ARTICLE

Prescribed fire effects on oak woodland advance regeneration at the prairie–forest border in Kansas, USA

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Abstract: Understanding the effects of fire on advance regeneration of oak (*Quercus* L.) species and their competitors is an important step in determining the role of prescribed fire in regenerating and restoring upland oak ecosystems. Our study aimed to understand how dormant-season prescribed fire affects advance regeneration of chinkapin oak (*Quercus muehlenbergii* Engelm.), black oak (*Quercus velutina* Lam.), and their major competitors at sites targeted for woodland restoration and management. We analyzed relationships between stem size and survival probability; determined the effect of fire temperature on survival probability; and compared how mortality, sprouting, and survival differed among species. For chinkapin oak, black oak, and bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch), mortality was low and rate of sprouting was high after shoot dieback. Initial basal diameter was significantly related to survival probability after one fire for all species except chinkapin oak and black oak. Height was a significant predictor of survival probability for all species except chinkapin oak. Although sugar maple (*Acer saccharum* Marsh.) also responded to fire by sprouting, it did so at a much lower rate than oaks and hickory (20% versus 43%–68%). These data reveal that heavily invaded, fire-suppressed woodlands on the prairie–forest border region may not experience major structural and compositional shifts without repeated burning or mechanical treatments.

Key words: chinkapin oak, prescribed fire, mortality, logistic models.

Résumé : La compréhension des effets du feu sur la régénération préétablie des espèces de chêne (*Quercus* L.) et de leurs concurrents est une étape importante pour déterminer le rôle du brûlage dirigé dans la régénération et la restauration des écosystèmes bien drainés de chêne. Notre étude visait à comprendre comment le brûlage dirigé appliqué pendant la saison de dormance influence la régénération préétablie des chênes jaune (*Quercus muehlenbergii* Engelm.) et noir (*Quercus velutina* Lam.) et celle de leurs principaux concurrents sur des stations destinées à la restauration et l'aménagement de zones boisées. Nous avons analysé les relations entre la taille des tiges et la probabilité de survie, déterminé l'effet de la température du feu sur la probabilité de survie, et comparé les différences de mortalité, de repousse et de survie entre les espèces. Pour le chêne jaune, le chêne noir et le caryer cordiforme (*Carya cordiformis* (Wangenh.) K. Koch), la mortalité était faible et le taux de repousse était élevé après la mort des tiges. Le diamètre initial à la souche était significativement lié à la probabilité de survie après un feu pour toutes les espèces sauf les chênes jaune et noir. La hauteur était une variable prédictive importante de la probabilité de survie de toutes les espèces, à l'exception du chêne jaune. Bien que l'érable à sucre (*Acer saccharum* Marsh.) ait aussi réagi au feu en produisant des repousses, le taux de repousse était beaucoup plus faible que celui des chênes et du caryer (20 % contre 43 % à 68 %). Ces données révèlent que les zones boisées fortement envahies et protégées du feu, et établies dans l'écotone entre la prairie et la forêt peuvent se développer sans profonds changements structurel et compositionnel si des brûlages dirigés ou des traitements mécaniques ne sont pas appliqués de façon répétée. [Traduit par la Rédaction]

Mots-clés : chêne jaune, brûlage dirigé, mortalité, modèles logistiques.

1. Introduction

Fire has been an important driver in shaping plant communities in the Central United States (US) for millennia (Abrams 1992; Anderson et al. 1999; Nelson 2010). As a result, the transitional region between the Eastern US deciduous forests and the Great Plains contains diverse assemblages of forest, woodland, prairie, and savanna communities — a mosaic created in part by the spatial and temporal variation in fire regimes (Braun 2001; Nuzzo 1986; Anderson et al. 1999; Nelson 2010). Although climate, topography, soils, and grazing undoubtedly played important roles in this landscape, the influence of anthropogenic fire, specifically frequent fires of low to moderate intensity, has largely been credited for the development and perpetuation of open plant communities such as savannas and woodlands in the Central US (Abrams

1992; Stambaugh et al. 2006, 2011, 2014; Guyette et al. 2006; McEwan et al. 2007; Nelson 2010; Brose et al. 2013). The historical variation in fire frequency and severity was heavily influenced by human population density, culture, and land use; furthermore, the development and succession of plant communities reflects the temporal and spatial shifts of these fire regime characteristics (Abrams 1992; Delcourt and Delcourt 1997; Anderson et al. 1999; Guyette et al. 2006; Stambaugh et al. 2014).

Across the Central US, oaks (*Quercus* L. spp.) were historically a principal component of savannas and woodlands (Nuzzo 1986; Anderson et al. 1999; Nelson 2010; Hanberry and Nowacki 2016). The link between landscape-level fire and historical oak dominance is a widely discussed hypothesis with a growing body of support (Abrams 1992; Brose et al. 2001; Nowacki and Abrams 2008; Arthur et al. 2012). Oaks have physiological adaptations such

as thick bark, large ratios of roots to shoots, ability to sprout after shoot dieback, and wound compartmentalization — traits that can support a resilience to fire (Smith and Sutherland 1999; Johnson et al. 2009). Fire as a natural disturbance has perpetuated oak communities by providing necessary canopy openings, as oaks commonly have low to moderate shade tolerance, while also promoting oak domination by excluding fire-sensitive oak competitors (Abrams 1992; Johnson et al. 2009).

