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Is a Prescribed Fire Sufficient to Slow the Spread of Woody Plants in an Infrequently Burned Grassland? A Case Study in Tallgrass Prairie ☆,☆☆

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ABSTRACT

In many mesic grasslands, such as the central Great Plains in North America, frequent fire is a key regulator of ecological processes. Long periods of infrequent fire facilitate the conversion of herbaceous-dominated grassland to woody-dominated shrubland or woodland. At the Konza Prairie Biological Station in northeast Kansas, one infrequently burned portion of the landscape has undergone transformation from grassland to woodland after nearly 30 yr without fire. In Spring 2017, a prescribed burn was implemented to assess fire effectiveness on woody plant mortality. A postfire census of 3 000+ individual woody plants identified the distribution of species by size (height), topographic position, and slope on the landscape. Mortality and canopy fire damage were calculated for each individual. In lowland locations with near-continuous shrub cover (30.7% of the landscape), woody plants were unaffected by fire. However, in upland and slope locations, where shrubs and trees were sparser, survival probability varied by topographic position and species. In these locations 68% of all woody individuals experienced 90% or greater fire damage to the canopy, with 56% of these individuals exhibiting new canopy regrowth within 2 mo after the fire. The two most abundant woody shrubs, *Cornus drummondii* and *Rhus aromatica,* showed high survival at all height classes and landscape positions. The two abundant tree species, *Gleditsia triacanthos* and *Juniperus virginiana,* showed increased survival probability with tree height that varied by landscape position. Survival of *J. virginiana* also varied according to proximity and size of neighboring clonal shrubs, providing a mechanism for persistence of this fire-sensitive tree species even at small height classes. The probability survival curves developed here are useful for managers assessing when to prescribe fire to maximize mortality for *J. virginiana* and provide insight relevant for broader ecological understanding of woody encroachment within grasslands throughout the world.

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Introduction

Grassland ecosystems face multiple threats including conversion to cultivated agriculture, climate change, invasive species, and increases in the cover and abundance of woody species (White et al. 2000; Sherow 2007; Gibson 2009; Blair et al. 2014). An increase in occurrence and cover of woody species in grassland is a process often referred to as *woody encroachment.* Woody encroachment is a global phenomenon, impacting grassy ecosystems in temperate (Knapp et al. 2008; Ratajczak et al. 2014a, 2014b), tropical (Mitchard and Flintrop, 2013; Stevens et al. 2017), semiarid (Van Auken 2000; Gibbens et al. 2005), subarctic (Goetz et al. 2010), and alpine environments (Brandt et al. 2013; Formica et al. 2014). Many drivers have been attributed to increased woody encroachment (Archer et al. 2017) including overgrazing (Walter 1964; Archer 2010; Stevens et al. 2016), altered fire frequencies (Briggs et al. 2005; Ratajczak et al. 2014a), reduced fire intensity (Twidwell et al. 2016; Smit et al. 2016), loss of browsing herbivores (Staver and Bond 2014; O'Connor et al. 2020), increased propagule sources (Woods et al. 2019) (i.e., windbreak tree plantings and fragmentation of rural landscape for human development—Briggs et al. 2005), and rising atmospheric CO_2 concentrations (Buitenwerf et al. 2012; Higgins and Scheiter 2012; Devine et al. 2017). Changes in

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these drivers, or interactions among multiple drivers, typically benefit the growth and persistence of woody species compared with the grass species being replaced and increase the difficulty for land managers to maintain functionality of grassland ecosystems (Berg et al. 2016; Archer et al. 2017; Wilcox et al. 2018).

The consequences of woody encroachment in grasslands vary among locations (Archer et al. 2017) but can include altered species diversity (Eldridge et al. 2011; Ratajczak et al. 2012), reduced forage for livestock (Allred et al. 2012; Anadón et al. 2014), reduced pollination services (Kettenbach et al. 2017; Lavorel et al., 2018), and altered carbon, water, and nutrient cycling (Throop and Archer 2007; Knapp et al. 2008; Honda and Durigan 2016; Mureva et al. 2018). Because of the myriad of ways that increased abundance of woody plants negatively impact ecosystem services, an investigation into potential solutions for remediation or recovery from woody encroachment has become a primary research focus in many grassland ecosystems.

Grasslands, shrublands, or woodlands are thought to represent alternative ecosystem states for many ecosystem types (Staver et al. 2011; Ratajczak et al. 2014b; Wilcox et al. 2018). Due to the nonlinear dynamics that regulate the transition from grassland state to a shrubland/woodland state, warning signs that precede thresholds between ecosystem states are often difficult to identify (Bowman et al. 2015). When present, these warning signs may provide windows of opportunity to preemptively implement management solutions (Bestelmeyer et al. 2011; Twidwell et al. 2013a; Ratajczak et al. 2017). For example, shrub or tree invasion of grassland ecosystems can be gradual at first, until a tipping point is reached where woody species rapidly expand (Ratajczak et al. 2014b). In addition, species interactions can vary on the basis of demographic stages of the woody plants, such that the greatest competitive interactions between grasses and shrubs occur at the youngest shrub demographic stages (Pierce et al. 2019). Thus, once woody species reach a critical age, size, abundance, or cover, competitive restrictions from co-occurring grasses are low and the original resilience of the grassland ecosystem is eroded, resulting in abrupt and nonlinear increases in woody plant abundance (Bestelmeyer et al. 2011; Ratajczak et al. 2014b, 2018). For these reasons, the best remedy for woody encroachment in grasslands is often prevention of initial spread (Ratajczak et al. 2014a).

