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Resprouting dynamics suggest different regeneration strategies for shortleaf pine and oak species following surface fires in Missouri Ozarks

Hope Fillingim [a,1], Benjamin O. Knapp [a,*], John M. Kabrick [b], Michael C. Stambaugh [a], Grant P. Elliott [c], Daniel C. Dey [b]

[a] School of Natural Resources, University of Missouri, 203 Anheuser-Busch Natural Resources Building, Columbia, MO 65211, USA
[b] USDA Forest Service, Northern Research Station, 202 Anheuser-Busch Natural Resources Building, Columbia, MO 65211, USA
[c] Department of Geography, University of Missouri, 202 Stewart Hall, Columbia, MO 65211, USA

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ABSTRACT

Prescribed burning is a common management tool for both shortleaf pine and associated oak species, as they can resprout following top-kill and are adapted to frequent surface fire regimes. In Missouri, shortleaf pine often occurs with oaks in mixedwood ecosystems, though its prevalence is diminished from historic levels. With interest in restoring shortleaf pine, research is needed on specific strategies for using prescribed fire to promote shortleaf pine in mixed pine-oak ecosystems. We studied the survival and resprouting of shortleaf pine and oaks of different sizes following a prescribed burn in Missouri. Our results affirm the patterns of increasing stem size reducing the likelihood of top-kill and of greater fire intensity increasing the likelihood of top-kill for both shortleaf pine and oaks. We found that shortleaf pine can resist top-kill at a lower basal stem diameter threshold than oaks and that shortleaf pine and oaks differ in post-resprouting resource allocations, with shortleaf pine growing numerous shorter sprouts and oaks growing fewer taller sprouts. We suggest the use of well-timed prescribed burning to release shortleaf pine from oak competition and improve its viability in mixed pine-oak systems.

1. Introduction

Resprouting is an important mechanism that contributes to regeneration dynamics of tree communities (Bond and Midgley, 2001; Del Tredici, 2001). The ability to resprout after surface disturbances such as fire, flooding, or herbivory provides woody plants with the benefit of persistence of the population from existing rootstocks rather than requiring reestablishment from germination of new seeds. Consequently, species that resprout can persist under frequent disturbances or stressful conditions by accumulating abundant populations of regeneration through time without frequent or abundant seed production (Bellingham and Sparrow, 2000; Bond and Midgley, 2003), provided conditions are sufficient for survival and growth between disturbance events. Species that resprout vigorously often prioritize early development of root systems rather than aboveground growth (Bond and Midgley, 2003; Roberston and Hmielowski, 2014), but once established, relatively large root systems can support rapid height growth of resprouts (Larsen and Johnson, 1998; Dietze and Clark, 2008; Matula et al., 2019).

In frequent-fire ecosystems, basal resprouting is common for many tree species, especially for small-diameter trees that are vulnerable to stem mortality from surface fire (Clarke et al., 2013). For many species, the probability of resprouting decreases as stem diameter increases, becoming rare for large, mature trees (Dey et al., 1996; Keyser and Loftis, 2015). While resprouting provides a mechanism for persistence of seedling and sapling populations, eventual replacement of overstory trees also requires recruitment into larger sizes that are resistant to top-kill from recurring fires (Freeman et al., 2017; Hoffmann et al., 2020). Mortality or top-kill of small trees is commonly due to damage to conductive tissue at the base of the stem or damage to buds (Hood et al., 2018). As trees grow, they develop thicker bark that protects the vascular cambium (Reifsnyder et al., 1967; Schafer et al., 2015), and sensitive meristematic tissue on stems and branches gets positioned further from damaging heat energy of surface fires (Hood et al., 2018). Stem size is therefore an important factor of resprouting dynamics in frequent-fire ecosystems, affecting the likelihood of resprouting

* Corresponding author.
E-mail address: knappb@missouri.edu (B.O. Knapp).
[1] Present address: USDA Forest Service, Southern Research Station, 3734 SC-402, Cordesville, SC 29434

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following damage, the rate of stem growth following resprouting, and the likelihood of resisting top-kill (i.e., not needing to resprout but instead recruiting to the overstory).

Specific traits of the species within the tree community interact with fire behavior to affect regeneration and recruitment in frequently burned ecosystems. Tree species vary in their likelihood to resprout repeatedly with frequent surface fires (Dey and Hartman, 2005), and thus increasing fire frequency often changes the species composition of the regeneration cohort by favoring species capable of vigorous, frequent resprouting (Hutchinson et al., 2012; Brose et al., 2013; Knapp et al., 2015). Species resprouting responses are also influenced by the density of overstory (i.e., available light in the understory) in addition to fire frequency and seasonality (Brinkman and Liming, 1961; Waldrop et al., 1992; Grano, 1970; Fan and Dey, 2014). Additionally, species vary in the rate of bark development in relation to stem size, with species associated with frequent surface fire regimes observed to develop greater bark thickness than those associated with infrequent fire (Schafer et al., 2015). The variation in patterns of bark development among species provides an additional mechanism to manage the composition of the recruiting trees to favor those resistant to top-kill (Pausas, 2015). Variation in the rate of stem growth following resprouting can affect the time required to become resistant to top-kill as well as competitive dynamics of species within the regenerating population. Fire behavior can affect these dynamics: greater fire intensity can increase stem mortality rather than top-kill and increase the stem size necessary to persist without top-kill (Hood et al., 2018; Hoffmann et al., 2020).

In the central and eastern United States, open ecosystems of oak (*Quercus* spp.) and pine (*Pinus* spp.) species were historically maintained through frequent surface fires (Hanberry et al., 2020b). These tree species vary in their fire-adaptation traits (Varner et al., 2016; Pile et al., 2017), resulting in corresponding variation in structure and composition associated with differences in frequency or intensity of the surface fire regimes. In Missouri, shortleaf pine (*Pinus echinata* Mill.) occurs in mixtures with a variety of oak species in natural communities from savannas and woodlands to closed-canopy forests. Following European settlement, timber exploitation, conversion of forest to agriculture, free-range grazing coupled with annual burning, and subsequent fire exclusion changed the regeneration, composition, and structure of forests in the region (Record, 1910). These land use patterns contributed to a reduction in the estimated extent of shortleaf pine from 324,000 to 25, 000 km^2 across its 22-state range (Oswalt, 2012; Anderson et al., 2016), with approximately 22 % of the historical shortleaf pine abundance remaining in Missouri (Guyette et al., 2007). Current management efforts to restore shortleaf pine and open pine-oak ecosystems within the region commonly focus on re-establishing frequent surface fire (often initially combined with timber harvesting) to reduce stand density and promote shortleaf pine regeneration through site preparation and competition control (Dey et al., 2017; Guldin, 2019; Bragg et al., 2020). Despite evidence for the importance of frequent surface fire in shortleaf pine ecosystems, results of prescribed burning to promote shortleaf pine regeneration have been mixed, often resulting in abundant resprouting of hardwoods that may outcompete shortleaf pine regeneration (Elliott and Vose, 2005; Fan et al., 2012).