The Central and Eastern US saw major shifts in plant community structure and composition during the 19th and 20th centuries, with many historically open communities transitioning to closed-canopy forests (Nowacki and Abrams 2008; Hanberry et al. 2014a, 2014b). Several potential drivers of these shifts have been suggested, including climate change, shifts in levels of carbon dioxide and nitrogen, and loss of foundation or keystone species such as bison (*Bison bison* (Linnaeus, 1758)) and American chestnut (*Castanea dentata* (Marsh.) Borkh.) (McEwan et al. 2011). Additionally, fire suppression and exclusion during the 20th century has been linked to fire-sensitive, shade-tolerant, and mesophytic species encroaching into areas where fire previously constrained their existence. Throughout the eastern deciduous forests, species such as red maple (*Acer rubrum* L.) and sugar maple (*Acer saccharum* Marsh.) have increased in abundance, causing major structural, compositional, and functional changes to these communities (Fei and Steiner 2007; Nowacki and Abrams 2008; Fei et al. 2011; Knott et al. 2019). These species are hypothesized to contribute to the process of "mesophication", whereby they create shady, damp conditions through their canopy and litter traits that likely lead to reduced fuel flammability (Nowacki and Abrams 2008; Kreye et al. 2013; 2018; Varner et al. 2015). This may create a positive feedback loop that promotes the proliferation of fire-sensitive species at the expense of oaks and other fire-tolerant species (Nowacki and Abrams 2008).

The decline in oak savannas and woodlands is significant because of the high ecological value of these communities. Oak savannas have higher plant diversity at various scales than prairies or forests, as the heterogeneous canopy cover may promote species commonly seen in either of these communities (Peterson and Reich 2008). Savannas and woodlands are often associated with high wildlife diversity and habitat for rare species (Davis et al. 2000; Starbuck et al. 2014). For example, savanna and woodland restoration studies have documented increased abundance of bird species of conservation concern (Thompson et al. 2012; Reidy et al. 2014). The degradation of these communities has contributed to the loss of landscape diversity (Shifley and Thompson 2011; Hanberry 2013), which may be less resilient in the face of future threats such as climate change (Brandt et al. 2014; Janowiak et al. 2014).

There has been an abundance of research examining the effects of prescribed fire on advance regeneration (individuals or populations of juvenile trees already reproduced and already existing within the community (Johnson et al. 2009)) of oaks and competitor species in recent decades (Arthur et al. 1998; Hutchinson et al. 2005; Alexander et al. 2008; Vander Yacht et al. 2017); however, most of these studies have been located in the Eastern Deciduous Forest or Central Hardwood Region and have been focused in forest communities. In contrast, the Forest–Prairie Transition Region is a relatively understudied region with unique features relative to eastern oak forests. For example, the ranges of red maple and tulip poplar (*Liriodendron tulipifera* L.), common oak competitors of the Eastern US, do not extend into the Forest–Prairie Transition Region. The goals of prescribed fire can also vary depending on the community of interest. For example, in eastern forests with higher productivity, prescribed fire can be used to facilitate oak regeneration; however, in the context of woodland and savanna management, regeneration of oak species must be balanced with maintaining the desired open midstory and abundant herbaceous cover.

Understanding the effects of fire on advance regeneration of oak species and their competitors is an important step in determining the role of prescribed fire in regenerating and restoring upland oak ecosystems. Our goal was to understand how a dormant-season prescribed fire affects advance regeneration of two oak species, chinkapin oak (*Quercus muehlenbergii* Engelm.) and black oak (*Quercus velutina* Lam.), as well as bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch), sugar maple, and eastern redcedar (*Juniperus virginiana* L.). The objectives of this study were to (*i*) determine percent mortality and percent shoot dieback with sprouting for five different tree species; (*ii*) assess relationships between initial stem size (basal diameter and height) and survival probability; (*iii*) determine the effect of fire temperature on survival probability; and (*iv*) compare how mortality, sprouting, and survival probability differ among the five species.

2. Methods

2.1. Study areas and design

This study was conducted at Marais des Cygnes (MDC) Wildlife Area (38°15′25.7″N, 94°40′59.9″W) and La Cygne Wildlife Area (LCWA; 38°24′33.6744″N, 94°39′42.4908″W) in Linn and Miami counties of eastern Kansas, USA. These wildlife areas are managed by the Kansas Department of Wildlife, Parks and Tourism, an agency responsible for maintaining habitat for multiple game species. MDC, located in the floodplain of the Marais des Cygnes River, is 3097 ha of mainly wetlands and bottomland hardwood forest, but also includes a smaller component of upland forest where the MDC replication of this study is located. Located 19 km north of MDC, LCWA is 810 ha of mostly wooded uplands adjacent to La Cygne Lake, a 1050 ha cooling reservoir for a coal-fired generating plant owned by Kansas City Power and Light. Two replications of this study are located within the upland forest of LCWA.

