Effects of Megafire on Woody Species in the Mixed-Grass Prairie

Matthias W. Sirch[1*], Daniel S. Sullins[2], Nicholas J. Parker[2], David A. Haukos[3], John D. Kraft[1], Christian A. Hagen[4], and Kent A. Fricke[5]

Abstract - Lack of fire in contemporary grasslands has contributed to the invasion of woody plants that can survive low-intensity fire upon maturity, but knowledge of the effects of megafire (>100,000 ac [40,000 ha]) on mortality of woody species within grasslands is limited. We used remote sensing and ground surveys to estimate tree canopy cover change and rates of top-kill and mortality of woody species in the mixed-grass prairie following the Starbuck megafire. After the megafire, we detected 63% tree canopy cover loss, 17 ± 4% (mean ± SD) tree death, and 56 ± 5% tree top-kill with resprouting. We conclude that further postfire management (e.g., targeted herbicide, mechanical removal) may be required to limit woody encroachment following megafire.

Introduction

Fire within the mixed-grass prairie has historically been a key ecological driver in maintaining treeless landscapes (Askins et al. 2007, Gleason 1913, Keeley and Rundel 2005). However, land management in the form of fire suppression and intensive livestock grazing has encouraged encroachment of woody species onto grasslands (Briggs et al. 2005, DeSantis et al. 2011, Engle et al. 2008, Van Auken 2000). Such alterations, alongside land conversion for row-crop agriculture and energy development, have resulted in a mixed-grass prairie ecoregion with grasslands that are fragmented and invaded by woody and non-native species (Dodson and Fiedler 2006, Keeley 2006, Samson et al. 2004). As woody biomass increases, the additional fuels can promote megafires, a term typically defined as a fire burning >100,000 ac (40,000 ha) (Bracmort 2013, Brown 2018, Lindley et al. 2019).

Today, the Great Plains region is recognized as one of six global hotspots for high grassland wildfire risk, and climate change models predict future increases of very large wildfires throughout the region (Barbero et al. 2015, Cao et al. 2015, Donovan et al. 2017). In support of these predictions, the two largest wildfires recorded in Kansas history occurred in 2016 and 2017 within the southern mixed-grass prairie of the Great Plains. The 2017 fire, known as the Starbuck Fire, burned approximately 662,737 ac (268,200 ha) from March 6th to 10th (Lindley et al. 2019).

The Starbuck Fire burned 41,374 ac (16,744 ha, 6% of burned area) at moderate severity and 526,890 ac (213,225 ha, 80%) at low severity, with the remaining 91,737 ac (37,125 ha, 14%) classified as unburned or charred (Monitoring Trends in Burn Severity 2020) by using the differenced Normalized Burn Ratio (dNBR) index. In contrast to forests, grasslands have minimal fuel loads and grassland fires spread and burn through an area rapidly, accounting for the

[1]Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, 205 Leasure Hall, 1128 N. 17th Street, Manhattan, KS 66506, USA. [2]Department of Horticulture and Natural Resources, Kansas State University, 1602 Throckmorton Hall, 1712 Claflin Road, Manhattan, KS 66506, USA. [3]U.S. Geological Survey, Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, 205 Leasure Hall, 1128 N. 17th Street, Manhattan, KS 66506, USA. [4]Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, 2820 S.W. Campus Way, Corvallis, OR 97331, USA. [5]Kansas Department of Wildlife, Parks, and Tourism, 1830 Merchant Street, Emporia, KS 66801, USA. *Corresponding author: msirch@uvm.edu

Associate Editor: Sean Jenkins, Department of Biological Sciences, Western Illinois University.

low severity as the fire removes less vegetation and moisture from the soil than slower moving forest fires (Dillon et al. 2020, Keeley 2009, Miller et al. 2009). Accordingly, even areas burned at low severity experience a near-complete removal of vegetation. This low severity estimate for the Starbuck Fire is similar to all other recent large grassland fires (eight wildfires >50,000 ac [20,000 ha], 2016–2018) in the mixed-grass prairie (Monitoring Trends in Burn Severity 2020).

The Starbuck Fire extensively burned portions of one of the largest remaining tracts of intact grasslands in the region, which provides habitat for several vulnerable grassland-dependent wildlife species, including *Tympanuchus pallidicinctus* Ridgway (Lesser Prairie-chicken; Haukos and Boal 2016, Rosenberg et al. 2019). As Lesser Prairie-chickens are sensitive to tall features (>3.28 ft [1 m]) on the landscape (Boggie et al. 2017, Falkowski et al. 2017, Lautenbach et al. 2017, Plumb et al. 2019), woody encroachment has become a regionally important threat to maintaining grassland habitat for wildlife. Prescribed burning is frequently used to limit woody encroachment, which, when incorporated with mechanical tree removal, can control woody encroachment and produce habitat for grassland-dependent species in the mixed-grass prairie (Fuhlendorf et al. 2017, Lautenbach 2017, Ratajczak et al. 2014).

Two woody species that have substantially encroached onto the Great Plains include the native *Juniperus virginiana* L. (Eastern Redcedar) and non-native *Tamarix ramosissima* Ledeb. (Saltcedar). Encroachment by Eastern Redcedar can reduce grassland biodiversity, lower livestock productivity, increase carbon volatilization, and reduce wildfire suppression potential (Ratajczak et al. 2012, Twidwell et al. 2013). Several studies of Eastern Redcedar and other *Juniperus* species have demonstrated high postfire mortality rates that decrease as trees mature or surrounding vegetation is cut or grazed (Briggs et al. 2002, Noel and Fowler 2007, Ratajczak et al. 2014, Weir and Engle 2017). For Saltcedar, prescribed burning mortality rarely exceeds 30% as it vigorously sprouts from roots following most disturbances (Delwiche 2009, Hohlt et al. 2002, Racher et al. 2003). Further, Saltcedar serves as a fuel ladder that propels flaming embers onto surrounding vegetation beyond the fire perimeter, making prescribed burning challenging (Delwiche 2009).