Shortleaf pine and associated oak species have differences in their fire-adaption traits, which may result in generalizable differences in fire effects on their regeneration. Young shortleaf pines have a unique morphological adaptation to fire known as the basal crook, which is a J-shaped curve above the root collar that creates a horizontal section of upper root tissue approximately 2.5 cm in length (Mattoon, 1915). The basal crook is often positioned just below the surface of the mineral soil, where dormant buds are protected from damage by fire. Shortleaf pine seedlings resprout from the basal crook following top-kill, although factors such as stem size, fire intensity, and position of the basal crook relative to the soil surface can affect resprouting probability (Lawson, 1990; Lilly et al., 2012). Oaks resprout from buds located at or near the root collar and are known to resprout vigorously following top-kill (Larsen and Johnson, 1998). During early seedling development, oaks typically allocate a relatively high proportion of growth to belowground structures, developing a large root system that can persist for decades with repeated surface fires and provides energy for rapid stem growth following resprouting (Larsen and Johnson, 1998). Previous research has found crucial differences in survival rates following prescribed burns between shortleaf pine and oaks growing in a mixedwoods forest, with greater mortality among shortleaf pine than oaks after repeated burns, as well as differences in survival among oak species, with greater mortality for red oak species than white oak species (Dey and Hartman, 2005; Fan et al., 2012).

This study compares resprouting dynamics of shortleaf pine and co-occurring upland oak species, with the goal of evaluating the use of prescribed fire as a tool for promoting shortleaf pine regeneration in mixed shortleaf pine-oak forests. Specifically, we aim to: 1) determine size thresholds at which shortleaf pines and oaks can either resist top-kill or survive through resprouting; 2) determine effects of fire intensity on these size thresholds; 3) compare post-fire resprouting performance (number of sprouts produced per stem and maximum sprout height growth) of shortleaf pines and oaks following fire; and 4) determine if there is an optimal size of shortleaf pine to favor it over neighboring oak through either differential top-kill or greater growth rate after resprouting. Results from this study will improve our understanding of shortleaf pine and oak resprouting dynamics and provide managers with recommendations for prescribed burning to promote shortleaf pine regeneration.

2. Methods

2.1. Study site

In 2000, the Missouri Department of Conservation (MDC) established the 900-ha Midco Shortleaf Pine Restoration Area (referred to as Midco) within the southern part of the Peck Ranch Conservation Area in Carter County, Missouri, with the goal of restoring shortleaf pine woodland natural communities. The elevation of Midco ranges from 190 to 295 m above sea level, with rolling topography and dry to dry-mesic, cherty Ultisol and Alfisol soils (Olson and Olson, 2016). The predominant soils in the study area are mapped as Clarksville (Loamy-skeletal, siliceous, semiactive, mesic Typic Paleudults), Alred-Rueter (Loamy-skeletal over clayey, siliceous, semiactive, mesic Typic Paleudalfs and Loamy-skeletal, siliceous, active, mesic Typic Paleudalfs, respectively), and Alred-Gepp (Very-fine, mixed, semiactive, mesic Typic Paleudalfs) soil series, which are very deep, strongly acid, well drained to somewhat excessively drained soils, composed of hillslope sediments over gravelly and/or clayey residuum (Soil Survey Staff). Slopes range from 0 % to 35 %. Carter County has a 30-year (1991–2020) average precipitation of 1247 mm and temperature of 13.8 °C (NOAA National Centers for Environmental information, 2022). The Missouri ecological classification system uses ecological and geological information to categorize landscapes into landtype associations (LTAs). Midco is described as a Current River Oak-Pine Woodland/ Forest Hills LTA (Nigh and Schroeder, 2002; Olson and Olson, 2016) and as a Current-Eleven-Point Oak-Pine Woodland Dissected Plains LTA (Tuttle and Houf, 2007, Olson and Olson, 2016).

The original project at Midco was designed to be an example of operational, adaptive restoration management but with interest in comparing the effectiveness of prescribed burning, mechanical release, and herbicide in association with timber harvest. There were originally ten management units that received different silvicultural prescriptions through time, applied at the unit scale. Our current study uses only the three management units that focused on frequent prescribed burning as the primary management treatment (Table 1). Timber harvest was done in 2001 and 2003, with focus on salvaging declining red oaks and the goal of leaving approximately 4.6 m^2/ha basal area of white oak

Table 1
History of management treatments in the three units designated as prescribe fire management in the Midco Shortleaf Pine Restoration Area at the Peck Ranch Conservation Area in Carter County, MO.

Management action	Unit 1	Unit 4	Unit 6
Harvest	2001 2003	2001	2001
Plant shortleaf pine seedlings	2005 2006	2006	2005
Prescribed burn	2002 2007 2010 2014	2002 2013	2002 2015
Mechanical release (slashing or mulching)	2007	2007 2011	2005 2009

(*Quercus alba* L.) and post oak (*Q. stellata* Wangenh.) along with shortleaf pine seed trees. Following harvest, stands were planted at a spacing of 3.6 × 3.6 m with bare-root shortleaf pine seedlings produced from the MDC George O. White State Nursery in Licking, MO. At the time of planting or soon after, the sites were treated with a slashing treatment by cutting the remaining suppressed oak and hickory trees (Tuttle and Houf, 2007). Two of the units (Unit 4 and 6) received additional mechanical release in 2011 and 2009, respectively, to control woody competition (Table 1). These treatments were applied by cutting woody competition within 1.83 m of pine seedlings with a chainsaw or forestry mulching machine.

