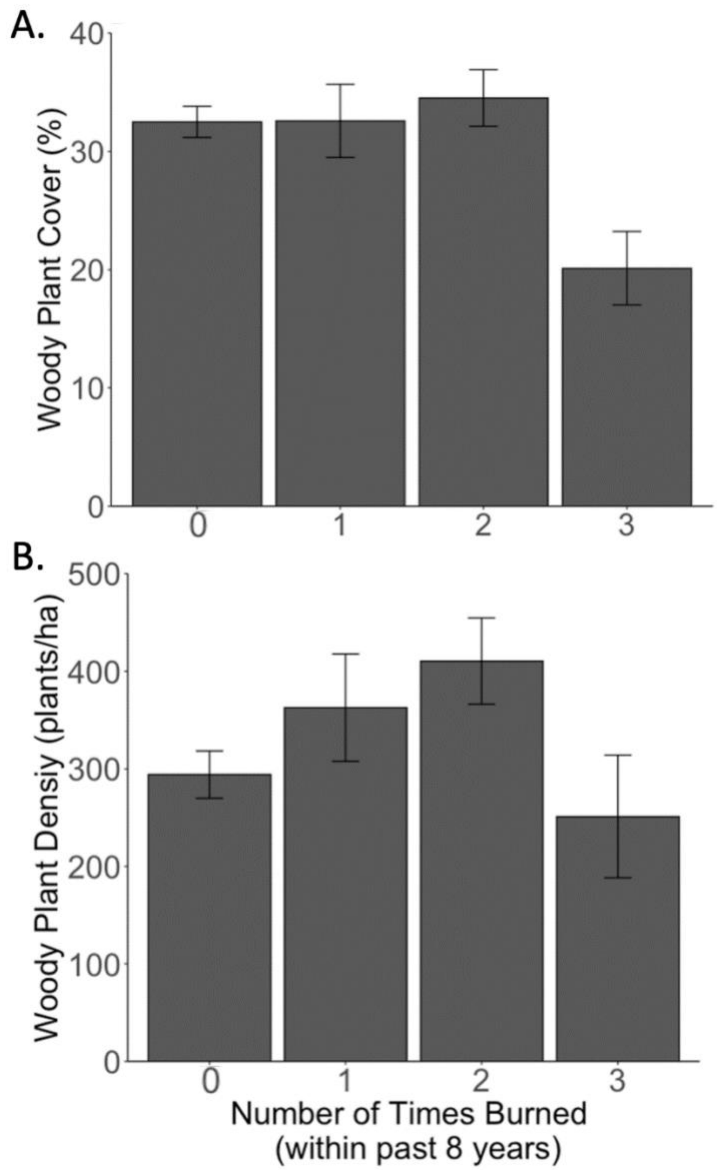

Figure 4. A) Woody cover (%) and **B)** woody density (plants/ha) measurements for the number of times vegetation had been burned in the past 8 years across Beaver River, Packsaddle, Sandy Sanders, and Cross Timbers Wildlife Management Areas, Oklahoma, USA, 2018-2019. Error bars equal ± 1 SE. Because both methods of woody cover estimation yielded similar patterns among number of times burned, Daubenmire frame woody cover (**A.**) is shown above as a representative graph to describe this relationship.