Because controlled wildfire experiments are not easily replicated, the effects of wildfire on vegetation should be evaluated when possible. Although ecological effects of prescribed burning have been studied extensively, vegetation responses to prescribed burning cannot be directly transcribed to vegetation exposed to more intensive wildfires such as megafires (Arkle and Pilliod 2010, Eisenberg et al. 2019). Most notably, prescribed burns are conducted in predictable low-wind and moderate-high humidity conditions, even during extreme and large-scale experiments (Bidwell et al. 2018, Dey and Hartman 2004, Weir 2014). As landscape-scale and intensive grassland wildfires in the Great Plains become more frequent (Donovan et al. 2017, Polley et al. 2013, Pyne 2017), knowledge of how megafires influence woody species in the highly altered mixed-grass prairie remains limited.

To better understand the effects of megafires within the mixed-grass prairie, our objectives were to (1) estimate tree canopy change from ground surveys and remote-sensing techniques, and (2) evaluate woody species conditions including rates of dead and top-killed plants. We hypothesized that mortality of woody vegetation following the Starbuck Fire would be high but vary by species, and canopy cover would be substantially reduced.

Materials and Methods

Study Area

We examined the effects of the 2017 Starbuck Fire on the mixed-grass prairie of Clark County, Kansas, USA (Fig. 1). The climate was characterized by a warm growing season (mid-April to mid-October) followed by months of little moisture, with precipitation averaging 22.25 in (56.49 cm) annually between 1895 and 2018 (NOAA 2020a). Wildfires typically occur in March and April as vegetation has senesced after the dry period of December–February, which on average receives 0.66 in (1.67 cm) of precipitation per month (Lindley et al. 2019, NOAA 2020a). Wind speed averages are also highest during March and April as air pressure fluctuates due to a convergence of warm air from the Gulf of Mexico and cold air from the Rocky Mountains and the Arctic (Jones and Cushman 2004). Fire return intervals are thought to range 1 to 10 years with an average fire return interval of 5 to 10 years (Fryer and Luensmann 2012, Joern and Keeler 1995).

The warm and dry conditions preceding the 6–10 March 2017 Starbuck Fire intensified effects of the megafire (Lindley et al. 2019). October, November, and December 2016 were particularly dry, receiving less than 1.41 in (3.58 cm) of precipitation cumulatively, 0.63 in (1.6 cm) below historical average (1895–2016) (NOAA 2020a). February 2017 accumulated only 0.07 in (0.18 cm) of precipitation with mean temperatures 9° F (5° C) above historical average (1895–2016) (NOAA 2020a), further desiccating vegetation. Fire ignited by a downed power line in western Oklahoma quickly spread northward on 6 March 2017. Only five hours after ignition, winds of 35 knots (40 mph [65 km/h]), with gusts of 50 knots (57 mph [92 km/h]), pushed flames the height of utility poles (~30 ft [9 m]) from the southwest before rapidly and repeatedly changing directions (Frazier 2018, NOAA 2020b). The Starbuck Fire burned most actively and expanded in size over a two-day period (March 6–7, 2017) and has been described as a short-duration evolution type fire (Lindley et al. 2019). In total, the fire burned an estimated 662,737 ac (268,200 ha).

We conducted ground surveys to evaluate the effects of the fire on 38,500 ac (15,580 ha) of accessible private land within Clark County, Kansas (Fig. 1). The mosaic of land cover types included native grass pastures, Conservation Reserve Program (CRP) fields, alkali flats, sand dunes, and row-crop agriculture. Trees, primarily *Populus deltoides* W. Bartram ex Marshall (Eastern Cottonwood), *Sapindus saponaria* L. (Western Soapberry), *Gleditsia triacanthos* L. (Honey Locust), and *Maclura pomifera* (Raf.) C.K. Schneid (Osage Orange), generally grow in windbreaks along agricultural field edges. Several woody species, including Eastern Redcedar,

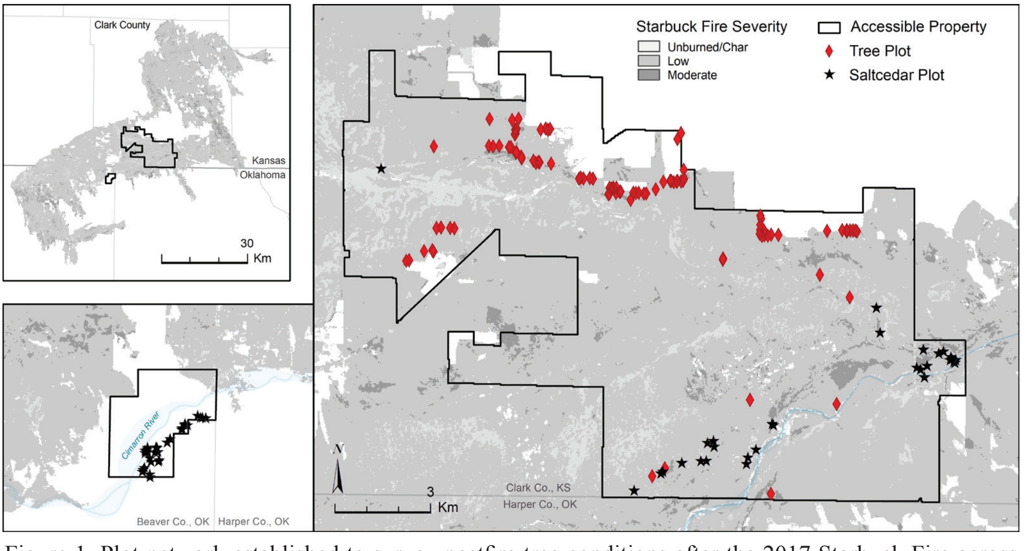

Figure 1. Plot network established to survey postfire tree conditions after the 2017 Starbuck Fire across accessible property in Clark County, Kansas, and Beaver County, Oklahoma. Ground surveys were conducted between 28 August and 1 October 2018, on woodland (n = 98) and Saltcedar plots (n = 60). The differenced Normalized Burn Ratio (dNBR) severity index of the Starbuck Fire was calculated by the Monitoring Trends in Burn Severity program. Tree canopy cover loss was estimated from change in June 2015 and July 2017 National Agricultural Imagery Program (NAIP) imagery.