Prescribed burning was done across all units in 2002 and at least one other time before the current study. Unit 1 received a low-intensity burn in February 2002, and Units 4 and 6 received a moderate-to-intense burn in April 2002. Unit 1 was burned again in September 2007, March 2010, and in 2014. Unit 4 was burned again in 2012, and Unit 6 was burned again in 2013. As a result of various treatments applied through time, the Midco Shortleaf Pine Restoration Area has shortleaf pine and oak regeneration across a range of sizes that occurs intermixed. While it may not be possible to distinguish natural from artificial regeneration of shortleaf pine or to estimate the age of individuals in the regeneration layer, the population structure provides opportunity to evaluate resprouting responses following fire for individuals across a wide range of stem sizes in a field setting. Oak species include post, white, black (*Quercus velutina* Lam.), and blackjack (*Q. marilandica* Münchh.).

2.2. Experimental design

We used the three prescribed burn management units at Midco, ranging from 68 to 94 ha, for the study. Within each burn unit, we established 30 plots to sample regeneration from two species groups (shortleaf pine vs upland oaks) and five size classes, based on basal diameter (0–1.50 cm, 1.51–4.00 cm, 4.01–6.50 cm, 6.51–10.00 cm, 10.01–15.00 cm). Sampling plots were established in the fall/winter of 2019. To determine locations of sampling plots, we first used ArcMap software to overlay a grid of uniform points at 50 m spacing across each burn unit. We randomly selected an initial 50 points along the grid and visited these in the random order they were generated. Within 30 m of each selected grid point, we established a circular plot 10 m in diameter, within which we tagged regeneration that met the study criteria for species and size class, resulting in 10 individuals sampled in each plot. Grid points that did not have the required 10 seedlings within 30 m were excluded and the next grid point was evaluated. Because the first 50 points failed to generate the 30 sample plots within each burn unit, a second set of 50 points were randomly selected until 30 suitable plots were found.

2.3. Data collection

At each plot, one shortleaf pine and one oak in each of the five size classes were tagged. The height and basal diameter (measured 2.5 cm from ground) of all tagged trees were measured and recorded in the fall of 2020 (prior to prescribed burning). Height was recorded as the distance from the ground to the terminal portion of the stem, and seedlings were straightened if leaning. Oaks were identified and species recorded. Given their close proximity, each shortleaf pine and oak within the same size class was considered a paired sample that was assumed to experience similar fire behavior. In June 2021 (after prescribed burning, see below), all tagged trees were re-visited, and status was recorded as: alive (resisted top-kill), resprouted (survive with top-kill), or dead. In fall 2021, the number of sprouts and height and basal diameter of the largest sprout for each seedling were recorded, and trees not top-killed were remeasured for height and basal diameter.

As a surrogate for fire intensity, an aluminum tag painted with temperature sensitive paints designed to melt at specific temperatures (Tempil® Temperature Indicating Liquids) was staked by each tagged tree at a height of 10 cm above the ground prior to prescribed burns. Paint temperatures included: 80, 121, 149, 177, 204, 232, 260, 288, 316, 343, and 399 °C. Temperature paint tags were installed adjacent to all seedlings in Units 1 and 4. In Unit 6, 25 of the 30 plots had at least 1 temperature painted tag, with most at the smallest size class of pine and oak seedlings only, due to time constraints. All tags were collected 1 – 2 days following burning to determine the highest temperature at which the paint melted. Any plots that did not burn were noted.

2.4. Prescribed burns

The prescribed burns were conducted by Missouri Department of Conservation personnel in February and March of 2021. All plots were burned in Units 1 and 4, and 22 of the 30 plots were at least partially burned in Unit 6. Rates of spread and flame lengths were estimated visually by different fire crew members, with 5 – 12 observations per burn, and fire weather and behavior are summarized in Table 2.

2.5. Data analysis

To address our first objective, to determine size thresholds at which shortleaf pines and oaks can either resist top-kill or survive through resprouting, we used a generalized linear mixed model with a binomial distribution and logit link function to test the probability of resisting top-kill as the dependent variable. The model included basal diameter as a continuous variable and species (shortleaf pine vs oaks) as a categorical variable, as well as their interaction, as fixed effects. Plot within unit was included as a random effect, but models would not converge and the random effect was dropped.

To address our second objective, determining effects of fire intensity on size thresholds for resisting top-kill, we used generalized linear mixed models with a binomial distribution and a logit link function to model likelihood of resisting top-killed. We binned the fire temperatures based on the maximum temperature that melted on the paint tags into four categories: Low (paint temperatures of 80 and 121 °C), Low-Med (paint temperatures of 149, 177, and 204 °C), Med-High (paint temperatures of 232 and 260 °C), and High (paint temperatures of 288, 316, 343, and 399 °C). We modeled the likelihood of resisting top-kill with maximum fire temperature, basal diameter, and their interactions included as fixed effects. We ran models for temperature effects separately for shortleaf pine and for oaks. Models included a random effect of plot within unit; models for shortleaf pine would not converge and the random effect was dropped, but the model for oaks converged with the random effect included.

Our third objective, to compare post-fire resprouting performance (number of sprouts produced and maximum shoot growth) of shortleaf pines and oaks after one growing season following fire, was accomplished by creating separate models for dependent variables of number of sprouts and maximum sprout growth for resprouting stems using generalized linear mixed models. For number of sprouts, we used a

Table 2
Prescribed burn weather and fire effects.

Unit	Date	Time	Air Temp (°C)	Relative Humidity (%)	Flame Length (cm)	ROS (m/hr)	Fire Temp. (°C)
1	3.3.21	13:51 – 16:03	16 – 23	~ 35	37	46	290
4	3.3.21	10:58–12:51	16 – 23	~ 35	27	27	220
6	2.3.21	11:40 – 15:46	5 – 13	43–68	24	36	-

Air temperature and relative humidity were estimated with a Kestrel by the burn crew
ROS = rate of spread
Fire temperature was estimated from painted tags

negative binomial distribution with a log link function, and for sprout height we used a lognormal distribution. Models included pre-fire basal diameter, species group, and their interaction as fixed effects and plot within unit as a random effect.