The identification of grassland regions susceptible to woody encroachment (Ratajczak et al. 2016) and implementation of proactive versus reactive controls is a key goal of sustainable natural resource management (Holling and Meffe 1996). However, the vastness of this ecosystem type (e.g., North America Great Plains alone has 1.3 M km^2 of grassland), the scale of woody encroachment, and the rapidity of ecosystem change have limited our ability to implement widespread proactive control. In addition, insufficient funds for removal of undesirable woody plants, research, and outreach has made the solution of prevention often difficult to achieve (Tanaka et al. 2011). In locations where woody encroachment has already occurred, grassland conservation requires novel solutions to facilitate restoration and promote state transitions from an undesirable ecosystem state (here, shrubland or woodland) back to functional grasslands. The existence of alternative ecosystem states implies the presence of hysteresis (May 1977; Walker et al. 1981; Collins et al. 2021) whereby the resumption of ecosystem drivers that once maintained the grassland state (e.g., fire frequency) are no longer sufficient to generate its recovery. Stated another way, reversal of woody encroachment requires changes in drivers of a magnitude greater than that which facilitated the original transition. The mechanistic underpinning of hysteresis is often one or more shifts in feedbacks (Collins et al. 2021). For instance, as woody plants expand into grasslands, they can reduce surface fuel loads, making subsequent fires less intense in and around shrub canopies (Ratajczak et al. 2014b). For many mesic grassland ecosystems, fire, grazing, and climate are key drivers that regulate ecosystem dynamics (Knapp et al. 1998; Blair et al. 2014), and reductions in fire frequency and intensity are the most proximal local drivers of woody encroachment (Briggs et al. 2005; Twidwell et al. 2013b; Ratajczak et al. 2014b). Given that historic fire frequencies and intensities that once maintained the grassland state are often no longer effective in its restoration (Case and Staver 2017), management prescriptions that incorporate species-specific and landscape-specific recommendations may be one of our best long-term management goals for recovering grasslands from woody encroachment.

This study used a landscape perspective to investigate the impacts of a single prescribed fire in a mesic grassland ecosystem that transitioned from grassland to shrubland/woodland following decades of fire suppression. Here, we measured the consequences of a single spring fire on the 3 000+ woody plants that exist within the 23.77-ha study area. To identify the effectiveness of fire as a management option, we measured the species identity, landscape location, height, and basal diameter for the vast majority of woody species on the landscape after a spring prescribed fire in 2017, and then again in 2019/2020. Attributes of individual species were then related to landscape characteristics including topographic position (upland, slope, lowland) and slope that may impact fire intensity and overall effectiveness as a management option. Our objectives were to 1) identify the effectiveness of fire as a management tool on a woody-encroached grassland system that still retains a fragmented heterogeneous grassy fuel layer; 2) identify if lags in mortality occur such that initial assessments of fire impacts underestimate true mortality; 3) develop a predictive model that delineates the impacts of fire damage and mortality according to species identity, size, and physical landscape attributes; and 4) identify if shrub island size on the landscape accentuates, buffers, or has no impact on fire effectiveness for neighboring tree species. While this research was conducted in a single, well-studied tallgrass prairie in eastern Kansas, an assessment of these objectives may serve to broadly inform managers developing prescriptions that include fire as a method to recover grassland ecosystems lost to encroaching woody species.

Methods

Study site

Data were collected at the Konza Prairie Biological Station (KPBS), located in northeastern Kansas (39.1069°N, 96.6091°W). KPBS is an experimental landscape that maintains decadal fire prescriptions manipulated at the watershed level. Replicate watersheds at KPBS were burned at 1-yr, 2-yr, 4-yr, and 20-yr frequencies in the spring (March–April), in addition to other 1-yr fire treatments prescribed during other seasons of the year (summer, fall, winter). We measured woody plant species located on watershed 20B during the summer of 2017 and 2019. Watershed 20B is 23.77 ha, ungrazed by large ungulates (no cattle or bison present), and the infrequent burn schedule has led to a large increase in woody plants (Briggs et al. 2005; Ratajczak et al. 2014a). Before this study, the last prescribed burn on watershed 20B occurred in 1975 with only two unplanned wildfires since then, both of which occurred in 1991. A prescribed fire was conducted on April 13, 2017, using a headfire initiated on the western boundary of the watershed (**Fig. 1**). Weather conditions during the burn included an air temperature of 23°C, relative humidity of 53%, wind speed of 4.7 m/s, and a wind direction of 230 degrees (southwest) (Nippert 2020). Between January 1 and April 13, 2017 (day of the burn), this location had received a cumulative of 181.1 mm of rainfall, with no rain in the week before the burn (Nippert 2021).

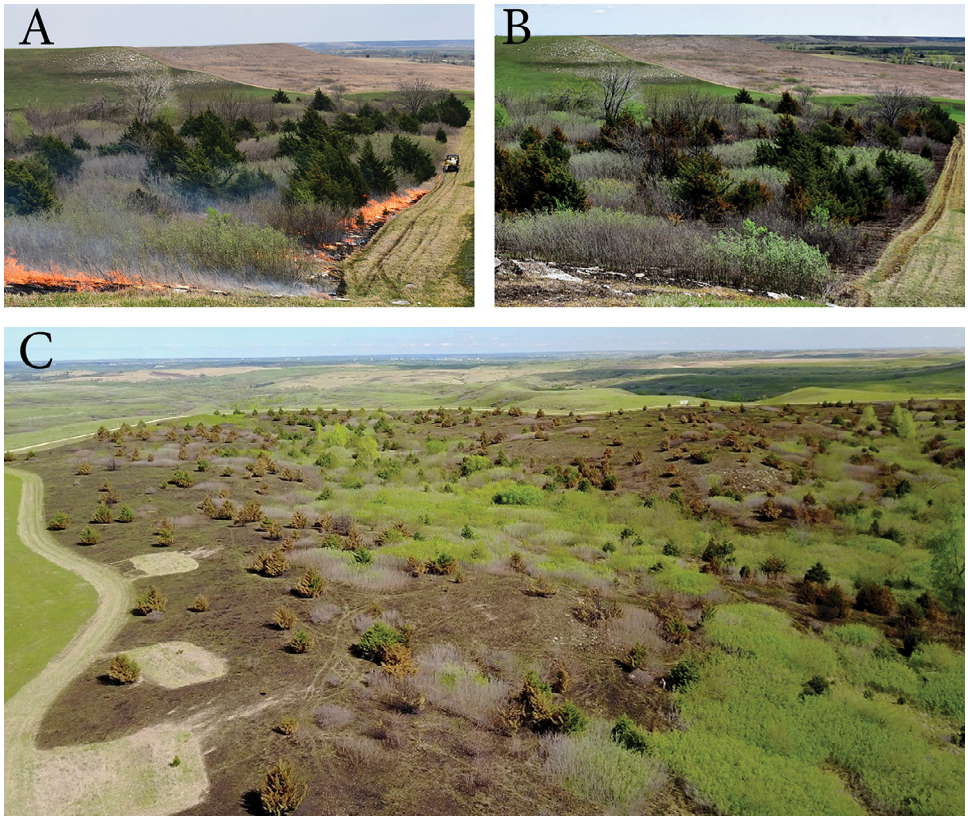

Fig. 1. Prescribed fire and immediate impacts on watershed 20B. **A** and **B,** Southern vantage on the western side of the watershed taken on April 13 and 17, 2017, respectively (photo credit: Barb Van Slyke). **C,** Aerial view with a northern vantage on the western border from April 20, 2017 (photo credit: Scott Stebner). The green shrub matrix is primarily *Cornus drummondii* and the widely distributed evergreen is *Juniperus virginiana*.