Ulmus L. spp. (Elm spp.), *Elaeagnus angustifolia* L. (Russian Olive), and *Salix nigra* Marshall (Black Willow) have encroached into the grasslands. Saltcedar has established in dense stands along riverine lowlands of the Cimarron River.

Change in Canopy Cover

To remotely estimate tree canopy cover, we examined defined woodland areas using the 2015 USDA Forest Service Tree Canopy layer, compiled by Paull et al. (2017), throughout the study area. We manually refined the woodland canopy layer across accessible private land using 1-meter resolution National Agricultural Imagery Program (NAIP) imagery for June 2015 and July 2017 to identify tree canopy cover both before and after the wildfire. Tree canopy was distinguished from surrounding vegetation by a distinct shadow at a 1:1000 scale. Pre- and postfire tree canopy layers were manually drawn using ArcGIS 10.6 (ESRI 2018).

Field Collected Data

To ground-truth our remotely-sensed tree canopy estimates and estimate woody species mortality on the ground, we randomly generated 100 non-overlapping 65.62 ft (20 m) diameter woodland ground survey plots within the 2015 pre-fire woodland canopy layer. Two woodland plots were later excluded because of documented aerial application of herbicide in the area. We then used the remotely-sensed postfire 2017 canopy values to compare with 2018 field observations. We evaluated the relationship of remotely-sensed and woodland ground survey canopy estimates using a generalized linear regression in Program R 3.6.1 (R Development Core Team 2019).

Our woodland plots mostly focused on wooded uplands and hedgerows interspersed throughout the predominantly grassland study area. To better evaluate Saltcedar mortality following the Starbuck Fire, we established an additional 60 plots (Saltcedar plots) centered in riparian areas largely invaded by Saltcedar. The areas were manually delineated in ArcGIS 10.6 using the 2015 NAIP imagery to identify Saltcedar stands by their characteristic clustering. We randomly generated 30 plots in both burned and unburned areas within Saltcedar clusters. Because there were no accessible unburned Saltcedar clusters in Clark County, we established the unburned Saltcedar plots within accessible private property in Beaver County, Oklahoma, ~7 mi (11 km) from the closest burned plot (Fig. 1).

For each 65.62 ft (20 m) diameter woodland and Saltcedar plot, we estimated composition of woody species and percentage of intact, dead, and top-killed plants. Top-kill was defined as appearing dead except for new resprout branches growing from the living root system, whereas intact individuals had living canopy branches. We tallied plants as an individual if the diameter at breast height (DBH) was >1 in (2.54 cm) and branches appeared to have emerged from the same root system. For every intact, dead, and top-killed woody species, we measured height of the plant and height of the tallest resprouting branch. In each plot, we also measured largest DBH of each species. We ocularly estimated heights between 10 ft (3 m) and 30 ft (10 m) and used a clinometer for branches taller than 30 ft (10 m). For each woodland plot, we estimated canopy cover ocularly in groups of 0, 1–5, 5–25, 25–50, 50–75, 75–95, and 95–100%. We estimated canopy cover ocularly rather than with a densiometer because of thick understory (<16 ft [5 m] tall; Korhonen et al. 2006). We conducted ground surveys a year and a half after the wildfire, between 28 August and 1 October 2018.

Estimation of Woody Species Mortality

To evaluate megafire effects on each woody species, we estimated the proportion that were dead and top-killed within burned plots. We estimated proportions of mortality and top-kill among all plots, SD of proportions as $(pq/(n-1))$ where p is proportion, q is $(1-p)$, and n is number of samples, and adjusted Wald 95% confidence intervals following Zar (2010). If p = 0 or 1, we used confidence intervals derived from nth root of α = 0.025 following methods in Zar (2010).

Analysis of Woody Species Mortality

To evaluate if tree mortality and top-kill rate varied by species, we logit transformed percent dead and top-kill estimates as our response variables for each ground survey plot and then performed a multivariate analysis of variance (MANOVA) with burned and unburned treatments as independent variables (Warton and Hui 2011). Although MANOVA can handle correlated dependent variables, we examined correlation between mortality and top-kill rates using a Pearson's product-moment correlation test. We then performed an analysis of variance (ANOVA) to evaluate influence of fire on logit transformed dead and resprout rates separately. Finally, we performed Welch's t-tests to examine woody species height and DBH difference between burned and unburned plots. All analyses were conducted using Program R 3.6.1 (R Development Core Team 2019).

Results

Change in Canopy Cover

Our remotely-sensed analysis indicated a 63% woodland canopy cover loss within the burned portion of the study area, decreasing from 126.5 ac (51.2 ha) pre-fire (0.33% of study area) to 46.95 ac (19.0 ha, 0.12%) postfire. Within woodland plots, remotely-sensed canopy cover decreased from 61.8 ± 31.2% to 18.9 ± 28.8% after the wildfire. This woodland canopy estimate using remotely-sensed data was comparable to canopy cover estimated at postfire ground-truth plots (11.0 ± 20.4%), with remotely-sensed canopy slightly greater than ground canopy within woodland plots ($Y_{\text{remotely sensed}} = 1.01 * X_{\text{ground estimate}} + 7.82$; $r^2 = 0.51$, $t_{153.2} = 2.1$, $P = 0.04$). For Saltcedar plots, ground-measured postfire canopy cover was 0.6 ± 3% of the surveyed area.

Species Composition

Each woodland plot contained 1.7 ± 0.9 tree species on average. Woody species within woodland plots were predominantly Honey Locust (26 ± 4%), Western Soapberry (23 ± 4%), Osage Orange (13 ± 3%), Elm spp. (9 ± 3%), Saltcedar (6 ± 2%), Eastern Cottonwood (5 ± 2%), and Eastern Redcedar (4 ± 2%). *Artemisia filifolia* Torr. (Sand Sagebrush) (5 ± 13%) and *Prunus angustifolia* Marshall (Sand Plum) (5 ± 12%) were the predominant shrub species. Within Saltcedar plots, Saltcedar accounted for 97 ± 2% of woody species (Table 1).