We used a paired approach to address our fourth objective, determining if there is an optimal size of shortleaf pine to favor it over neighboring oaks through either differential top-kill or greater growth rate after resprouting. At each plot, we considered the shortleaf pine and the oak stem within the same size class to be a paired sample, experiencing similar growing conditions and prescribed burn conditions, and compared the performance of each pair. To test for differences in resprouting, we recorded the frequency of each of four possible resprouting outcomes: 1) both stems resist top-kill, 2) both stems are top-killed, 3) shortleaf pine resists top-kill and the oak is top-killed, and 4) shortleaf pine is top-killed and the oak resists top-kill. We used a Chi-square analysis to test if the observed frequencies differed from expected frequencies by size class, using a Bonferroni adjusted alpha value of 0.0025. To test for differences in height growth of shortleaf pine and oak sprouts, we calculated the difference in height between seedlings in each pair one growing seasons after resprouting by subtracting the height of the oak sprout from the height of the shortleaf pine sprout. Negative values indicated that the oak sprout was taller than the shortleaf pine sprout. We used a generalized linear mixed model with height difference as the dependent variable and the basal diameter of shortleaf pine of each pair as a fixed effect. Plot within unit was included as a random effect.

3. Results

Overall, survival following burns was very high for pines and oaks, with 99 % alive after one growing season. Smaller seedlings were more likely to survive through resprouting, while larger trees were more likely to survive by resisting top-kill (Table 3). There was a significant interaction between species and basal diameter ($p < 0.001$) on the probability of resisting top-kill. For both species, the probability of resisting top-kill increased with increasing basal diameter (Fig. 1A), although shortleaf pine was resistant to top-kill at smaller basal diameters than oaks. The probabilities of oaks and pines to resist top-kill diverged at a basal diameter greater than about 2.3 cm. Across all stems sampled, shortleaf pine reached 50 % probability of resisting top-kill at a threshold of 2.4 cm basal diameter and a 90 % probability of resisting top-kill at 3.0 cm basal diameter, whereas oaks reached the same probabilities at 3.5 cm and 5.5 basal diameter, respectively.

The paint tags indicated that fire intensity affected resprouting response. For pines and oaks, the proportion of stems that resisted top-kill decreased as the temperature at which the paint tags melted increased, although the largest size classes resisted top-kill regardless of paint tag temperature (Fig. 2). Including paint tag temperature in the model for shortleaf pine resulted in no significant interaction between temperature and basal diameter ($p = 0.735$). Paint tag temperature had a significant effect on the probability of resisting top-kill ($p < 0.001$), with increasing paint tag temperature reducing probability of resisting top-kill (Fig. 1B). Model results were similar for oak, with no interaction between paint tag temperature and basal diameter ($p = 0.099$) and significant effect of paint tag temperature ($p = 0.008$) and basal diameter ($p < 0.001$) on probability of resisting top-kill (Fig. 1C). As the paint tag temperature increased, the basal diameter required for a given probability of resisting top-kill increased at a greater rate for oaks than for shortleaf pine, suggesting that species differences in the size threshold for resisting top-kill becomes more pronounced at greater fire intensity (Figs. 1B and 1C).

We found differences in resprouting performance between shortleaf pine and oak species. For the number of sprouts per stem after resprouting, there was a significant interaction between species and pre-fire basal diameter ($p < 0.001$). The number of sprouts significantly increased with increasing basal diameter for shortleaf pine ($p < 0.001$) but did not for oak species ($p = 0.180$). Oak species produced a mean of 3.5 sprouts per stem. Across all pre-fire basal diameters, shortleaf pine produced more sprouts than oak, with an overall mean of 12.8 sprouts per stem but increasing to over 30 sprouts for pre-fire basal diameters > 3 cm (Fig. 3A). There was no interaction between species and pre-fire basal area for the height of sprouts after one growing season ($p = 0.371$). Species differed in shoot length ($p < 0.001$), with a mean of 28.6 cm for shortleaf pine and a mean of 59.1 cm for oaks. For all species, shoot length increased with increasing basal diameter ($p < 0.001$), with oak shoots nearly double the length of shortleaf pine shoots across the range of pre-fire basal diameters (Fig. 3B).

We used a paired analysis to compare resprouting performance of shortleaf pine and neighboring oak stems of similar pre-fire stem size. Resprouting outcomes were similar for shortleaf pine and oak stems for most of the size classes, other than size class 2 (Fig. 4A). For the smallest size class, both the shortleaf pine and oak were top-killed in 88.6 % of the pairs, significantly greater than what would be expected by chance ($p < 0.001$). For size classes 3, 4, and 5, both the shortleaf pine and oak species group resisted top-kill in > 90 % of the pairs, significantly greater than what would be expected ($p < 0.001$). For size class 2, both species groups were top-killed 33.8 % of the time and both resisted top-kill 28.6 % of the time. In cases for which one of the paired stems was

Table 3
The percent of shortleaf pine and oak stems that died, resprouted, or resisted top-kill in immediately following a prescribed burn by basal diameter class; n = 82 for each species group in each size class.

	Shortleaf pines			Oak species		
Size class (cm)	Dead	Sprouted	Resisted top-kill	Dead	Sprouted	Resisted top-kill
1 (< 1.5)	2.5	92.5	5.0	0.0	92.7	7.3
2 (1.5–3.9)	2.5	34.6	64.1	0.0	66.7	34.6
3 (4.0–6.4)	0.0	0.0	100	0.0	7.4	92.6
4 (6.5–9.9)	0.0	0.0	100	0.0	3.7	96.3
5 (10.0–14.9)	0.0	0.0	100	0.0	0.0	100