Field methods

From late May to early August, 2017, we identified 3 020 individual woody species within the watershed and measured them for a suite of physical characteristics (**Fig. 2**). In 2017, we encountered 15 different woody species within the watershed (**Table S1,**), of which four species were disproportionately more abundant than the others (> 200 individuals/species). These focal species included 1) *J. virginiana* L., a nonclonal and nonresprouting evergreen tree; 2) *Cornus drummondii* C. A. Mey., a clonal and resprouting shrub; 3) *Gleditsia triacanthos* L., a resprouting deciduous tree; and 4) *Rhus aromatica* Aiton, a clonal and resprouting shrub. The tallest height for each individual was assessed using a height pole, and stem diameter at ground level was measured for tree species using a dbh tape. In 2017, location within the watershed was recorded using a Garmin 60CSx global positioning system unit (Garmin International, Inc., Olathe, KS). For each individual, total plant percent damage from fire was visually estimated using 5% interval categories (e.g., 0%, 5%, …, 95%, 100%). Many of the woody individuals were completely damaged by fire but had begun basal resprouting. In these cases, individuals were assessed as 100% damage from fire but classified as "alive." Woody individuals that were completely damaged from fire (i.e., 100%) but not resprouting were classified as "dead." In the lowland portions of this watershed, individuals of the shrub *C. drummondii* have grown together, creating a large amorphous shrub island that makes it difficult to penetrate and identify distinct individuals (see Fig. 1C, Fig. 2A, white shading). For this reason, the number of individual *C. drummondii* shrubs in the lowland region is underestimated. Outside of the lowland locations, estimates of *C. drummondii* on the watershed are frequency based and refer to discrete shrub islands. Although abundant at KPBS as a whole, the small-statured shrub *Rhus glabra* L. (smooth sumac) was not measured in this study because of low abundance in this watershed (< 0.05 ha cumulative canopy cover).

To assess if woody species marked as "alive" in 2017 had delayed mortality, we censused the majority of living trees and select shrubs during July–August 2019 using Trimble Juno 3B GPS units (Trimble, Sunnyvale, CA). Individual trees were marked as points, while shrubs were mapped as either polygons or points depending on size and growth form. If a shrub was < 1 m at its widest dimension, it was marked as a point at the plant's center and its dimensions were visually estimated. If > 1 m wide, a perimeter polygon was obtained at the shrub periphery where new clonal stems are recruited. During late winter and early spring 2020, all *J. virginiana* trees were recensused to assess mortality (living or dead) since 2017.

Global information system analyses

Ground survey data were analyzed and displayed using ArcGIS 10.8 (ESRI 2020). We digitized areas of the watershed as either herbaceous vegetation (no woody species), woody burned (which includes herbaceous plants plus woody plants impacted by the fire), and woody unaffected (regions unimpacted by the fire–see Fig. 1) using 2017 National Agriculture Imagery Program (NAIP) imagery and the 2017 ground survey (**Fig. 3A**). US Geological Survey light detection and ranging (LiDAR)-derived elevation with a 2-m spatial resolution was reclassified to represent landscape positions of upland (> 430 m above sea level [ASL]), lowland (< 420 m ASL), and slope (between 420 m and 430 m ASL). The elevation at the site varied from 405 m at the lowest topographic position to 435 m at the highest topographic position. Using the same LiDAR data, we also calculated slope and elevation for the watershed. We next