Estimation of Woody Species Mortality

We collected data on woody species mortality and condition after the Starbuck Fire. Overall, 17 ± 4% of trees were dead within burned woodland plots while 56 ± 5% were top-killed and resprouted from roots (Table 2). Percentages of dead individuals were greatest for Eastern Redcedar (100%) and Eastern Cottonwood (86 ± 3%), and lowest for Russian Olive and Black Willow (0%) (Table 2). Of 117 burned ground survey plots, 116 plots (99%) had a tallest branch at >3.28 ft (1 m) tall. Tallest branches in burned ground survey plots averaged 29.36 ± 14.60 ft (8.95 ± 4.45 m).

Percentage of dead and top-killed tree species in each plot were negatively correlated, which reflects that if trees were not killed by fire they typically were top-killed ($r = -0.62$, $t_{391} = -15.41$, $P < 0.001$). Combined mortality and top-kill rates varied among burned and unburned treatments (Wilk's $\lambda = 0.53$, $F_{2,357} = 159.5$, $P < 0.001$) and by species (Wilk's $\lambda = 0.48$, $F_{26,714} =$

12.3, $P < 0.001$). The interactive effect of the burn on each species was also significant, indicating that mortality and top-kill rates from the megafire were species-specific (Wilk's $\lambda = 0.87$, $F_{18,714} = 2.8$, $P < 0.001$). Black Willow, Russian Olive, Honey Locust, Western Soapberry, and Osage Orange all showed high rates of top-kill, with branches resprouting from the tree base (Table 2). Among shrub species, Sand Sagebrush exhibited the greatest mortality, followed by Sand Plum and *Rhus aromatica* Aiton (Fragrant Sumac).

Saltcedar Mortality and Top-kill

Our comparison among burned and unburned treatments revealed that Saltcedar was largely top-killed by the megafire and resprouted from the base. In all burned ground survey plots, 33 ± 9% of Saltcedar were dead, 65 ± 9% were top-killed, and 2 ± 4% remained living with intact canopy cover (Table 2). Percentage of dead and top-kill Saltcedar varied among burned and unburned plots (Wilk's $\lambda = 0.20$, $F_{2,149} = 292.6$, $P < 0.001$). However, this difference was mostly due to the difference in top-kill rates among burned and unburned treatments ($F_{1,150} = 88.8$, $P < 0.001$). In unburned plots, Saltcedar were 21 ± 8% dead, 1 ± 3% top-killed, and 78 ± 8% intact.

Tallest Saltcedar branches in burned plots were on average 12.40 ± 2.46 ft (3.78 ± 0.75 m) tall, similar to 13.19 ± 2.20 ft (4.02 ± 0.67 m) unburned Saltcedar branches ($t_{58.693} = -1.31$, $P = 0.19$). We observed 1 dead Saltcedar >16.4 ft (5 m) tall and 4 dead Saltcedar >13.1 ft (4 m) tall, indicating the megafire likely killed large Saltcedar trees. A year and a half after the Starbuck Fire, resprouting branches of top-killed Saltcedar grew to 6.40 ± 1.74 ft (1.95 ± 0.53 m) tall.

Table 1. Overall mean woody species composition and standard deviation within woodland (n = 98) and Saltcedar plots (n = 60) surveyed in Clark County, Kansas, and Beaver County, Oklahoma, USA between 28 August and 1 October 2018.

		Woodland plots				Saltcedar plots			
				Plants/ha				Plants/ha	
	Woody species	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Trees	Honey Locust	0.26	0.04	83	149	0	NA	0	NA
	W. Soapberry	0.23	0.04	76	247	0	NA	0	NA
	Osage Orange	0.13	0.03	42	91	<0.01	<0.01	3	21
	Elm Spp.	0.09	0.03	31	71	<0.01	<0.01	7	25
	Saltcedar	0.06	0.02	21	103	0.97	0.02	1514	1282
	E. Cottonwood	0.05	0.02	15	35	0	NA	0	NA
	E. Redcedar	0.04	0.02	12	52	<0.01	<0.01	6	15
	Mulberry	0.02	0.01	6	26	0	NA	0	NA
	Black Locust	0.02	0.01	6	30	0	NA	0	NA
	Black Willow	<0.01	<0.01	<1	3	0	NA	0	NA
	Ash Spp.	<0.01	<0.01	1	10	0	NA	0	NA
	Russian Olive	0	NA	0	NA	<0.01	<0.01	4	19
	Overall	0.9	0.03	293	272	0.98	0.03	1534	1278
Shrubs	Sand Sagebrush	0.05	0.02	16	86	0.01	0.02	23	106
	Sand Plum	0.05	0.02	15	108	0	NA	0	NA
	Fragrant Sumac	<0.01	<0.01	<1	3	<0.01	<0.01	2	9
	Overall	0.1	0.02	31	148	0.02	0.02	25	111

Table 2. Tree and shrub species counts and proportion of dead and top-killed following the Starbuck Fire within all burned ground survey plots (n = 117) in Clark County, Kansas, USA between 28 August and 1 October 2018. Plots were established where trees were remotely detected in 2015.