Located in the Forest–Prairie Transition ecoregion, the management areas occur within the Wooded Osage Plains physiographic region of Kansas (McNab and Avers 1994; Chapman et al. 2001). The Wooded Osage Plains is a broad transition region shifting from prairie to woodland, characterized by a series of roughly parallel escarpments oriented southwest to northeast, separated by gently rolling to level plains (McNab and Avers 1994; Chapman et al. 2001). Historically, tallgrass prairie was the dominant vegetation of the ecoregion (70%), with corridors of oak–hickory forest along drainages (McNab and Avers 1994). Today, agriculture, particularly corn and soybean, is the predominant land use in the ecoregion, although pastureland and rangeland comprise a smaller, but sizable, component of the area (Penner 1981). Most land is privately owned; however, numerous federal- and state-owned areas are found throughout the region. Remnant natural communities cover <10% of the total area of the region, are highly fragmented, and mainly occur on the sites that are least agriculturally productive (Hamilton et al. 2000).

The study areas comprise mainly ridge, shoulder, and backslope topographic positions, with elevations ranging from 260 to 310 m and slopes of 0%–45%. Soils are Mollisols, mainly of the Clareson series, with limestone rock outcrops and are moderately deep and well drained (Soil Survey Staff 2017). Tree species composition includes chinkapin oak, post oak (*Quercus stellata* Wangenh.), black oak, bur oak (*Quercus macrocarpa* Michx.), sugar maple, and hickories (*Carya* Nutt. spp.) in the overstory (diameter at breast height (DBH; breast height = 1.37 m) ≥ 11.4 cm), with sugar maple, eastern redbud (*Cercis canadensis* L.), elms (*Ulmus* L. spp.), ironwood (*Ostrya virginiana* (Mill.) K. Koch), and roughleaf dogwood (*Cornus drummondii* C.A. Mey.) in the midstory (3.8 cm ≤ DBH < 11.4 cm) and understory (DBH < 3.8 cm). Common shrub and vine species include coralberry (*Symphoricarpos orbiculatus* Moench), fragrant sumac (*Rhus aromatica* Aiton), blackberries (*Rubus* L. spp.), Virginia creeper (*Parthenocissus quinquefolia* (L.) Planch.), and grapes (*Vitis* L. spp.). Prior to study initiation, stands averaged 80% stocking

(Gingrich 1967), mean basal area was between 19.8 and 24.0 m²·ha⁻¹, and closed-canopy conditions existed. Many of the oaks at the study areas have tree architectures expressing past open-canopy, woodland conditions, namely spreading crowns, primary branches located low on the bole, and trees of shorter stature (Nelson 2010).

The study is a complete randomized block design with three blocks (replications): one block was established at MDC and two blocks were established at LCWA (the two blocks at LWCA are hereafter referred to as LC1 and LC2). Six treatment types were randomly assigned to treatment units of approximately 2.4 ha within each of the three blocks. Treatments included a single dormant-season prescribed fire (burn only), thinning to a basal area of 13.8 m²·ha⁻¹, thinning to a basal area of 6.9 m²·ha⁻¹, a combination of fire and thinning to a basal area of 13.8 m²·ha⁻¹, a combination of fire and thinning to a basal area of 6.9 m²·ha⁻¹, and an untreated control. Within each treatment unit, six permanent, 0.08 ha, fixed-radius, circular vegetation plots were randomly located, creating 36 plots per replication and a total of 108 plots. For the purpose of this study, only the plots (N = 32 plots) within the burn-only treatment units and the control treatment units were examined.

2.2. Prescribed fire treatment

A dormant-season prescribed fire was applied at the MDC study area on 5 March 2016 and at LC1 and LC2 on 17 March 2016. Fuels at all burns were mainly deciduous leaf litter, although cool- and warm-season grasses also occurred adjacent to study areas. All fires occurred before leaf emergence of woody species. On burn days, daytime air temperatures ranged from 11 to 18 °C, relative humidity ranged from 25% to 45%, and wind speed ranged from 4 to 16 km·h⁻¹. Flame lengths varied, but observed values averaged 0.3 to 0.9 m at all three areas. Rates of spread between 39 and 138 cm·min⁻¹ were observed.

Fire temperature was measured using Tempilaq temperature-sensitive paints (LA-CO Industries, Elk Grove Village, Ill., USA) applied to aluminum tags. The methods for the use of paint tags as pyrometers were adapted from Iverson et al. (2004). Ten different paints were applied to each tag, and the temperatures at which they liquefied were rated as 79, 121, 149, 177, 204, 232, 260, 288, 343, and 427 °C. Paint tags were covered with a blank tag to avoid the accumulation of char and soot on the paint's surface. The paint tags were suspended 15 cm above the litter layer using a wire pin flag and were deployed in the field just prior to prescribed fire (day of burn or day before). Tags were deployed at five positions within plots in the burn treatment unit: at plot center and at 8 m to the north, south, east, and west of plot center (five tags per plot in 18 plots = 90 tags deployed). After each fire, pyrometers were collected within 24 h, and each tag was evaluated by two independent observers. The highest temperature paint that melted was recorded as the fire temperature for that location. This temperature represented the minimum of a range of possible temperatures between the temperature paint that melted and the next highest temperature paint. Mean fire temperature per plot was calculated from the five pyrometers in each plot.

2.3. Data collection

Within the established burn-only and control treatment units, individuals of five tree species were permanently tagged in the summer of 2015, before the prescribed fire treatment. Species were selected based on a range of recognized fire-tolerance designations (Nowacki and Abrams 2014), with chinkapin oak (Tirmenstein 1991a) and black oak (Carey 1992) defined as fire tolerant and bitternut hickory (Coladonato 1992), sugar maple (Tirmenstein 1991b), and eastern redcedar (Anderson 2003) defined as fire sensitive. Additionally, these species were selected based on their occurrence and abundance at all three blocks (MDC, LC1, and LC2). Tagging occurred on seedlings and saplings (DBH < 11.4 cm), and best efforts were made to tag individuals

Table 1. Mean (and standard error (SE)), minimum, and maximum fire temperatures recorded at each site.