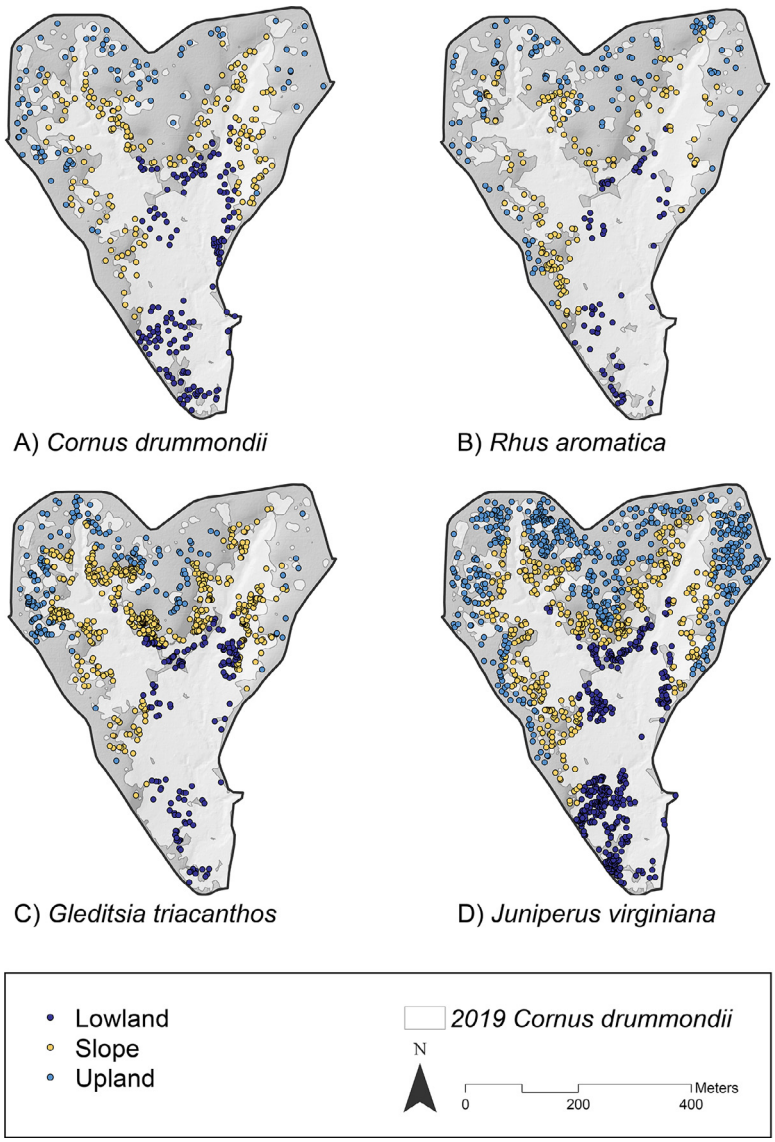

Fig. 2. Census of the four most abundant woody species on watershed 20B in 2017. Points are color coded based on topographic position. The large white polygon in the lowlands depicts complete coverage by the clonal shrub *Cornus drummondii* (as measured in 2019).

used ArcMap10.8 (ESRI 2020) to join the topographic categories, slope, and elevation values to each individual woody plant. Maps were created to display the recorded species-specific data from 2017. Data were symbolized to depict the individuals that were highly impacted by fire (i.e., those with > 90% damage) and resprouted (see Fig. 3B).

Additional global information system analyses were conducted for the *J. virginiana* individuals to assess proximity to shrub polygons. Heights and fire damage from 2017 were classified to correspond with 2019/2020 height and damage categories. We buffered each *J. virginiana* tree 2 m. We next dissolved all shrub polygons together. Next, we intersected the 2-m buffer and the dissolved shrubs to calculate the area of overlap of these two datasets. These analyses were not conducted for *G. triacanthos* because this tree species is not fire sensitive and resprouts following fire damage.

Statistical analysis

All analyses were done in program R with RStudio (R Core Team 2017). We analyzed the 2017 survey data using model selection of binary multiple logistic regression models. Our response variable was woody plant mortality (i.e., dead or alive), with explanatory variables of woody plant height (m), topographic position, slope, and woody plant species. Using the R package glmulti (Calcagno, 2019, version 1.0.7.1), an automated model selection method that compares all possible models using Akaike information criteria, we compared main and crossed effects, which resulted in 250 individual models. We subset one-third of our dataset to train our model, and then once our top model was selected we used the remaining two-thirds of the data to evaluate model performance. Our top model included woody plant species, woody plant height, topographic position (i.e., lowland, slope, and upland), and the interaction term of woody plant height and topographic position. We then used this model to predict woody plant survival among species, woody plant height, and topographic position. To assess our top model's predictive sensitivity, we used a receiver operating characteristic curve and calculated the area under the curve using the R package pROC (Robin et al. 2011, version 1.16.2). Using the Car package (Weisberg 2011, version 3.0-2), we used a type III analysis of variance function to test model significance. "Species" was significant in the top model, so individual models were analyzed by species to test plant height and landscape topographic positions.

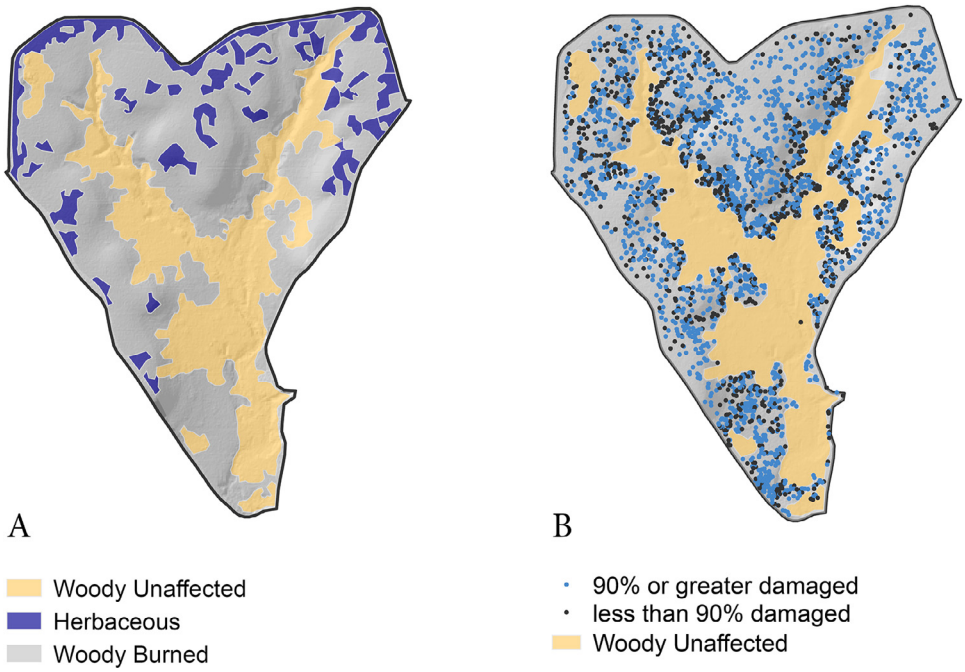

Fig. 3. Impacts of the fire on woody species in 2017. **A,** Herbaceous litter promoted fire spread in regions with herbaceous fuel only (blue) and herbaceous and woody species (gray shading). Areas marked with yellow shading were not impacted by the fire. **B,** Estimated visual impacts of fire damage for each woody stem are identified.

All model results were determined statistically significant at an α-level of 0.05.

We used a binary logistic regression model to test if *J. virginiana* survival was impacted by growth within or adjacent to the clonal shrubs on the landscape. *J. virginiana* was selected for this analysis because it is a fire-sensitive species that does not resprout after disturbance. We used woody plant mortality (i.e., dead or alive) as the response variable with height and percent area within a shrub as the predictor variables. Model significance was determined with an α-level of 0.05.

We assessed delayed mortality effects of the 2017 fire on *J. virginiana* with a second survey in 2019/2020. To determine the percent of mortality and percent delayed mortality, we located the dead *J. virginiana* after the 2017 fire and divided this number of individuals by the total number of *J. virginiana* surveyed. Delayed mortality was calculated the same way but used the 2019/2020 survey to establish the number of dead/living *J. virginiana* on the landscape. No newly found or established *J. virginiana* in 2019/2020 were included in this analysis.