				Dead (proportion)			Top-kill (proportion)		
	Woody species	No. total	No. plots present	$\bar{x}$	SD	95% CI	$\bar{x}$	SD	95% CI
Trees	E. Redcedar	35	9	1	0	0.91–1.00	0	0	0.00–0.09
	E. Cottonwood	42	21	0.86	0.03	0.72–0.94	0.05	0.02	0.00–0.17
	Ash Spp.	3	1	0.67	0.04	0.20–0.94	0.33	0.04	0.06–0.80
	Mulberry	10	4	0.4	0.05	0.17–0.69	0.3	0.04	0.10–0.61
	Saltcedar	901	37	0.33	0.09	0.25–0.43	0.65	0.09	0.55–0.74
	Elm Spp.	97	28	0.22	0.04	0.15–0.31	0.42	0.05	0.33–0.52
	Honey Locust	219	40	0.1	0.03	0.06–0.14	0.75	0.04	0.69–0.81
	Osage Orange	99	24	0.08	0.03	0.04–0.15	0.53	0.05	0.43–0.62
	Black Locust	18	5	0.06	0.02	0.00–0.28	0.78	0.04	0.54–0.92
	W. Soapberry	225	16	0.02	0.01	0.01–0.05	0.54	0.05	0.41–0.54
	Black Willow	1	1	0	NA	0.00–0.78	1	NA	0.22–1.00
	Russian Olive	3	2	0	0	0.00–0.53	1	0	0.47–1.00
	Overall Woodland Plots	872	87	0.17	0.04	0.12–0.29	0.56	0.05	0.54–0.74
	Overall Saltcedar Plots	873	30	0.35	0.09	0.26–0.44	0.63	0.09	0.53–0.72
	Overall	1796	117	0.26	0.04	0.16–0.31	0.6	0.05	0.42–0.60
Shrubs	Sand Sagebrush	92	9	0.08	<0.01	0.03–0.15	0.92	0.03	0.85–0.97
	Sand Plum	47	2	0.02	<0.01	0.00–0.12	0.98	0.01	0.88–1.00
	Fragrant Sumac	3	2	0	0	0.00–0.53	1	0	0.47–1.00

Discussion

Variation in postfire mortality and top-kill rates by species in our study highlights the complex nature of woodland response to disturbance, even in areas with limited tree diversity such as our study site in the mixed-grass prairie of western Kansas. Our study contributes to a small but growing body of evidence on the impacts of megafires on grassland plant communities in the Great Plains (Donovan et al. 2020, Rideout-Hanzak et al. 2011), and specifically advances knowledge on the impact to woody species interspersed within grassland-dominated landscapes. Results indicated that megafire in mixed-grass prairie initially reduced canopy cover, but many burned deciduous trees resprouted from their root systems. For example, complete mortality of Saltcedar was not substantially greater in burned areas relative to unburned areas. However, Saltcedar in a burned area experienced a 65% top-kill rate that removed nearly all riverine canopy cover. In contrast to the high prevalence of resprouting from top-killed Saltcedar and other deciduous species, we documented substantial mortality among Eastern Cottonwoods and complete mortality for the invasive Eastern Redcedar.

Our results suggest that megafires historically restricted woody encroachment into grasslands in the Great Plains by eliminating mature stands of *Juniperus* and *Populus* spp. Eastern Cottonwoods that died following the Starbuck Fire were fairly tall, with at least 6 individuals >60 ft (18 m) tall and >31.5 in (80 cm) DBH. Resprouting was also limited for many Eastern Cottonwood across the study area. In contrast to our findings, Wonkka et al. (2018) observed high Eastern Cottonwood regeneration rates following an early May wildfire ~105 m (170 km) west of our study area. Differences in the size or timing of fires, as well as location of trees among hedgerows in our study rather than in riparian areas, may have influenced conflicting regeneration rates between the two studies. In addition, our reduced regeneration may have been caused by an interaction of browsing on resprouting branches by cattle or deer and the effect of the fire (Glinski 1977, Stromberg 1997).

Our high postfire mortality estimates for Eastern Cottonwood and Eastern Redcedar were substantially greater than estimates historically observed in the region's woodlands. Percentages of dead *Populus* and *Juniperus* spp. across Kansas in typical unburned woodlands have been estimated by the USDA Forest Inventory and Analysis (FIA) Program as 19 ± 3% and 2 ± 1%, respectively (>5 in [12.7 cm] DBH, 2006–2016). The FIA standing dead baseline for Populus spp. was the greatest of all examined species, though still well below the 86% we recorded following the megafire (Table 2). This suggests substantial mortality of Eastern Cottonwood despite the thick insulating bark for which the species is known (VanderWeide and Hartnett 2011). For Eastern Redcedar, we documented complete mortality of all trees following the megafire, even trees >20 ft (6 m) tall and with DBH >10 in (25 cm). An Eastern Redcedar of this size would more likely survive a smaller and less intense prescribed fire (Briggs et al. 2002, Nippert et al. 2021, Owensby et al. 1973), but the crown damage of the megafire's larger flames likely killed the mature juniper trees (Weir and Engle 2017). Eastern Redcedar lacks the adventitious buds at the root collar that allow other fire-adapted woody species to resprout (Glasgow and Bidwell 2009).

Although our reported mortality rates suggest megafires may have restricted encroachment of native Eastern Redcedar and Eastern Cottonwood into mixed grass prairie, mortality of the exotic invasive Saltcedar was substantially lower. The Saltcedar mortality rate of 33% from this study coincides with rates of prescribed burn studies across the region (Delwiche 2009, Hohlt et al. 2002, Racher et al. 2003). However, Saltcedar mortality was not substantially different between burned and unburned areas. Our comparison among burned and unburned areas may have been confounded by *Diorhabda* spp. Desbrochers (Tamarisk Beetle). The relatively high Saltcedar mortality rate in unburned areas was likely caused by Tamarisk Beetles, which have been introduced across the Southwest since 2001 as a Saltcedar defoliator biocontrol (Bean and Dudley 2018, Hatten 2016) and has recently expanded into portions of the study area. Although the Saltcedar mortality rate was low, we documented near-complete removal of canopy from riverine lowland Saltcedar stands. Additionally, our estimates suggest that 65% of Saltcedar were top-killed and resprouted, with new sprouts growing to nearly 6.5 ft (2 m) tall over a year and a half after the fire.

This rapid growth rate corresponds with previous research noting faster growth rates for recently disturbed Saltcedar (Goldsmith and Smart 1982). We recognize that wildfire alone has limited potential for returning established Saltcedar stands to grassland habitat, particularly due to this resprouting capacity and the species' ability to disperse millions of seeds annually (Bond and Midgely 2003, Di Tomaso 1998, Stevens 2002). Similar to patterns of Saltcedar, we documented high resprouting potential in several other deciduous taxa, including Elm spp., Honey Locust, Osage Orange, and Western Soapberry (Bond and Midgely 2003). Our results suggest that future megafires, if not selecting for herbaceous cover, will select for native or invasive non-native woody species with strong resprouting potential, similar to postfire woody vegetation shifts in Arizona following decades of fire suppression (Taylor et al. 2021).