Site	Mean fire temperature (°C)	SE (°C)	Minimum fire temperature (°C)	Maximum fire temperature (°C)
MDC	95.8	9.7	25	204
LC1	119.4	12.5	25	260
LC2	85.3	11.6	25	232

Note: MDC, Marais des Cygnes; LC, La Cygne.

evenly across this range of sizes. A total of 725 individuals were tagged (approximately equal proportions for the five species) across the burn and control treatment units.

At each individual tree, a wire pigtail stake was placed in the ground 5–10 cm to the north of the stem, and a stainless-steel tag with a unique number was attached. Most tagged trees were within the boundaries of the 0.08 ha vegetation plots, but some were located up to 50 m outside of plots to obtain the desired number of individuals per species. We selected only seedlings and saplings that existed in a continuous fuel bed, for example those in herbaceous or tree leaf litter, to ensure that tagged stems were not in locations that could not carry a surface fire (e.g., on rocky outcrops). Mean fire temperatures ranged from 85.3 to 119.4 °C across the three study areas (Table 1). The minimum temperature measured was 25 °C at all areas. Maximum temperatures recorded at the study areas ranged from 204 to 260 °C. The initial height, stem basal diameter 2.5 cm above the ground, and DBH (if present) were recorded for all tagged individuals. Height was measured to the nearest centimetre for individuals ≤ 2 m tall and estimated to the nearest metre for individuals > 2 m tall.

In the summer of 2016, tagged individuals were located and examined to determine survival following prescribed fire. A tree was considered to have survived if there was no shoot dieback or if there was shoot dieback and sprouting. An individual was dead if the shoot was killed and no sprouting was evident, indicating complete death of all portions of the tree. The percent mortality and percent shoot dieback for each species were calculated. Shoot dieback was defined as the death of only the aboveground portion of the tree, with the rootstock still alive. This was determined by the presence of sprouting after the aboveground portion of an individual was killed. Total damage was calculated as the sum of mortality and shoot dieback (Dey and Hartman 2005).

2.4. Data analysis

For each of the five tree species, logistic regression (PROC GLIMMIX, SAS version 9.4, SAS Institute, Cary, N.C., USA) was used to model survival probability of advance regeneration in the burn treatment units from 2015 (preburn) to 2016 (postburn). Independent variables were fire temperature, initial height, and initial basal diameter. Fire temperature was calculated as the mean temperature of the five temperature paint tags for each plot. The binary dependent variable in this analysis was the fate of each tagged seedling or sapling (i.e., alive or dead). As previously mentioned, an individual survived if there was no shoot dieback or if there was shoot dieback and sprouting. To account for the randomized block experimental design and the nesting of individual trees within plots, as well as the nesting of plots within the three study areas, the generalized linear mixed models developed here contained random effects in addition to the fixed effects (basal diameter, height, and fire temperature).

The eight a priori models for each species included a null model (intercept only), single independent-variable models (basal diameter (BD), height (HT), and fire temperature (Temp)), two-variable models (BD + Temp and HT + Temp), and the two-variable models including a two-way interaction (BD + Temp + BD × Temp and HT + Temp + HT × Temp) (Table 2). Because basal diameter and

Table 2. Ranking of survival probability models for advance regeneration following prescribed burn treatment.

Model	K	AIC_c	ΔAIC_c	w_i	c
Black oak					
BD + Temp + BD × Temp	4	17.40	5.02	0.0342	0.926
HT + Temp + HT × Temp	4	14.53	2.15	0.1435	0.993
BD + Temp	3	16.46	4.08	0.0547	0.912
HT + Temp	3	12.38	0.00	0.4206	0.993
BD	2	15.23	2.85	0.1012	0.919
HT	2	13.50	1.12	0.2402	0.985
Temp	2	22.53	10.15	0.0026	0.765
Null	1	22.27	9.89	0.0030	
Chinkapin oak					
BD + Temp + BD × Temp	4	27.81	5.78	0.0228	0.694
HT + Temp + HT × Temp	4	28.11	6.08	0.0196	0.649
BD + Temp	3	25.50	3.47	0.0722	0.694
HT + Temp	3	25.81	3.78	0.0619	0.649
BD	2	23.49	1.46	0.1974	0.649
HT	2	23.79	1.76	0.1699	0.604
Temp	2	23.37	4.34	0.0468	0.549
Null	1	22.03	0.00	0.4095	
Bitternut hickory					
BD + Temp + BD × Temp	4	23.17	4.99	0.0264	0.933
HT + Temp + HT × Temp	4	22.22	4.04	0.0425	0.917
BD + Temp	3	22.62	4.44	0.0348	0.925
HT + Temp	3	19.96	1.78	0.1316	0.942
BD	2	18.43	0.25	0.2827	0.917
HT	2	18.18	0.00	0.3203	0.913
Temp	2	22.39	4.21	0.0390	0.688
Null	1	20.10	1.92	0.1227	
Sugar maple					
BD + Temp + BD × Temp	4	33.34	13.77	0.0007	0.973
HT + Temp + HT × Temp	4	27.76	8.19	0.0119	0.986
BD + Temp	3	19.57	0.00	0.7154	0.974
HT + Temp	3	25.59	6.02	0.0353	0.986
BD	2	22.93	3.36	0.1333	0.974
HT	2	23.44	3.87	0.1033	0.987
Temp	2	77.84	58.27	0.0000	0.534
Null	1	75.93	56.36	0.0000	
Eastern redcedar					
BD + Temp + BD × Temp	4	66.07	5.54	0.0248	0.916
HT + Temp + HT × Temp	4	61.85	1.32	0.2041	0.934
BD + Temp	3	67.28	6.75	0.0135	0.914
HT + Temp	3	60.53	0.00	0.3950	0.932
BD	2	71.51	10.98	0.0016	0.891
HT	2	60.71	0.18	0.3610	0.905
Temp	2	101.69	41.16	0.0000	0.685
Null	1	115.15	54.62	0.0000	