Results

The distribution of individuals varied by location on the landscape. *J. virginiana* had the largest number of individuals measured in 2017 (see Fig. 2D, Table S1), with 38.4% of individuals located in upland, 30.2% on slopes, and 31.3% in lowland locations. The second most abundant species on this watershed was *G. triacanthos,* with 22.3% in uplands, 58.3% on slopes, and 19.3% in lowland locations (see Fig. 2C, Table S1). As noted in the Methods section, individual *C. drummondii* shrub islands have grown together in lowland locations, creating a large amorphous shrub island that is now buffered against fire (see Fig. 1). This shrub island encompassed the largest portion of the watershed, although discrete shrub islands were present throughout the watershed including 20.6% in uplands, 42.9% in slopes, and 36.5% in lowlands (see Fig. 2A). *R. aromatica* was also broadly distributed across the watershed, with 36.7% in uplands, 44.1% in slopes, and 19.2% in lowland topographic positions (see Fig. 2B).

Table 1
Binary logistic type III analysis of variance χ^2 results of woody plant survival from fire based on species, landscape position, plant height, and the interaction of landscape topographic position. Model variable significance is represented through bolded values ($\alpha = 0.05$).

	χ^2	Standard error	*P* value
Species	**1 413.40**	**3**	**< 0.001**
Topographic position	**7.63**	**1**	**0.022**
Plant height (m)	**82.12**	**1**	**< 0.001**
Topographic position−to−plant height (m)	**11.96**	**2**	**0.003**

The prescribed fire on April 21, 2017 resulted in differential severity by species and landscape position (**Fig. 3A**): 12.9% of the watershed had a significant herbaceous layer without woody plants and was completely burned; 56.4% of the watershed had mixed grass/woody layers and supported the prescribed fire; and 30.7% of the watershed, mostly in the lowland region, was unimpacted by the prescribed fire largely because a grassy layer is no longer present (see Fig. 3A). For woody species in locations that burned, 68% of all woody individuals experienced 90% or greater fire damage to the canopy (see Fig. 3B). Surveys of individuals on the landscape between June and July of 2017 showed that 56% of the individuals that experienced 90% or greater fire damage had new canopy regrowth.

Using the species-specific assessments of fire mortality in 2017 along with LiDAR-based landscape characteristics, we created models to identify the probability of survival following fire based on woody plant species, individual height, and landscape location. The ROC results showed that our top model had an 81.02% rate of accuracy in predicting woody plant death and that it had an 81.16% rate of accuracy in predicting woody plant survival (**Table S2**, available online at …). The top model illustrated species-specific mortality as a function of height and topographic location on the landscape (see Fig. 4). Overall, woody plant mortality was impacted by individual height and the combined effect of individual height and topographic position (see Table 1). Clear differences exist among

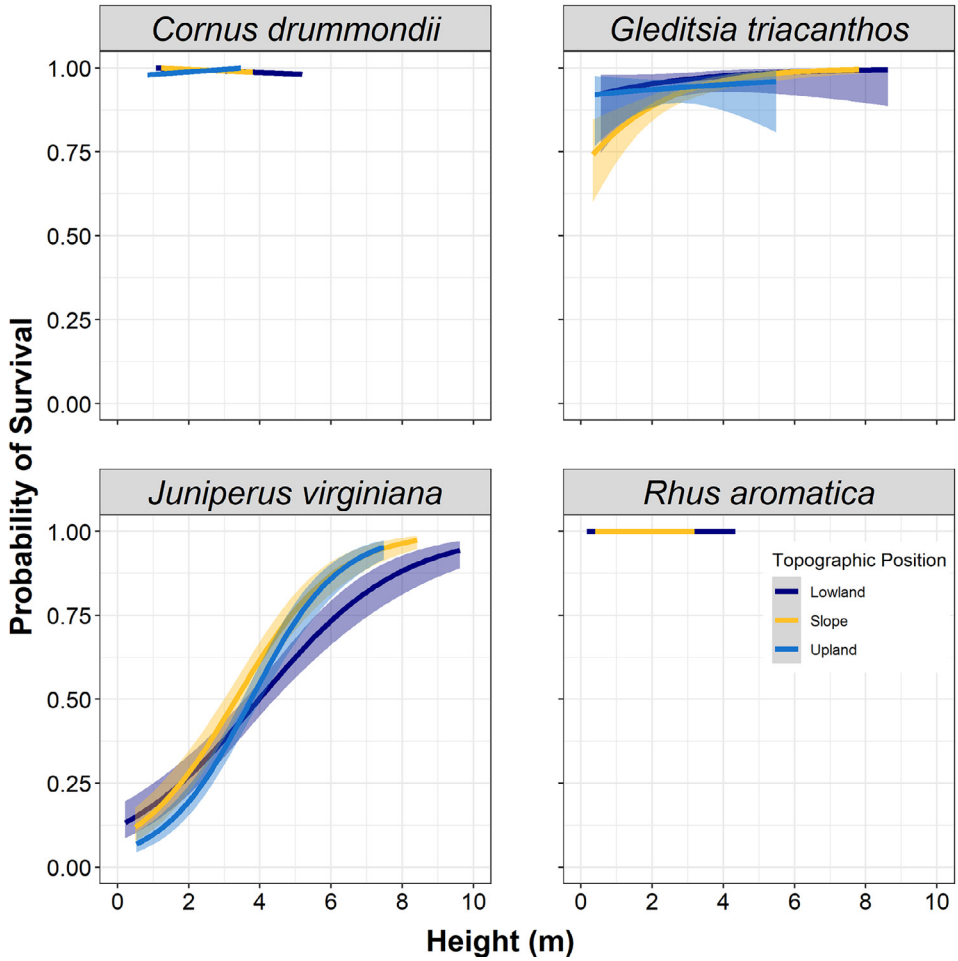

Fig. 4. Species-specific probability of survival from fire as a function of stem height (m) and location on the landscape (topographic position). Probability values of 0 indicates no survival, while a value of 1.00 indicates 100% survival following fire. The solid line represents the modeled mean, while the shading indicates the 95% confidence interval for each mean.