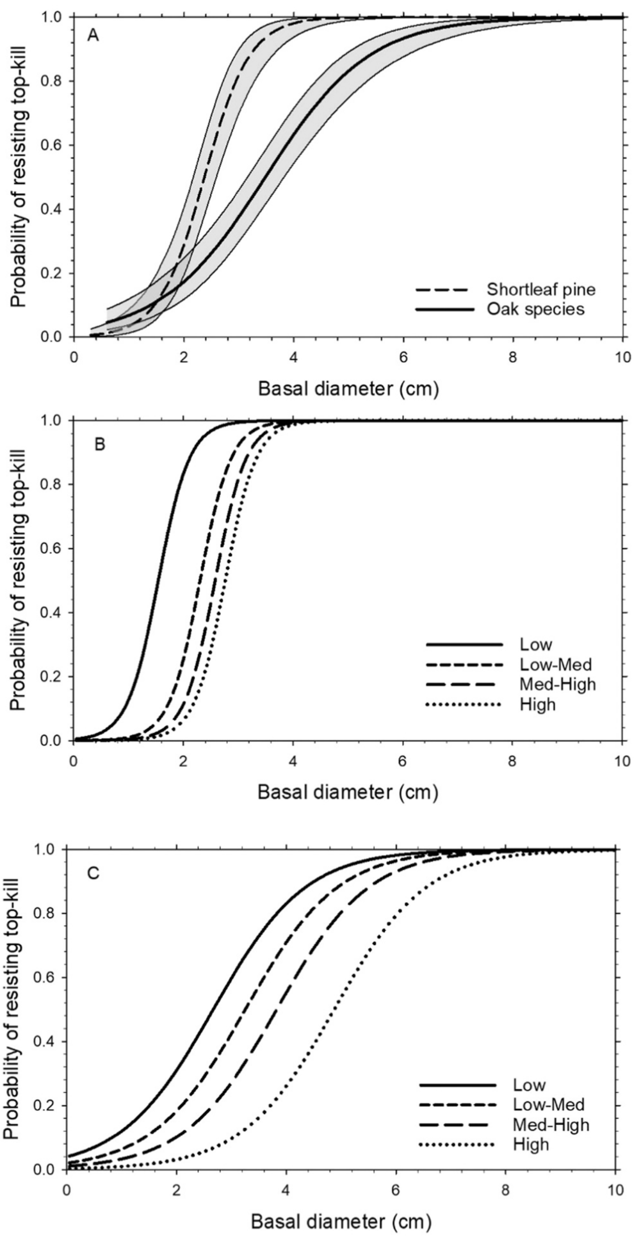

Fig. 1. Predicted probability of resisting top-kill for A) shortleaf pine and oak species, with 95 % confidence intervals shaded; B) shortleaf pine and C) oak species for paint tag temperatures binned into four fire intensity classes.

top-killed, shortleaf pine resisted top-kill and the oak stem was top-killed 33.8 % of the time, while the opposite occurred only 3.8 % of the time. The likelihood of pine resisting top-kill while oak did not was significantly higher than expected ($p < 0.001$) (Fig. 4A).

There were 91 seedling pairs where both shortleaf pine and oak resprouted, for which 81.3 % resulted in greater shoot growth of the oak sprout than the shortleaf pine sprout after one growing season (Fig. 4B). The resulting height advantage for oak sprouts increased with increasing pre-fire basal diameter ($p = 0.012$).

4. Discussion

Our results show the reliable resprouting ability of shortleaf pine and oak regeneration, as expected, but offer novel insights into implications for regeneration of each species type based on resprouting performance. Mortality in our study was lower than that reported in other studies, although Cain and Shelton (2000) also reported < 5 % mortality for shortleaf pine and oak seedlings burned in winter in a study from Arkansas. For shortleaf pine, other studies have reported mortality rates of 19 % (Phares and Crosby, 1962), 37 % (Lilly et al., 2012), 38 % (Dey and Hartman, 2005), 31–53 % (Clabo and Clatterbuck, 2019), and approximately 15–79 % (Willis et al., 2025) following one growing season after burning. For oaks, Dey and Hartman (2005) reported that after one spring burn in Missouri, white oak, post oak, and black oak regeneration experienced 5 %, 9 %, and 10 % mortality, respectively, although other studies have reported mortality rates of oak regeneration of 10–55 % (Brose and Van Lear, 1998).

A variety of factors could explain differences in mortality observed in our study and others, including differences in the size or age of seedlings, overstory shade and site quality. For example, Phares and Crosby (1962) and Clabo and Clatterbuck (2019) studied 3-year-old planted shortleaf pine seedlings that were smaller and likely younger than those in our study. Similarly, Lilly et al. (2012) also reported higher mortality for shortleaf pine seedlings that were smaller in basal diameter than those in our study. Differences in fire seasonality or intensity may have also resulted in the observed differences in survival. However, fire intensity as measured by temperature-sensitive paints in our study (<79–343 °C in units 1 and 4, and from <79–232 °C in unit 6) was generally similar to that reported using similar methods by Lilly et al. (2012) (79–593 °C) and Dey and Hartman (2005) (121–316 °C).

Resprouting was common for both shortleaf pine and oaks in our study, and for both, resistance to top-kill increased with stem size (Dey and Hartman, 2005; Ferguson, 1957; Lilly et al., 2012). However, relationships between stem basal diameter and the probability of resisting top-kill differed between shortleaf pine and oaks, with shortleaf pine stems being more resistant to top-kill at smaller sizes than oaks. Because of the lower size threshold for resisting top-kill, more shortleaf pines than oaks survived by resisting top-kill rather than through resprouting, with only 25 % of surviving shortleaf pine sprouting compared to 34 % of oaks. A similar pattern was observed in another study in Missouri, where after repeated burns shortleaf pine was more likely to survive by resisting top-kill and associated oak species were more likely to survive through resprouting (Dey and Hartman, 2005; Fan et al., 2012).

Although not measured in our study, previous research shows that the time required for shortleaf pine and associated oak species to reach their top-kill resistant size thresholds varies. Factors such as stand density and amount of competition, seedling age or origin (resprout or germinant), site quality, and weather or climate conditions can affect growth rates. Planted shortleaf pine seedlings in the Missouri Ozarks ranged from ~0.4–4 cm basal diameter after five years, largely based on overstory stocking (Kabrick et al., 2015), and shortleaf regeneration in the South Carolina piedmont ranged from 3.9 to 12.7 cm basal diameter five years after re-sprouting due to top-kill by fire (Bohannon et al., 2025). Black and white oak planted from acorns in Pennsylvania under different light levels ranged from ~0.4 cm basal diameter in low light to ~1–1.3 cm basal diameter in 75 % light after 5 years (Brose and Rebbeck, 2017), while resprouting oaks in our current study reached a similar size (0.2 – 2.1 cm basal diameter) after only one growing season. Additional research is needed to model shortleaf pine and oak stem growth rates under various conditions to inform fire-free intervals appropriate for preventing top-kill.