Note: Independent variables in the models included basal diameter (BD), height (HT), and fire temperature (Temp). K is the number of parameters in each model and includes the intercept and each independent variable. c is the area under the receiver operating characteristic (ROC) curve. AIC_c, Akaike's information criterion corrected for small sample size; w_i, Akaike weight; ×, interaction.

height are correlated variables, they were never in the same model to avoid the issue of multicollinearity.

An information-theoretic approach was used to model survival probability for advance regeneration (Burnham and Anderson 2002). Models were ranked using Akaike's information criterion (AIC_c); ΔAIC_c and Akaike weight (w_i) were calculated from AIC_c values and were used to determine the best models. AIC_c was used rather than AIC because of a smaller sample size. Models containing lower ΔAIC_c and greater w_i and simpler models with $\Delta AIC_c < 2$ had the most support for being the best model. All models were evaluated using the area under receiver operating characteristic (ROC) curve (c statistic).

3. Results

3.1. Mortality and sprouting of advance regeneration

Mean fire temperatures ranged from 85.3 to 119.4 °C across the three study areas (Table 1). The minimum temperature measured was 25 °C at all areas. Maximum temperatures recorded at the study areas ranged from 204 to 260 °C. Rates of mortality and shoot dieback with sprouts varied by species. In the first growing season following the 2016 dormant-season prescribed burns, the total damage to advance regeneration ranged from 38.7% to 72% for all five species (Table 3). Chinkapin oak had the greatest total damage (72% of tagged stems damaged), whereas sugar maple had the lowest total damage (38.7%). Most of the damage to black oak, chinkapin oak, and bitternut hickory was attributed to shoot dieback with sprouting; mortality was low (<4%) for all three species. Sugar maple experienced nearly equal proportions of mortality and shoot dieback, whereas eastern redcedar experienced 44% mortality and no shoot dieback.

The size of advance regeneration that experienced mortality and shoot dieback between 2015 and 2016 varied by species (Table 4). The maximum basal diameter and height of individuals that were dead following the prescribed burn were lowest in chinkapin oak, black oak, and bitternut hickory and highest in sugar maple and eastern redcedar. Similarly, the minimum basal diameter and height of individuals experiencing shoot dieback with sprouts were lowest for chinkapin oak, black oak, and bitternut hickory and greatest for sugar maple.

Similar low mortality rates were found in the control treatment for chinkapin oak, black oak, and bitternut hickory, which ranged from 1.6% to 3.5% (Table 5). Conversely, sugar maple and eastern redcedar had 0% mortality from 2015 to 2016 in the control treatment, which was markedly different from the mortality for those species in the burn treatments.

3.2. Survival probability

The best model based on AIC_c was the single-variable height model for both eastern redcedar and black oak (Table 6). For chinkapin oak and bitternut hickory, the null model ranked as the best model. The basal diameter and fire temperature model with no interaction ranked best for sugar maple. The c statistic ranged from 0.905 to 0.985 in the best models.

Basal diameter was a significant fixed effect in the single-variable models for bitternut hickory, eastern redcedar, and sugar maple. For these three species, the probability of survival increased with increasing basal diameter (Fig. 1). Survival probability of bitternut hickory increased from 79.1% to 99.0% as basal diameter increased from 0.2 to 2.2 cm, survival probability of sugar maple increased from 9.4% and 99.0% as basal diameter increased from 0.2 to 3.0 cm, and survival probability of eastern redcedar increased from 17.2% to 99.0% as basal diameter increased from 0.2 to 8.7 cm. At the smallest diameters, bitternut hickory was most likely to survive, followed by eastern redcedar and sugar maple; however, eastern redcedar required the greatest diameter to obtain a 99.0% probability of survival.

Height was a significant fixed effect in the single-variable models for all species except chinkapin oak, with the probability of survival increasing with increasing height (Fig. 2). At a height of 11 cm, the models predicted 100% survival probability for black oak. Survival probability of bitternut hickory increased from 68.5% to 99.0% as height increased from 11 to 61 cm, survival probability of sugar maple increased from 8.5% to 99.0% as height increased from 11 cm to 2.4 m, and survival probability of eastern redcedar increased from 7.9% to 99.0% as height increased from 11 cm to 3.5 m.

4. Discussion

In this study, we found that the effect of a single dormant-season fire on advance regeneration mortality and sprouting var-

Table 3. Preburn (2015) mean basal diameter (BD) and height (HT) for all tagged advance regeneration in the burn treatment units, and percent damage following the 2016 prescribed burn.