In addition to better understanding direct responses of both exotic and native invasive woody species, the accurate prediction of future woody species response to megafire will need to account for interactions with other ecological drivers including climate (Askins et al. 2007). As the mixed-grass prairie experiences warmer and drier conditions, greater variability of weather linked to climate change could result in more intense wet seasons followed by intense drought during dormant seasons. Such a scenario would promote the growth and drying of grasses as fuel for fire (Courtwright 2011). When combined with increased woody encroachment throughout the region, megafires may become more prominent and challenging to suppress (Lindley et al. 2019). Megafires like the Starbuck Fire have the potential to reduce the abundance of trees on the landscape, creating habitat for grassland wildlife species. However, once undesirable trees become established, it will require substantial disturbance and effort for the woody species to be removed.

Management Implications

Even following a megafire, resprouting Saltcedar and other tree species were prevalent. Mechanical removal of root systems or multiple years of herbicide may be required to eliminate Saltcedar from an area (Duncan and McDaniel 2009, Fick and Geyer 2010, McDaniel and Taylor 2003). In areas suitable for Saltcedar, aggressive efforts to prevent establishment of Saltcedar and other resprouting species may be more cost effective. In contrast, large fires and megafires may present an opportunity to reclaim grasslands previously invaded by Eastern Redcedar. Although Eastern Redcedar will not resprout, dead Eastern Redcedar may continue to stand for many years, functionally limiting habitat availability for grassland-obligate species like the Lesser Prairie-chicken (Fuhlendorf et al. 2017, Lautenbach et al. 2017, Oberle et al. 2018).

Acknowledgments

We thank Corrie Desilets who helped collect field data and all private landowners for allowing access. For financial and logistical support, we thank Kansas State University, Kansas Department of Wildlife, Parks, and Tourism, United States Department of Agriculture (USDA) Natural Resources Conservation Service, Pheasants Forever, and Lesser Prairie-Chicken Initiative. The research which is the subject of this manuscript has been financed, in part, with federal funds from the Fish and Wildlife Service, a division of the United States Department of Interior, and administered by the Kansas Department of Wildlife, Parks, and Tourism. The contents and opinions, however, do not necessarily reflect the views or policies of the United States Department of Interior or the Kansas Department of Wildlife, Parks and Tourism. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Literature Cited

Arkle, R.S., and D.S. Pilliod. 2010. Prescribed fires as ecological surrogates for wildfires: A stream and riparian perspective. Forest Ecology and Management 259:893–903.

Askins, R.A., F. Chávez-Ramírez, B.C. Dale, C.A. Haas, J.R. Herkert, F.L. Knopf, and P.D. Vickery. 2007. Conservation of grassland birds in North America: Understanding ecological processes in different regions. Ornithological Monographs 64:1–46.

Barbero, R.J., T. Abatzoglou, N.K. Larkin, C.A. Kolden, and B. Stocks. 2015. Climate change presents increased potential for very large fires in the contiguous United States. International Journal of Wildland Fire 24:892–899.

Bean, D., and T. Dudley. 2018. A synoptic review of *Tamarix* biocontrol in North America: Tracking success in the midst of controversy. BioControl 63:361–376.

Bidwell, T.G., J.R. Weir, J.D. Carlson, R.E. Masters, and D.M. Engle. 2018. Fire prescriptions for restoration and maintenance of native plant communities. Oklahoma Cooperative Extension Service Report F-2878. Stillwater, OK, USA. 8 pp.

Boggie, M.A., C.R. Strong, D. Lusk, S.A. Carleton, W.R. Gould, R.L. Howard, C. Nichols, M.J. Falkowski, and C.A. Hagen. 2017. Impacts of mesquite distribution on seasonal space use of Lesser Prairie-chickens. Rangeland Ecology and Management 70:68–77.

Bond, W.J., and J.J. Midgley. 2003. The evolutionary ecology of sprouting in woody plants. International Journal of Plant Sciences 164:S103–S114.

Bracmort, K. 2013. Wildfire fuels and fuel reduction. Congressional Research Service Report R40811. 15 pp. Washington, D.C., United States.

Briggs, J.M., G. Hoch, and L. Johnson. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. Ecosystems 5:578–586.

Briggs, J.M., A.K. Knapp, J.M. Blair, J.L. Heisler, G.A. Hoch, M.S. Lett, and J.K. Mccarron. 2005. An ecosystem in transition: Causes and consequences of the conversion of mesic grassland to shrubland. BioScience 55:243–254.

Brown, H. 2018. Fire control and the 2015 Canyon Creek Complex fire. Fire Management Today 76:36–40.

Cao, X., Y. Meng, and J. Chen. 2015. Mapping grassland wildfire risk of the world. Pp. 277–283, In P. Shi and R. Kasperson (Eds.). World Atlas of Natural Disaster Risk. Springer-Verlag, Berlin, Heidelberg, Germany. 368 pp.

Courtwright, J. 2011. Prairie Fire: A Great Plains History. University Press of Kansas, Lawrence, KS, USA. 288 pp.

Delwiche, J. 2009. Saltcedar: Is burning an option? Joint Fire Science Program Briefs Issue 50. Boise, ID, USA. 7 pp.

DeSantis, R.D., S.W. Hallgren, and D.W. Stahle. 2011. Drought and fire suppression lead to rapid forest composition change in a forest-prairie ecotone. Forest Ecology and Management 261:1833–1840.

Dey, D.C., and G. Hartman. 2004. Effects of different large-scale prescribed burning regimes of advanced production in Missouri Ozarks. Pp. 168–176, In M.A. Spetich (Ed.). Proceedings of the Upland Oak Ecology Symposium: History, current conditions, and sustainability. US Department of Agriculture, Forest Service, Southern Research Station General Technical Report SRS-73. Asheville, NC, USA. 311 pp.

Di Tomaso, J.M. 1998. Impact, biology, and ecology of Saltcedar (*Tamarix* spp.) in the southwestern United States. Weed Technology 12:326–336.