species and growth forms. The two clonal shrub species *C. drummondii* and *R. aromatica* had a high probability of survival regardless of topographic position and/or height (*C. drummondii* – P = NS, *R. aromatica*—all individuals surviving; see Table 2). *C. drummondii* had only three individuals die (see Table S1). In contrast, the two abundant tree species measured on this watershed, *J. virginiana* and *G. triacanthos,* experienced mortality from the fire (see Table S1). *G. triacanthos* had > 90% survival, even at the smallest height classes measured here for lowland, slope, and upland locations on this watershed (**Table 2**). Individuals < 2.5 m in height and on the slope positions had lower survival (**Fig. 4**). *J. virginiana*, a nonclonal and nonresprouting species, had the highest mortality following fire (see Table 2). Despite this susceptibility, this species had a 50% survival rate at heights > 3.75 m (see Fig. 4). The probability of survival varied for *Juniperus virginiana,* with higher survival in the lowland and slope locations for individuals < 2.5 m tall, and reduced probability of survival for individuals > 5 m tall in the lowlands, compared to the other topographic positions (see Fig. 4).

To assess how the presence of shrub islands composed of *C. drummondii, R. aromatica, Rhus glabra, Prunus americana, Zanthoxylum americanum,* and *Amorpha fruiticosa* buffered the impacts of fire, we estimated the probability of *J. virginiana* survival as a function of juniper height and percent shrub cover within 2 m (**Fig. 5**). Regardless of the basal area of the neighboring shrubs, probability of survival following fire was low when *J. virginiana* individuals were small (< 1 m; $P < 0.001$) (see Fig. 5; **Table 3**). As individual

Table 2
Binary logistic regression model results of woody plant survival following fire based on each species by landscape topographic position, plant height, and the interaction. *Rhus aromatica* is not included because it had zero mortality and could not be analyzed in the model. Model variable significance is represented through bolded values ($\alpha = 0.05$).

	Estimate	Standard error	*P* value
Cornus drummondii			
(Intercept)	6.705	3.647	0.066
Slope position	0.687	6.035	0.909
Upland position	−3.722	4.936	0.451
Plant height (m)	−0.628	1.268	0.620
Slope−to−plant height (m)	−0.266	2.245	0.906
Upland−plant height (m)	1.419	2.183	0.516
Gleditsia triacanthos			
(Intercept)	**2.294**	**0.841**	**0.006**
Slope position	−1.434	0.918	0.118
Upland position	0.110	1.119	0.922
Plant height (m)	0.359	0.271	0.186
Slope−to−plant height (m)	0.240	0.303	0.428
Upland−to−plant height (m)	−0.220	0.384	0.567
Juniperus virginiana			
(Intercept)	**−1.990**	**0.252**	**< 0.001**
Slope position	−0.366	0.371	0.324
Upland position	**−1.046**	**0.368**	**0.004**
Plant height (m)	**0.501**	**0.061**	**< 0.001**
Slope−to−plant height (m)	**0.208**	**0.093**	**0.026**
Upland−to−plant height (m)	**0.309**	**0.095**	**0.001**