Species	N	BD (cm)	HT (m)	Mortality (%)	Shoot dieback with sprouts (%)	Total damage (%)
Black oak	70	6.0 (0.2–23.0)	3.5 (0.1–10)	2.9	42.9	45.7
Bitternut hickory	62	4.2 (0.2–23.0)	2.7 (0.1–11)	3.2	66.1	69.4
Chinkapin oak	74	4.0 (0.1–34.0)	1.5 (0.07–10)	2.7	68	72
Sugar maple	75	7.1 (0.1–26.8)	3.8 (0.07–11)	18.7	20	38.7
Eastern redcedar	81	4.7 (0.1–21.6)	2.1 (0.04–8)	44.4	0	44.4

Note: Ranges for basal diameter and height are presented in parentheses. Mortality is defined as the complete death of the individual, and shoot dieback is defined as the death of only the aboveground portion of the tree. Total damage is the sum of mortality and shoot dieback (Dey and Hartman 2005).

Table 4. The mean, minimum, and maximum initial basal diameter (BD) and height (HT) of advance regeneration that was alive or dead (no sprouts) or experienced shoot dieback with sprouts following the 2016 prescribed burn.

Species	N	BD (cm)			HT (cm)		
		Mean	Minimum	Maximum	Mean	Minimum	Maximum
Alive							
Black oak	36	10.3	0.7	23.0	577	51	1000
Bitternut hickory	19	3.6	0.7	23.0	523	66	1100
Chinkapin oak	21	0.2	0.2	34.1	418	11	1000
Sugar maple	46	10.1	3.5	26.8	550	200	1100
Eastern redcedar	45	0.3	0.3	21.6	324	20	800
Shoot dieback with sprouts							
Black oak	32	1.0	0.3	3.3	91	11	300
Bitternut hickory	41	2.3	0.3	22.2	159	16	900
Chinkapin oak	51	0.7	0.1	3.0	46	7	200
Sugar maple	15	1.9	0.9	4.1	191	41	500
Eastern redcedar	0	—	—	—	—	—	—
Dead							
Black oak	2	0.4	0.2	0.6	14	12	16
Bitternut hickory	2	0.5	0.2	0.7	26	11	40
Chinkapin oak	2	0.5	0.4	0.6	39	21	56
Sugar maple	14	0.6	0.1	2.3	34	7	172
Eastern redcedar	36	1.2	0.1	3.9	66	4	200

Table 5. Preburn (2015) mean basal diameter (BD) and height (HT) for all tagged advance regeneration in the control treatment units, and postburn (2016) percent mortality.

Species	N	BD (cm)	HT (m)	Mortality (%)
Black oak	61	7.2	4.2	1.6
Bitternut hickory	86	5.4	3.4	3.5
Chinkapin oak	86	6.3	3.4	3.5
Sugar maple	66	6.9	3.6	0.0
Eastern redcedar	38	2.5	1.2	0.0

ied by species. As we expected, mortality was low for chinkapin oak, black oak, and bitternut hickory during the first growing season after a dormant-season burn. In fact, almost identical numbers of individuals for these three species did not survive in the control treatment between 2015 and 2016. Although mortality was low, these three species also showed high rates of sprouting after shoot dieback. This finding was expected, as the ability of these species to sprout following shoot dieback has been well documented, especially for oaks (Dey and Hartman 2005; Blankenship and Arthur 2006; Johnson et al. 2009). Mineral soil is a poor conductor of heat and acts as an insulating layer from the heat of a fire (Iverson and Hutchinson 2002). Dormant buds of oak and hickory root collars are generally located at or beneath the surface of the soil, allowing sprouting even when the entire aboveground portion of an individual is killed by fire (Smith 1990; Johnson et al. 2009). Bitternut hickory is the most prolific sprouter of all northern hickories, with sprouts arising from stumps, root collar, and roots (Smith 1990). Additionally, oak species preferentially allocate carbohydrates into their root systems, creating a reserve that supports the growth of sprouts more readily than their hardwood competitors (Huddle and Pallardy 1999; Brose and Van Lear 2004; Johnson et al. 2009). Dey and Hartman (2005) found similar sprouting rates after one dormant-season fire for chinkapin oak and black oak advance regeneration, with 76% and 70% experiencing shoot dieback with sprouting, respectively.