Dillon, G.K., M.H. Panunto, B. Davis, P. Morgan, D.S. Birch, and W.M. Jolly. 2020. Development of a severe fire potential map for the contiguous United States. US Department of Agriculture, Forest Service, Rocky Mountain Research Station General Technical Report RMRS-GTR-415. Fort Collins, CO, USA. 107 pp.

Dodson, E.K., and C.E. Fiedler. 2006. Impacts of restoration treatments on alien plant invasion in *Pinus ponderosa* forests, Montana, USA. Journal of Applied Ecology 43:887–897.

Donovan, V.M., C.L. Wonkka, and D. Twidwell. 2017. Surging wildfire activity in a grassland biome. Geophysical Research Letters 44:5986–5993.

Donovan V.M., D. Twidwell, D.R. Uden, T. Tadesse, B.D. Wardlow, C.H. Bielski, M.O. Jones, B.W. Allred, D.E. Naugle, and C.R. Allen. 2020. Resilience to large, "catastrophic" wildfire in North America's grassland biome. Earth's Future 8, e2020EF001487.

Duncan, K., and K. McDaniel. 2009. Chemical weed and brush control for New Mexico rangelands. New Mexico State University Cooperative Extension Service Circular 579. Las Cruces, NM, USA. 20 pp.

Eisenberg, C., C.L. Anderson, A. Collingwood, R. Sissons, C.J. Dunn, G.W. Meigs, D.E. Hibbs, S. Murphy, S.D. Kuiper, J. SpearChief-Morris, L. Little Bear, B. Johnston, and C.B. Edson. 2019. Out of the ashes: Ecological resilience to extreme wildfire, prescribed burns, and Indigenous burning in ecosystems. Frontiers in Ecology and Evolution 7:436.

Engle, D.M., B.R. Coppedge, and S.D. Fuhlendorf. 2008. From the dust bowl to the green glacier: Human activity and environmental change in Great Plains grasslands. Pp. 253–271, In O.W. Van Auken (Ed.). Western North American *Juniperus* Communities: A Dynamic Vegetation Type. Springer-Verlag, New York, NY, USA. 316 pp.

ESRI. 2018. ArcGIS Desktop: Release 10.6. Redlands, CA: Environmental Systems Research Institute.

Falkowski, M.J., J.S. Evens, D.E. Naugle, A.H. Khalyani, C.A. Hagen, A. Ponzanovic, and J.D. Maestas. 2017. Mapping tree canopy cover in support of proactive prairie grouse conservation in western North America. Rangeland Ecology and Management 70:15–24.

Fick, W.H., and W.A. Geyer. 2010. Cut-stump treatment of Saltcedar (*Tamarix ramosissima*) on the Cimarron National Grasslands. Transactions of the Kansas Academy of Science 113:223–226.

Frazier, I. 2018. The day the Great Plains burned. The New Yorker, 5 November 2018. Available online at https://www.newyorker.com/magazine/2018/11/05/the-day-the-great-plains-burned. Accessed 1 July 2021.

Fryer, J.L., and P.S. Luensmann. 2012. Fire regimes of the conterminous United States. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Fire Effects Information System (FEIS). Missoula, MT, USA. Available online at www.fs.fed.us.database/feis/fire_regime_table/fire_regime_table.html. Accessed 1 July 2021.

Fuhlendorf, S.D., T.J. Hovick, R.D. Elmore, A.M. Tanner, D.M. Engle, and C.A. Davis. 2017. A hierarchical perspective to woody plant encroachment for conservation of prairie-chickens. Rangeland Ecology and Management 70:9–14.

Glasgow, S., and T.G. Bidwell. 2009. Management after wildfire. Oklahoma Cooperative Extension Service Report NREM-2881. Stillwater, OK, USA. 4 pp.

Gleason, H.A. 1913. The relation of forest distribution and prairie fires in the middle west. Torrey Botanical Society 13:173–181.

Glinski, R.L. 1977. Regeneration and distribution of sycamore and cottonwood trees along Sonoita Creek, Santa Cruz County, Arizona. Pp. 116–123, In R.R. Johnson and D.A. Jones (Eds.). Importance, Preservation and Management of Riparian Habitat: A Symposium. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-43. Fort Collins, CO, USA. 217 pp.

Goldsmith, F.B., and N. Smart. 1982. Age, spacing and growth rate of *Tamarix* as an indication of lake boundary fluctuations at Sebkhet Kelbia, Tunisia. Journal of Arid Environments 5:43–51.

Hatten, J.R. 2016. A satellite model of Southwestern Willow Flycatcher (*Empidonax traillii extimus*) breeding habitat and a simulation of potential effects of tamarisk leaf beetles (*Diorhabda* spp.), southwestern United States. U.S. Geological Survey Open-File Report 2016-1120. Reston, VA, USA. 88 pp.

Haukos, D.A., and C.W. Boal (Eds.). 2016. Ecology and Conservation of Lesser Prairie-Chickens. CRC Press, Boca Raton, FL, USA. 294 pp.

Hohlt, J.C., B.J. Racher, J.B. Bryan, R.B. Mitchell, and C. Britton. 2002. Saltcedar response to prescribed burning in New Mexico, In G.R. Wilde and L.M. Smith (Eds.). Research Highlights 2002: Range, Wildlife, and Fisheries Management, Volume 33. Texas Tech University, College of Agricultural Sciences and Natural Resources, Lubbock, TX, USA. 25 pp.

Joern, A., and K. Keeler (Eds.). 1995. The Changing Prairie: North American Grasslands. Oxford University Press, New York, NY, USA. 244 pp.

Jones, S.R., and R.C. Cushman. 2004. A Field Guide to the North American Prairie. Houghton Mifflin Company, New York, NY, USA. 510 pp.

Keeley, J.E. 2006. Fire management impacts on invasive plants in the western United States. Conservation Biology 20:375–384.

Keeley, J.E. 2009. Fire intensity, fire severity and burn severity: A brief review and suggested usage. International Journal of Wildland Fire 18:116–126.

Keeley, J.E., and P.W. Rundel. 2005. Fire and the Miocene expansion of C4 grasslands. Ecology Letters 8:683–690.