Fire behavior affected relationships between probability of top-kill and stem size for shortleaf pine and oaks. As expected, greater fire intensity (as measured by higher paint tag temperatures) increased the basal diameter threshold for resisting top-kill. Previous studies have reported similar relationships between measures of fire intensity and top-kill or mortality of pine and oak species (Ferguson, 1957; Holmes et al., 2011; Knapp et al., 2018), including shortleaf pine (Lilly et al., 2012). Our results show that the effect of increasing fire intensity was less impactful on resistance to top-kill for shortleaf pine than for oak species. Mortality or top-kill of trees within the size range observed in the study is commonly due to damage to the vascular cambium because small trees have not developed thick bark, although damage to the

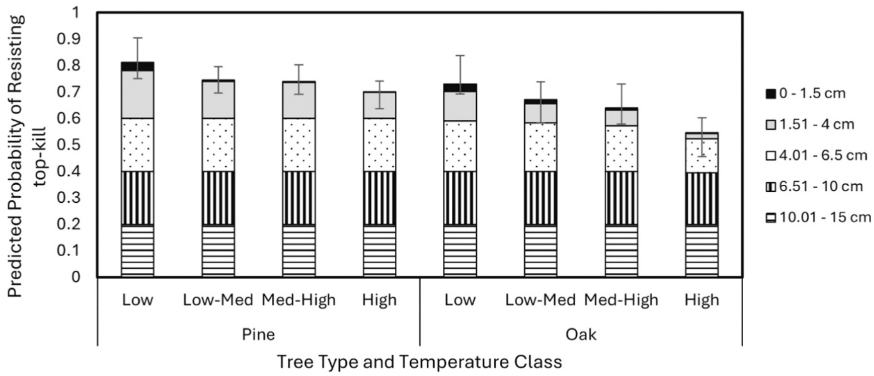

Fig. 2. Proportion of stems resisting top-kill for oak and shortleaf pine stems by temperature range. Whole bars represent total survival probability by temperature range. Bars are vertically divided by size class, with each size class representing ~20 % of the total sample size. Error bars are the 95 % confidence interval for all size classes combined.

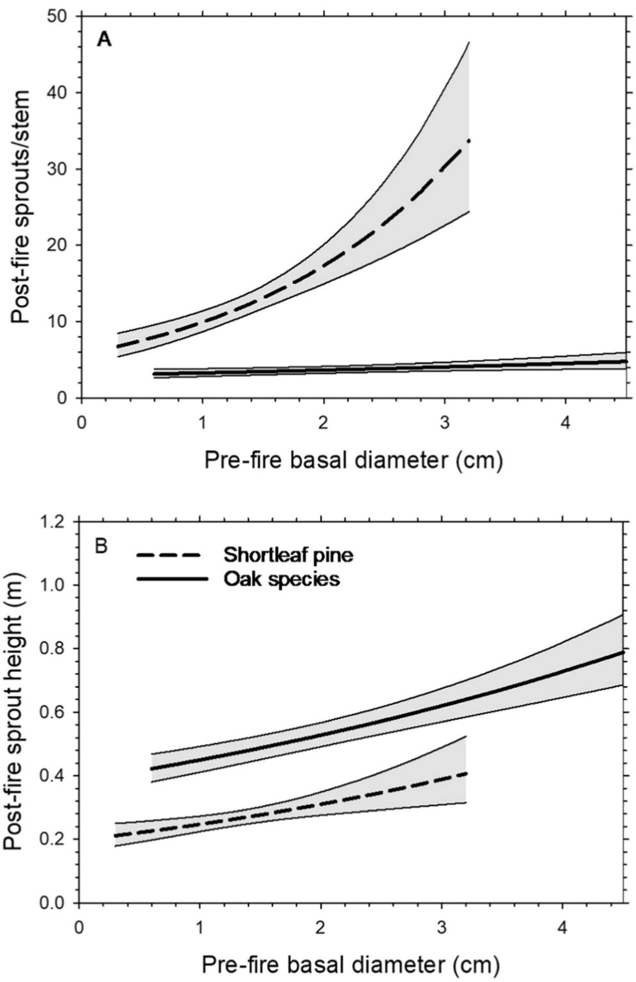

Fig. 3. Estimated mean and 95 % confidence intervals for A) number of sprouts per stem following resprouting of shortleaf pine and oak species in relation to pre-fire basal diameter, and B) height of tallest sprout one growing season after resprouting of shortleaf pine and oak species in relation to pre-fire basal diameter.

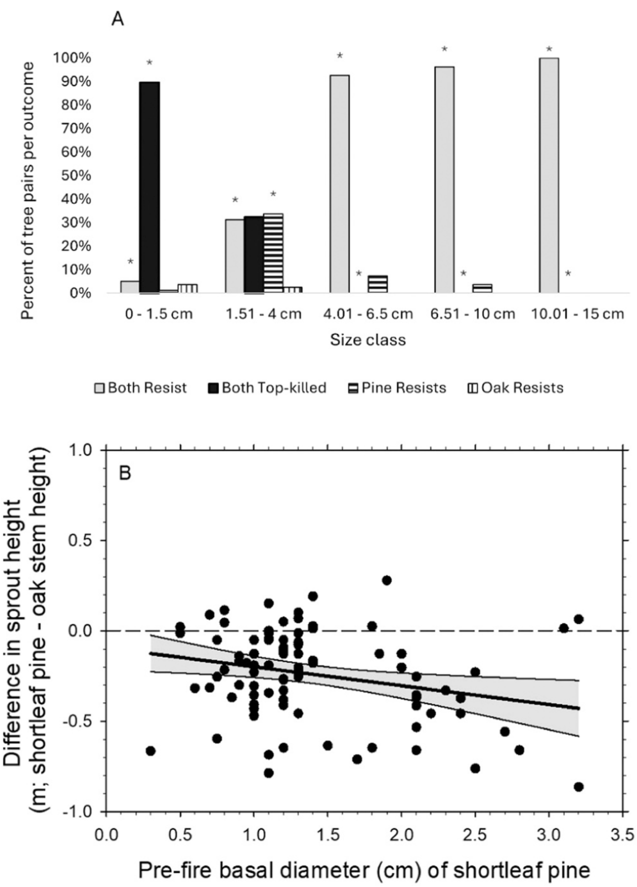

Fig. 4. Comparison of paired shortleaf pine and oak stems showing A) percent occurrence in each of four categories following prescribed burning: both resist top-kill, both are top-killed, only the pine resists top-kill, or only the oak resists top-kill; * indicates outcomes significantly different from the expected. Panel B) shows difference in maximum sprout height between paired shortleaf pine and oak one growing season after top-kill in relationship to pre-fire basal diameter of the shortleaf pine in the pair. Points below the reference line at 0 indicate the oak sprout was taller than the pine sprout.

crown (including foliage or buds) or roots may also contribute (Hood et al., 2018). The burns in our study were conducted prior to hardwood leaf-out. While we did not measure crown scorch, it has been reported to be related to shortleaf pine seedling mortality (Lilly et al., 2012). However, we expect differences in bark thickness between shortleaf pine and the neighboring oaks to be a driver of the relationships among top-kill, stem size, and fire intensity, as the bark of shortleaf pine thickens rapidly early in life, while the bark of many of the associated oaks thickens at a slower and more linear rate (Harmon, 1984).