Although sugar maple also responded to fire by sprouting, it did so at a lower rate than oaks and hickory (20% versus 43%–68%). Maples, like most hardwood species that occur in the Central US, can sprout after shoot injury (Dey and Hartman 2005; Blankenship and Arthur 2006); however, the buds of sugar maple root collars generally occur at or near the surface of the soil, increasing this species' vulnerability to fire damage and reducing the likelihood of sprouting (Godman et al. 1990; Brose and Van Lear 2004). Furthermore, we found that the proportion of sugar maple experiencing mortality was approximately equal to the proportion that sprouted following shoot dieback. In the control treatment, no sugar maple or eastern redcedar individuals experienced mortality, suggesting that the mortality rate in the burn treatment was likely related to fire. As expected, eastern redcedar showed no sprouting following the prescribed burn, as this species does not reproduce naturally by sprouting or suckering (Lawson 1990).
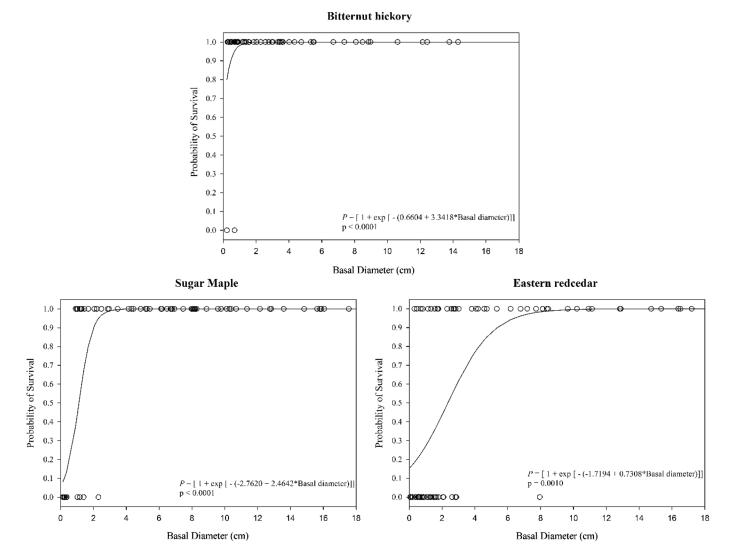
We found that size (basal diameter and (or) height) was an important predictor of survival probability for black oak, bitternut hickory, sugar maple, and eastern redcedar. Other studies have

Table 6. Highest ranked survival probability models for each species of advance regeneration.

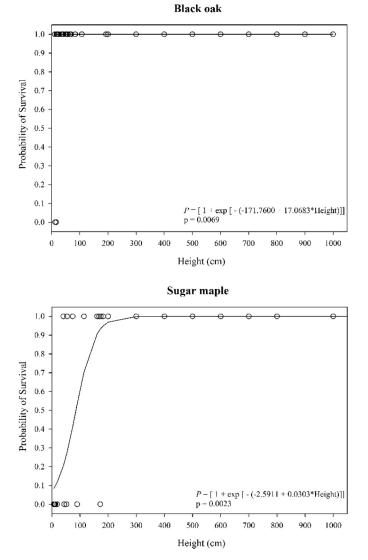| Species	Model	Intercept	BD	HT	Temp	Temp × BD	Temp × HT
Black oak	HT	–171.7600 (68.7036)		17.0683 (6.0763)			
Bitternut hickory	Null	10.2654 (4.4950)					
Chinkapin oak	Null	6.8857 (1.6506)					
Sugar maple	BD + Temp	–1.4544 (1.6035)	2.4680 (0)		–0.0119 (0)		
Eastern redcedar	HT	–2.6908 (0.6390)		0.0213 (0.0050)			

Note: Independent variables in the models included basal diameter (BD), height (HT), and fire temperature (Temp). Parameter estimates are presented with standard error in parentheses. Models are in the form of $P = \{1 + \exp[-(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_n X_n)]\}$, where P is the probability that an individual is alive following fire; β_i are the parameter estimates; and X_i are the independent variables BD, HT, and Temp. ×, interaction.
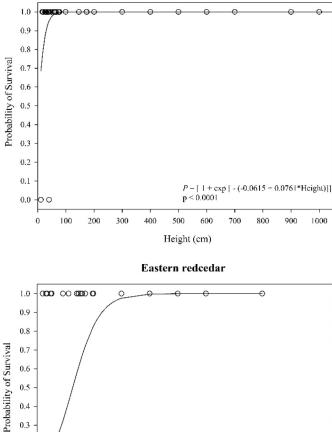
Fig. 1. The probability (P) that advance regeneration will be alive in the first growing season following a dormant-season prescribed fire based on the species and initial basal diameter. Models are in the form of $P = \{1 + \exp[-(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_n X_n)]\}$, where β_i are the parameter estimates and X_i are the basal diameter values. The significance of the fixed effect of basal diameter was determined by the p value shown. Open circles represent the basal diameter and fate of tagged individuals.

Bitternut hickory

$P - [1 + \exp [- (0.6604 + 3.3418*\text{Basal diameter})]]$
$p < 0.0001$

Sugar Maple

$P - [1 + \exp [- (-2.7620 - 2.4642*\text{Basal diameter})]]$
$p < 0.0001$

Eastern redcedar

$P - [1 + \exp [- (-1.7194 + 0.7308*\text{Basal diameter})]]$
$p - 0.0010$

found that as stem size increases, the resistance to mortality from fire also increases (Guyette and Stambaugh 2004; Dey and Hartman 2005; Ward 2015). Larger stems have thicker bark, particularly in species considered more fire tolerant, creating more thermal insulation for the cambium (Harmon 1984; Hammond et al. 2015). Even small increases in bark thickness can increase survival likelihood, as the time needed to kill the cambium of a tree is directly proportional to the square of bark thickness (Dickinson and Johnson 2001). Compared with sugar maple and eastern redcedar, oaks and hickories have thicker bark that better protects against cambial injury, especially as size increases

(Hengst and Dawson 1994; Smith and Sutherland 1999). The maximum basal diameters and heights of individuals that experienced mortality following fire were greater for sugar maple and eastern redcedar than for the other species. This suggests that whereas oaks and hickories are susceptible to fire-induced mortality at the smallest sizes of advance regeneration, sugar maple and eastern redcedar must reach larger sizes to avoid being killed by fire. Additionally, the minimum size of individuals that experienced shoot dieback with sprouts was at least three times higher for sugar maple than for oaks and hickory. Previous studies have shown that oaks sprouted when relatively small stems were top-

Fig. 2. The probability (*P*) that advance regeneration will be alive in the first growing season following a dormant-season prescribed fire based on the species and initial height. Models are in the form of $P = \{1 + \exp[-(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_n X_n)]\}$, where β_i are the parameter estimates and X_i are the height values. The significance of the fixed effect of height was determined by the *p* value shown. Open circles represent the height and fate of tagged individuals.

killed, whereas competing species such as maple were completely killed by fire at smaller sizes (Brose and Van Lear 1998; Barnes and Van Lear 1998).