Korhonen, L., K.T. Korhonen, M. Rautiainen, and P. Stenberg. 2006. Estimation of forest canopy cover: A comparison of field measurement techniques. Silva Fennica 40:577–588.

Lautenbach, J.D. 2017. The role of fire, microclimate, and vegetation in Lesser Prairie-chicken habitat selection. M.Sc. Thesis, Kansas State University, Manhattan, KS, USA. 133 pp.

Lautenbach, J.M., R.T. Plumb, S.G. Robinson, C.A. Hagen, D.A. Haukos, and J.C. Pitman. 2017. Lesser Prairie-chicken avoidance of trees in a grassland landscape. Rangeland Ecology and Management 70:78–86.

Lindley, T.T., D.A. Speheger, M.A. Day, G.P. Murdoch, B.R. Smith, N.J. Nauslar, and D.C. Daily. 2019. Megafires on the southern Great Plains. Journal of Operational Meteorology 7:164–179.

McDaniel, K.C., and J.P. Taylor. 2003. Saltcedar recovery after herbicide-burn and mechanical clearing practices. Journal of Range Management 56:439–445.

Miller, J.D., E.E. Knapp, C.H. Key, C.N. Skinner, C.J. Isbell, R.M. Creasy, and J.W. Sherlock. 2009. Calibration and validation of the relative differenced Normalized Burn Ratio (R*d*NBR) to three measures of fire severity in the Sierra Nevada and Klamath Mountains, California, USA. Remote Sensing of Environment 113:645–656.

Monitoring Trends in Burn Severity. 2020. US Department of Agriculture, Forest Service, and US Geological Survey. MTBS data access: National geospatial data. Available online at http://mtbs.gov/. Accessed 3 May 2020.

National Oceanic and Atmospheric Administration (NOAA). 2020a. National Climatic Data Center, Climate at a Glance. Available online at https://www.ncdc.noaa.gov/cag/county/time-series/KS-025/pcp/ann/. Accessed 3 May 2020.

National Oceanic and Atmospheric Administration (NOAA). 2020b. National Climatic Data Center. Local Climatological Data. Available online at https://www.ncdc.noaa.gov/cdo-web/datasets/LCD/stations/WBAN:13985/detail. Accessed 3 May 2020.

Nippert, J.B., L. Telleria, P. Blackmore, J.H. Taylor, and R.C. O'Connor. 2021. Is a prescribed fire sufficient to slow the spread of woody plants in an infrequently burned grassland? A case study in tallgrass prairie. Rangeland Ecology and Management 78:79–89.

Noel, J.M., and N.L. Fowler. 2007. Effects of fire and neighboring trees on Ashe juniper. Rangeland Ecology and Management 60:596–603.

Oberle, B., K. Ogle, A.E. Zanne, and C.W. Woodall. 2018. When a tree falls: Controls on wood decay predict standing dead tree fall and new risks in changing forests. PLoS One 13:e0196712.

Owensby, C.E., K.R. Blan, B.J. Eaton, and O.G. Russ. 1973. Evaluation of Eastern Redcedar infestations in the northern Kansas Flint Hills. Journal of Range Management 26:256–260.

Paull, D.A., J.W. Whitson, A.L. Marcotte, G.C. Liknes, D.M. Meneguzzo, and T.A. Kellerman. 2017. High-resolution land cover of Kansas (2015). US Department of Agriculture, Forest Service, Research Data Archive, updated 27 November 2017. Fort Collins, CO, USA. Available online at https://www.fs.usda.gov/rds/archive/catalog/RDS-2017-0025. Accessed 3 May 2020.

Plumb, R.T., J.M. Lautenbach, S.G. Robinson, D.A. Haukos, V.L. Winder, C.A. Hagen, D.S. Sullins, J.C. Pitman, and D.K. Dahlgren. 2019. Lesser Prairie-chicken space use in relation to anthropogenic structures. Journal of Wildlife Management 83:216–230.

Polley, H.W., D.D. Briske, J.A. Morgan, K. Wolter, D.W. Bailey, and J.R. Brown. 2013. Climate change and North American rangelands: Trends, projections, and implications. Rangeland Ecology and Management 66:493–511.

Pyne, S.J. 2017. The Great Plains: A Fire Survey. University of Arizona Press, Tucson, AZ, USA. 216 pp.

R Development Core Team. 2019. Program R version 3.6.1: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. Available online at https://www.r-project.org/. Accessed 3 May 2020.

Racher, B.J., C.M. Britton, R.B. Mitchell, and D.B. Wester. 2003. Fire application to Saltcedar-dominated riparian areas: Prescription development, hazardous fuels reduction, and ecosystem response. Annual progress report to Joint Fire Science Program, Project 00-2-29. Phoenix, AZ, USA. 1 pp.

Ratajczak, Z., J.B. Nippert, J.M. Briggs, and S.L. Collins. 2012. Woody encroachment decreases diversity across North American grasslands and savannas. Journal of Ecology 93:697–703.

Ratajczak, Z., J.B. Nippert, J.M. Briggs, and J.M. Blair. 2014. Fire dynamics distinguish grasslands, shrublands and woodlands as alternative attractors in the central Great Plains of North America. Journal of Ecology 102:1374–1385.

Rideout-Hanzak, S., D.B. Wester, C.M. Britton, and H.A. Whitlaw. 2011. Biomass not linked to perennial grass mortality following severe wildfire in the Southern High Plains. Rangeland Ecology and Management 64:47–55.

Rosenberg, K.V., A.M. Dokter, P.J. Blancher, J.R. Sauer, A.C. Smith, P.A. Smith, J.C. Stanton, A. Panjabi, L. Helft, M. Parr, and P.P. Marra. 2019. Decline of the North American avifauna. Science 366:120–124.

Samson, F.B., F.L. Knopf, and W.R. Ostlie. 2004. Great Plains ecosystems: Past, present, and future. Wildlife Society Bulletin 32:6–15.

Stevens, L.E. 2002. Exotic tamarisk on the Colorado Plateau. Available online at https://web.archive.org/web/20060206062038/http://www.cpluhna.nau.edu/Biota/tamarisk.htm. Accessed 1 July 2021.