For both shortleaf pine and oaks, pre-fire basal diameter was related to allocation of resources to post-fire recovery, but we observed opposite patterns for sprout production and growth between the species types, with sprout production increasing with pre-fire basal diameter for shortleaf pine but not for oaks, and shortleaf pine having more sprouts per individual. Abundant sprout production for shortleaf pine has been documented in other studies (Lilly et al., 2012; Clabo and Clatterbuck, 2019), with Bohannon et al. (2025) reporting a mean of 29 sprouts per individual (range of 1–99) one growing season following a wildfire in South Carolina, with the number of sprouts similarly correlated with pre-fire diameter. The multiple sprouts of shortleaf pine may be required to produce enough leaf surface area to meet the photosynthetic requirements for recovery compared to larger-leaved oaks. Within a few years after resprouting, shortleaf pine self-thins to a single dominant stem (Bohannon et al., 2025).

In contrast to the number of sprouts produced, oak sprout heights were correlated with pre-fire diameter, and oak sprouts consistently outgrew shortleaf pine sprouts during the first growing season after resprouting. Previous studies have reported shortleaf pine sprout shoot length to be about 50 cm after the first growing season following resprouting from fire (Cain and Shelton, 2000; Clabo and Clatterbuck, 2019; Bohannon et al., 2025). In general, most of the shortleaf pine sprouts in our study showed relatively low shoot growth, with estimated means of 20–40 cm across the pre-fire basal diameter range. Bohannon et al. (2025) found the shoot length of shortleaf pine sprouts increased rapidly after the first year, suggesting that the small stature of the sprouts in our study may change over the next few years. However, differences in sprout shoot length between shortleaf pine and oak competitors will likely have implications for recruitment and longer-term survival. Another study from Missouri found that planted shortleaf pine survival after 10 years was significantly reduced when the pine was shorter than neighboring hardwoods at 2 and 5 years after planting (Kabrick et al., 2015; Fillingim, 2023). While our study consistently found greater height growth of oak than pine sprouts within the paired design, Cain and Shelton (2000) reported that shortleaf pine shoots grew longer one year after resprouting from a winter prescribed burn than oak species. However, their study measured planted seedlings, which had not had a chance to develop large root systems and likely differ from the seedling populations in natural stands.

5. Management implications

There is a large body of evidence supporting the importance of frequent surface fire regimes for shortleaf pine (Hutchinson et al., 2019; Hanberry et al., 2020a; Stambaugh et al., 2020) and upland oak ecosystems (Nowacki and Abrams, 2008; McEwan et al., 2011; Hanberry et al., 2020a), making prescribed burning a common tool for their management (Arthur et al., 2012; Guldin, 2019). The establishment of new shortleaf pine seedlings is inhibited by the build-up of forest floor material (Grano, 1949; Boggs and Wittwer, 1993), and heavy shade from dense understory and midstory layers limit survival (Blizzard et al., 2007). Oaks, especially the more shade tolerant *Quercus alba*, are more likely to germinate and initially establish within the forest floor of unburned stands, but seedlings remain small or eventually die in dense shade (Dey, 2014). While frequent surface fire is understood to be important to the regeneration of both species, the resprouting responses observed in our study suggest some important differences between shortleaf pine and oaks that may affect regeneration outcomes with frequent fire regimes (Fig. 5).

For both shortleaf pine and oaks, resprouting provided a mechanism for **persistence** of seedlings that experience frequent fire. Given the low mortality rates in our study, we found no evidence that the probability for persistence following a single burn differed between species types, suggesting that the existing seedling population for both shortleaf pine and oaks remain viable as advance reproduction following prescribed burning. Individual oak advance reproduction has been documented at 50 years-old or older (Dee et al., 2022; Gross et al., 2024), but more research is needed to determine how long shortleaf pine can persist or how many times it can resprout with repeated burning. However, recruitment would not occur if prescribed burning occurred with a fire-return interval too frequent to allow seedlings to grow to the size that allows resistance to top-kill (Knapp et al., 2022) (Fig. 5). In such cases, very frequent burning may be used to maintain open woodland structure, create desired wildlife habitat, enhance understory plant communities, or as site preparation to develop advance reproduction, but a longer fire-free interval would be needed to recruit new shortleaf pine or oak trees.

Past studies have recommended frequent prescribed burning followed by a fire-free period for regeneration of shortleaf pine (Stambaugh et al., 2007; Kabrick et al., 2015) and oak species (Arthur et al., 2012). In situations for which both shortleaf pine and oak stems are top-killed, our results show very consistently that oak sprouts grow faster than shortleaf pine sprouts in their first year, favoring oak regeneration due to competition. We expect this pattern to occur reliably due to differences in resprouting behavior, with shortleaf pine allocating growth to numerous sprouts and oaks allocating greater growth rates to