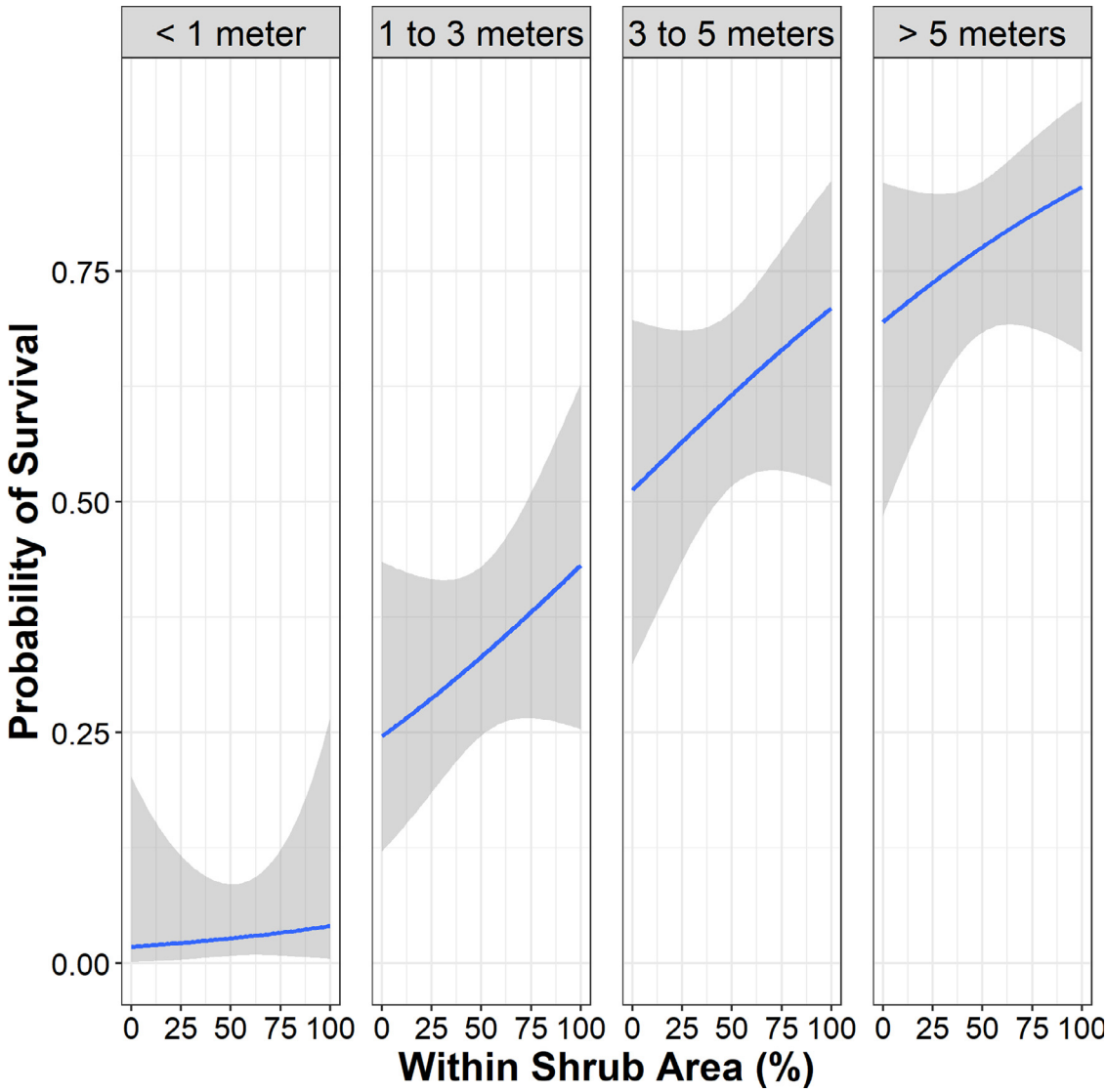

Fig. 5. Probability of survival for *Juniperus virginiana* individuals growing within 2 m of shrub islands as a function of tree height at the time of fire (< 1 m, 1–3 m, 3–5 m, and > 5 m). Shrub area refers to the square meters of shrubs growing within 2 m of the center point of *J. virginiana*. The blue line is the modeled mean, while the shading indicates the 95% confidence interval.

Table 3
Binary logistic regression model results of *Juniperus virginiana* mortality by height classes and within shrub islands. Model variable significance is represented through bolded values ($\alpha = 0.05$).

	Estimate	Standard error	*P* value
(Intercept)	**−4.01**	**0.72**	**< 0.001**
J. virginiana 1-3 m	**2.89**	**0.72**	**< 0.001**
J. virginiana 3-5 m	**4.07**	**0.72**	**< 0.001**
J. virginiana > 5 m	**4.84**	**0.75**	**< 0.001**
Percent shrub area	**0.01**	**0.00**	**< 0.001**

J. virginiana trees increased in height, a linear increase in probability of survival corresponded with the basal area of neighboring shrubs. Thus, greater area of proximal shrub cover resulted in a higher probability of survival for *J. virginiana* at all height classes > 1 m (see Fig. 5, Table 3).

J. virginiana mortality caused by fire was 53.9% when censused following the prescribed fire in 2017. A re-census of the surviving *J. virginiana* trees from 2017 in 2019/2020 found an additional 23.3% mortality (up to 77.2% of all *J. virginiana* censused), suggesting a delayed mortality following exposure to the 2017 fire.

Discussion

The encroachment of woody vegetation in temperate grassland ecosystems represents one of the greatest threats to sustainable management and long-term conservation of rangelands (Berg et al. 2016). As such, effective mitigation practices to recover functional grasslands from shrubland or woodland states is of the highest management concern. Woody plants are a natural part of most grassland ecosystems, but historically their abundance was restricted to isolated refugia like headwater stream regions and deep-soiled lowlands that provided abundant water and protected woody species from more intense fires (Gleason 1913). Their expansion and proliferation from these isolated regions likely reflects relaxation or shifts in local drivers (fire frequency, grazing intensity) and global drivers ($[CO_2]$, climate variability, nutrient deposition) that once minimized their spread (Archer et al. 2017;

Devine et al. 2017; Skowno et al. 2017; Stevens et al. 2017; Scholtz et al. 2018). Thus, the rate and trajectory of increases in woody plant expansion in many regions are no longer successfully managed using historic drivers (e.g., fire every 3–4 yr) (Ratajczak et al. 2014b, 2018; Wilcox et al. 2018). Current fire regimes in many key regions (here, North America tallgrass prairie) may be too infrequent for the long-term sustainability of functional grassland ecosystems (Ratajczak et al. 2016; Scholtz et al. 2020). The results from this study support this assertion, showing an ineffective role of prescribed fire as a moderator of woody plant expansion in this infrequently burned grassland (see Fig. 3).

The watershed used for this study was relatively unimpacted by the prescribed fire (nearly 31% of watershed area was unburned) (see Fig. 3A). Of the woody plants that experienced > 90% canopy damage, over 50% of the individuals had basal resprouting within 2 mo of the fire. The fire timing and intensity of this prescribed fire was conducted during a seasonal period that typically maximizes fire effectiveness (e.g., headfire, dry fuel loads). We measured delayed mortality for the fire-sensitive species, *J. virginiana*. After the 2017 fire, ~50% of *J. virginiana* survived and had new leaf growth. By 2019/2020, an additional ~20% of these individuals had died, illustrating delayed mortality for this species following fire exposure. We recognize that changes in fire regime and the site-specific attributes of this watershed studied may vary when compared with fire consequences at other sites. Fire effectiveness to negatively impact woody species (and promote grass species) depends on landscape fuel loads that support high fire intensity (Twidwell et al. 2013a; Krueger et al. 2015). When trees and shrubs become established in grasslands, their high canopy densities result in reduced understory growth and subsequent fuel for fires (Briggs et al. 2005; Limb et al. 2010; Ratajczak et al. 2011). Fire intensity and the corresponding sensitivity by fire-sensitive species varies according to type of fire (headfires vs. backfires) and season of year prescribed (Ewing and Engle 1988; Trollope et al. 2004; Hajny et al. 2011). In addition, the intensity of prescribed fires commonly used to meet management goals are lower than historical fires occurring over an unfragmented landscape during windy and low humidity periods. Maximizing the effectiveness of fire as a management tool requires reevaluation of how to prescribe fires with greater intensities (Smit et al. 2016; Twidwell et al. 2016) or frequencies (Case and Staver 2017) to achieve higher woody plant mortality for tall trees and woody shrubs while minimizing human risk.