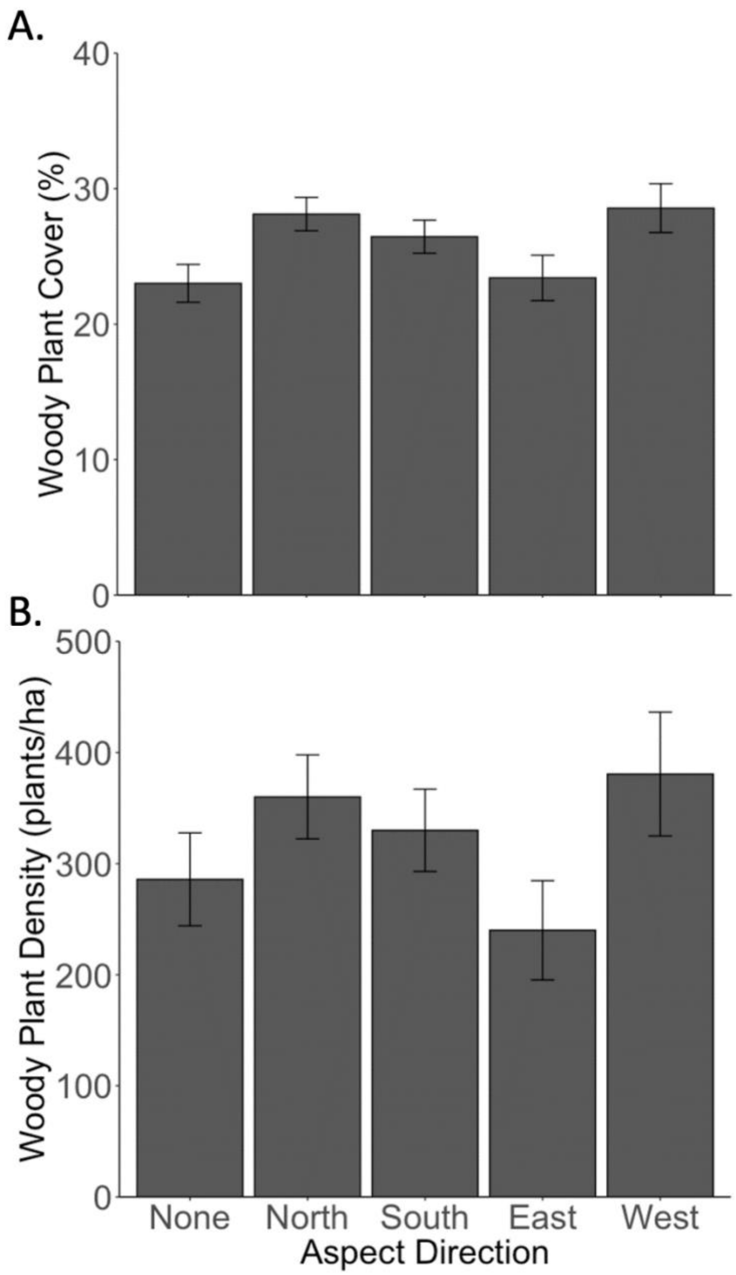

Figure 5. A) Woody cover (%) and **B)** woody density (plants/ha) measurements for each cardinal direction of aspect across Beaver River, Packsaddle, Sandy Sanders, and Cross Timbers Wildlife Management Areas, Oklahoma, USA, 2018-2019. Error bars equal ± 1 SE. Because both methods of woody cover estimation yielded similar patterns among aspect directions, Daubenmire frame woody cover (**A.**) is shown above as a representative graph to describe this relationship.

APPENDICES

Appendix A. Woody species presence data collected for each site across Beaver River, Packsaddle, Sandy Sanders, and Cross Timbers Wildlife Management Areas, Oklahoma, USA, 2018-2019. A total of 54 tree, shrub, and sub-shrub species were documented in this study.

Shrub Species	Beaver River WMA	Crosstimbers WMA	Packsaddle WMA	Sandy Sanders WMA
American Beautyberry		X		
American Elm		X	X	X
Ashe Juniper				X
Black Hickory		X		
Black Locust	X	X	X	X
Black Walnut		X		
Black Willow	X	X	X	X
Blackjack Oak		X		
Broom Snakeweed	X		X	X
Buckbrush		X		
Buffalo Currant	X	X	X	X
Buttonbush		X	X	X
Cedar Elm		X		
Chittamwood		X		
Common Hackberry	X	X	X	X
Common Persimmon		X		
Eastern Cottonwood	X	X	X	X
Eastern Prickly Pear		X		
Eastern Redcedar	X	X	X	X
Engelmann Prickly Pear				X
Four-winged Saltbush				X
Fragrant Mimosa				X
Great Plains False Willow	X		X	X
Greenbrier		X		
Honey Locust		X	X	X
Kentucky Coffeetree		X		
Oklahoma Blackberry		X		
Oklahoma Plum			X	
Osage Orange		X	X	X
Pecan		X		
Plains Prickly Pear	X	X	X	X

Shrub Species	**Beaver River WMA**	**Crosstimbers WMA**	**Packsaddle WMA**	**Sandy Sanders WMA**
Plains Yucca	X	X	X	X
Poison Ivy		X		
Post Oak		X		
Red Mulberry		X		
Redberry Juniper				X
Roughleaf Dogwood		X	X	
Saltcedar	X		X	X
Sand Plum	X	X	X	X
Sand Sagebrush	X		X	X
Shinnery Oak			X	
Siberian Elm	X		X	X
Skunkbush Sumac	X		X	X
Slippery Elm		X		
Smooth Sumac		X	X	X
Soapberry	X	X	X	X
Southern Hackberry	X	X	X	X
Tasajillo				X
Texas Hercules’ Club		X		
Tree Cholla	X			
Water Oak		X		
Winged Elm		X		
Winged Sumac		X	X	X
Total Species	**18**	**38**	**26**	**29**

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