The ranking of the models for chinkapin oak and bitternut hickory resulted in the null models being selected as the most supported. In a similar study, Dey and Hartman (2005) found that both height and basal diameter were significantly related to survival probability for hickory species, chinkapin oak, and black oak. The inability of our data to fit a given model form does not belie the underlying ecological phenomenon. Basal diameter and height models were likely not ranked higher as result of low mortality at any size class, perhaps an indication of the fire tolerance of these two species. Larger sample sizes and longer observational studies may better elucidate the relationship between size and fire survival probability of chinkapin oak and bitternut hickory.

The fire temperatures we measured were similar to those of other studies in eastern hardwood stands, in which maximum temperatures during low-intensity surface fires commonly ranged between 75 and 300 °C (Iverson et al. 2004; Blankenship and Arthur 2006; Ward 2015). We found no significant relationship between fire temperature and survival probability for all species except eastern redcedar. Although significant, fire temperature as a predictor of survival probability for eastern redcedar had very low support amongst all other model subsets. The lack of an effect of fire temperature on survival probability for most species was unexpected, as this relationship has been documented in other studies. Brose and Van Lear (1998) found that fire intensity was related to mortality in red maple, and Ward (2015) found that percent top kill increased with increasing thermocouple temperature for oaks, maples (*Acer* L. spp.), and birches (*Betula* L. spp.). Additionally, Dickinson and Johnson (2004) described an exponential dependence between mortality rates and temperature, but also found 60 °C to be the threshold for cambial necrosis within stems exposed to surface fires. Flame residence time, which reflects rate of spread and flame width, may also be an important factor in stem injury and mortality (Dickinson and Johnson 2001). Because our rate of spread and fire temperature measurements were collected at the burn unit level and plot level, respectively, the fire conditions that existed at individual stems could not be determined. An additional caveat of using the paint tags as pyrometers is that the temperature of the tag represents

the minimum of a range of temperatures. Additionally, although the measured temperature from the pyrometer may be correlated with the actual fire temperature, it does not directly represent the actual fire temperature. Despite these limitations, paint temperature tags are inexpensive and easy to deploy, making them well suited for fire ecology research. Future survival studies could obtain a more local fire temperature at each seedling or sapling to better elucidate the relationships between survival probability and fire temperature for a variety of species.

We anticipate that annual mortality rates and survival probability will change over time, particularly if the study areas are repeatedly exposed to prescribed fire. Some research suggests that there are different individual- and stand-level responses to prescribed fire depending on fire frequency and season of burn (Waldrop and Lloyd 1991; Arthur et al. 1998, 2015; Peterson and Reich 2001; Fan et al. 2012; Vander Yacht et al. 2017). For example, Dey and Hartman (2005) found that survival probability after one fire was high for all species examined in the Missouri Ozarks (USA), but it decreased for all species after three or four burns. This decrease was most prominent in mesophytic species such as flowering dogwood (*Cornus florida* L.) and blackgum (*Nyssa sylvatica* Marshall) and least prominent in the white oak group (i.e., white oak (*Quercus alba* L.), post oak, and chinkapin oak) and hickories. We expect that repeated fires will continue to top-kill advance regeneration and that sprouting and survival probability will continue to decrease with each burn as rootstocks become depleted and sprouts take time to recover to preburn sizes.

4.1. Management implications

Prescribed fire is a commonly recommended tool for restoring oak woodlands that are invaded by fire-sensitive, often mesophytic, oak competitors. Our results support those of other studies: oak regeneration shows greater resistance to fire than its competitors, but even fire-sensitive species can resist injury and death from a single dormant-season burn. All species analyzed in this study had at least a 99% survival probability at basal diameters > 9 cm. Our study was located in a relatively understudied region and focused on oak competitors that are somewhat less studied (i.e., eastern redcedar and sugar maple); however, we found that fire effects on advance regeneration in oak woodlands might behave similarly to those of eastern forests. The implication of these data reveals that heavily invaded, fire-suppressed woodlands may not experience major compositional shifts in the regeneration layer following a single fire, which is a finding in many other studies of eastern oak forests (Arthur et al. 2012; Brose et al. 2013).

Nowacki and Abrams (2008) conceptualized several alternative stable states of oak communities depending on the fire regime and site type. Beyond a theoretical threshold change in community state, restoring a community to a desired state that it no longer resembles requires considerably greater energy input than that required for its maintenance. Our short-term results support these theories, and we recommend the use of other treatments in combination with prescribed fire (e.g., targeted removal of large stems) to accelerate restoration of invaded oak woodlands.

Acknowledgements

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