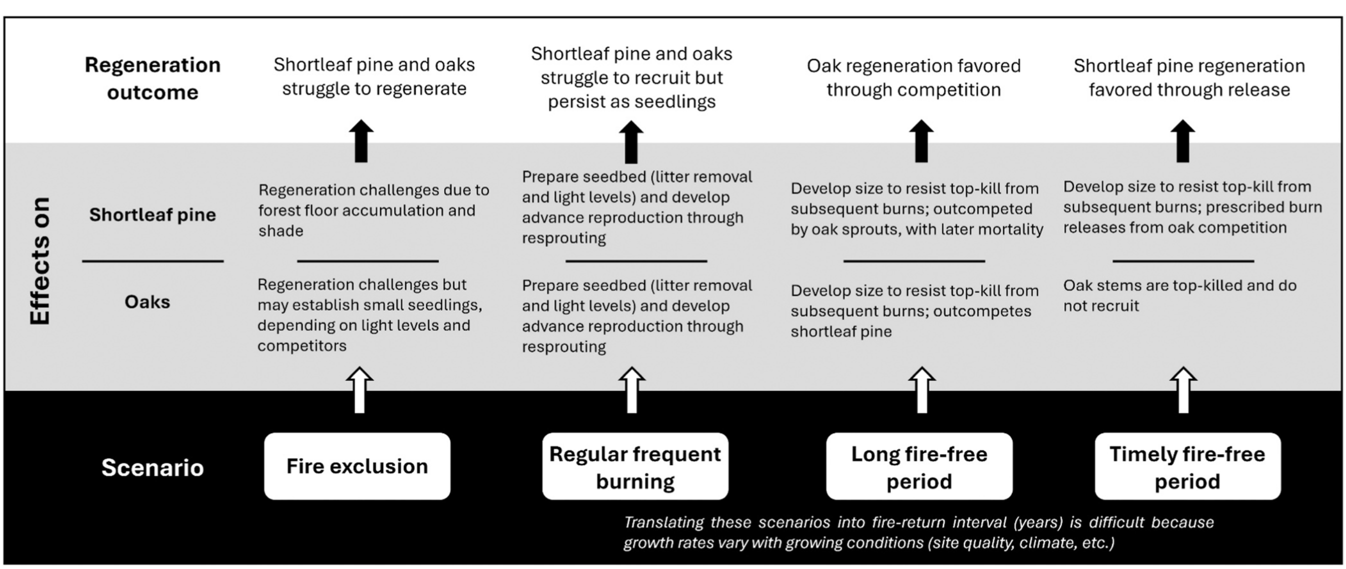

Fig. 5. Conceptualization of the effects of alternative fire return intervals on shortleaf pine and oak regeneration based on resprouting responses observed in our study.

fewer sprouts. Therefore, providing a fire-free interval that is long enough for oak stems to become resistant to top-kill would likely result in oaks outcompeting shortleaf pine during subsequent stand development. Arthur et al. (2012) recommended fire-free intervals of 10–30 years to allow recruitment of oaks. In contrast, Stambaugh et al. (2007) recommended fire-free intervals of 8–15 years for shortleaf pine recruitment.

Our results show that shortleaf pine became resistant to top-kill at a smaller stem diameter than neighboring oaks, providing a mechanism for prescribed burning to **release** shortleaf pine while top-killing oaks. These results suggest that there is an optimal fire-free interval to favor the recruitment of shortleaf pine (Fig. 5) and support the shorter fire-free interval recommended for shortleaf pine than for oaks in previous studies (Stambaugh et al., 2007; Arthur et al., 2012; Kabrick et al., 2015). However, the specific number of years needed to reach the size for fire resistance will vary with conditions that affect growth rates, such as site quality, growing season length, climate or weather conditions, and stand structure. Specific factors that can affect the early growth of shortleaf pine include soil properties, slope, precipitation (Shoulders and Walker, 1979) and overstory density (Kabrick et al., 2011). Stock type (Gwaze et al., 2006), timing, and storage (Hallgren and Tauer, 1989) can also affect the growth of planted shortleaf seedlings. While Stambaugh et al. (2007) recommended at least an 8-year fire-free period in a study from Missouri, Clabo and Clatterbuck (2019) reported that 3-year-old shortleaf pine seedlings survived fire without top-kill. Because of the variation in growth rates, a diameter threshold, rather than seedling age, time-since-planting, or universal fire-free interval, is a more reliable and transferable measure for predicting a seedling's ability to survive a burn. Our results showing that greater fire intensity magnified the difference in threshold size between shortleaf pine and oaks suggest that burning under conditions that increase fire intensity may offer greater flexibility for favoring shortleaf pine, especially with a longer fire-free period that would result in oaks of larger size.

While our study provides novel information on resprouting dynamics of shortleaf pine and oak species, inference from our results and implications for regeneration dynamics are limited by the constraints of our study. We report on results after only one growing season after burning but cannot assess long-term effects of repeated burning. Over long time periods of repeated burning, the likelihood of individual stems avoiding top-kill may increase due to local spatial variation in fire behavior (Hoffmann et al., 2020), allowing gradual recruitment to occur and accumulate through time. In a study from Florida, Robertson et al. (2021) found that prescribed burning at 1–2 year intervals for over 50 years increased shortleaf pine dominance, including in small diameter classes. Our study was also limited to dormant season burns, and effects of burning in other seasons on shortleaf pine-oak dynamics are not well understood. Previous studies have found growing season burns to increase mortality of hardwood regeneration (Glitzenstein et al., 1995; Brose and Van Lear, 1998), but results have been inconsistent for effects of fire season on shortleaf pine seedling survival. Cain and Shelton (2000) reported complete mortality of 1-year-old planted shortleaf pine after a summer burn in Arkansas, while Clabo and Clatterbuck (2019) reported little difference in burn season (November, April or July) on mortality of 1- to 3-year-old planted shortleaf pine seedlings in Tennessee.

6. Conclusion

Our study reveals differences in resprouting of shortleaf pine and oaks following prescribed burning that suggest different regeneration strategies between the species. Both shortleaf pine and oaks resprout vigorously, providing a mechanism of persistence with a frequent surface fire regime. Rapid shoot growth following resprouting provide oaks with a competitive advantage in fire-free periods; however, a larger threshold stem diameter is required for oaks to resist top-kill from subsequent fire than shortleaf pine. Thus, relatively long fire-free intervals would favor oak regeneration. Properly timed, shorter fire-free intervals would allow shortleaf pine but not oaks to reach the threshold size to resist top-kill from subsequent fires, effectively facilitating a release of shortleaf pine from competition. Additional research on other details of prescribed fire effects (e.g., fire seasonality, multiple burns, etc.) on shortleaf pine and oak regeneration would further refine management prescriptions and provide region- or site-specific guidance on appropriate prescribed burn intervals for reaching alternative objectives.

CRediT authorship contribution statement

Hope Fillingim: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Benjamin O. Knapp:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **John M. Kabrick:** Writing – review & editing, Methodology, Investigation. **Michael C. Stambaugh:** Writing – review & editing, Investigation. **Grant P. Elliott:** Writing – review & editing. **Daniel C. Dey:** Writing – review & editing, Investigation.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Benjamin Knapp reports financial support was provided by USDA Forest Service Northern Research Station. If there are other authors, they 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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Data availability

Data will be made available on request.

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