Site-specific factors including edaphic conditions, topography, and woody species identity have all been posited to influence fire effectiveness to mitigate woody encroachment (Briggs et al. 2002, 2005; Scholtz et al. 2018), but few ecosystem studies exist that integrate these factors into predictive models (but see Matson and Bart 2013). Predicted responses to resumed fire prescriptions are species specific as some species are less sensitive to fire than others (Pausas 1999; Pausas et al. 2004). The landscape-scale census of individuals following fire used here allowed us to create interspecific models of survival probability as a function of woody plant size (height) and topographic position (see Fig. 4). The two clonal shrub species in high abundance (*C. drummondii* and *R. aromatica*) were insensitive to fire with high survival probabilities for all height classes measured and all three topographic positions (see Fig. 4). For the probability curves for these clonal shrubs, the vast majority of individuals measured were from multistemmed established individuals, rather than newly established seedlings. Many clonal shrub species have the ability to resprout following severe fire damage (Twidwell et al. 2013a; Michielsen et al. 2017). For scenarios where clonal shrubs are recently established, we posit that probability of survival after fire would be lower than recorded here as the belowground bud reserve would be lower, with fewer carbohydrates to invest in stem regrowth/resprouting (Clarke et al., 2013; Pausas et al. 2016). By comparison, the two tree species at high abundance in this watershed show greater susceptibility to mortality at smaller height classes, especially *J. virginiana* (see Fig. 4). Probability of survival for *J. virginiana* is < 25% at height classes < 2.5 m for all topographic positions (see Fig. 4). For the larger height classes (> 5 m), probability of survival was higher in uplands and slopes compared with lowlands. Lowlands on Konza Prairie typically have deeper soil layers with greater water holding capacity, corresponding with greater grass biomass and herbaceous fuels in locations where an understory remains (Nippert et al. 2011). Uplands and slope locations typically have shallower soils, less fine fuels, and increased probability of survival once *J. virginiana* reaches critical size thresholds (see Fig. 4). Briggs et al. (2002) suggested that fire, even infrequent fire, should be effective for constraining the spread and inducing mortality in this species in scenarios before the formation of closed-canopy juniper woodlands. These predictions follow because *J. virginiana* does not resprout, oils in the leaves are flammable, and the thin bark makes it susceptible to fire (Fuhlendorf et al. 2008; VanderWeide and Hartnett 2011). The probability curves developed here for *J. virginiana* illustrate that fire is effective control for small individuals, but landscape characteristics influence the probability of survival for larger individuals (see Fig. 4).

Species interactions may act as ecosystem modifiers, resulting in ecological dynamics that vary dramatically beyond those with single species or among species with similar life history traits. For example, Briggs et al. (2005) speculated that clonal shrubs in woody encroached grassland may serve as a refugia for fire-sensitive tree species. Once established, seedlings in these locations are insulated from subsequent fire, facilitating sustained growth. **Figure 5** provides empirical evidence for this phenomenon and illustrates that the proximity and size of neighboring shrubs is a key regulator of survival for *J. virginiana,* a fire-sensitive tree species. For individual *J. virginiana* growing within 2 m of shrub islands, the area of the shrub island determines the potential for a buffering effect of the shrub on juniper survival. These shrub species have been shown to have high canopy density, low grassy biomass in the understory, and poorly propagate fire (Ratajczak et al. 2011). This facultative interaction between the shrub islands and the juniper also provides a mechanism for ecological state transitions in this mesic location, as the shrubs are facilitating the next state transition—from shrubland to woodland (Ratajczak et al. 2014). The landscape approach quantifying fire impacts used here provides necessary context for describing how juniper height and shrub island size interact to mediate survival from fire in *J. virginiana* (see Fig. 5). Taken together, the models developed here clearly illustrate reduced fire effectiveness in mesic grassland when the landscape has developed into mosaics of grassland, shrubland, and woodland. The reduced effectiveness of fire is a combination of species-specific demographic traits (clonal and resprouting), individual plant heights, and aspects of the physical environment including landscape position. Given this reduced effectiveness, successful long-term management and restoration of this tallgrass prairie site from shrubland/woodland back to grassland will probably require options beyond burning alone (Limb et al., 2010; Alford et al., 2012; O'Connor et al., 2020).

Given the ubiquity of woody encroachment in grassland ecosystems, the development of management options that aid in the removal of woody plants and the recovery of the grassland ecosystem state are desired. For prescribed fire to be an effective restoration tool requires options that promote the development of flammable herbaceous layers. Recovery of the grassy layer in the shrubland state controlled by resprouting and clonal woody species requires a multipronged approach for removal that includes fire after sufficient increases in herbaceous fuels (O'Connor et al. 2020). Opening the shrub canopy layer can be accomplished using brows-

ing herbivores or by cutting treatments that reduce the number of woody stems (O'Connor et al. 2020; Capozzelli et al. 2020). As noted here, promoting fire through regions with clonal shrub stems will reduce the buffering effect of shrub islands on tree development. Recovery of the grassy layer in the woodland state once trees are established requires *J. virginiana* removal, as this species is most susceptible to fire when young and short statured (Limb et al. 2010; Alford et al. 2012). Management actions that seek to reverse woody encroachment before the conversion to the closed canopy woodland state are preferred, due to the potential for extreme wildfire exposure and associated human risks associated with crown fires in juniper woodlands (Donovan et al. 2020).

Implications

Several key points can be derived regarding the overall effectiveness of fire as a management option in locations where fire exclusion has led to woody encroachment. The models developed in this study are directly applicable to land managers in mesic grasslands of the Great Plains region by specifying the height classes and landscape characteristics by which fire still effectively induces high mortality in *J. virginiana*. Similar to Twidwell et al. 2013a, we illustrate thresholds (see Figs. 4 and 5) by which fire effectiveness as a control on *J. virginiana* can be maximized. A single fire had minimal impacts on resprouting and clonal woody species, illustrating the need for novel solutions for future control including sequential fires (Hopkinson et al. 2020), extreme fires (Twidwell et al. 2016), or reintroducing large herd group browsers like goats or elk (O'Connor et al. 2020).

The detailed, site-based landscape perspective provided here aligns with the regional perspective of Scholtz et al. (2018). Specifically, for locations with > 800 mm rainfall in the Great Plains of North America, ecosystem states are regulated by plant height, site-specific soils, topography, and fire intensity (Scholtz et al. 2018). Using a detailed inventory of woody species on the landscape, we illustrate the mechanisms by which infrequent fire interacts with landscape topography and facultative interactions with clonal shrubs to facilitate establishment and survival in a fire-susceptible species *(J. virginiana)* that ultimately mediates the transition from shrubland to woodland. Going forward, these models require validation at other sites with a larger number of species to test the generality of fire impacts more broadly. These results provide more evidence to the developing paradigm that tallgrass prairie is a tristable system (Ratajczak et al. 2014a) such that the frequency of fire is a key driver of ecological dynamics and that the transition from grassland to shrubland is regulated by a varying set of drivers that is required to restore the ecosystem from woodland back to grassland (Collins et al. 2021).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.rama.2021.05.007.

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