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Response of advance reproduction of oaks and associated species to repeated prescribed fires in upland oak-hickory forests, Missouri

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ABSTRACT

The Chilton Creek prescribed burn project was initiated in 1996 by The Nature Conservancy (TNC) to restore native oak woodlands and test the effect of frequent, low intensity surface fires conducted in the dormant season (March–April) on upland oak-hickory forests in the Ozarks of Missouri. Burning treatments on five sites totaling 1000 ha were initiated in 1998. The prescribed burn treatments included: annual burns (one site was burned annually) and periodic burns (four sites were burned with a mean fire return interval of approximately 4 years). Approximately 3000 stems of advance reproduction with basal diameters $\leqslant$15.0 cm were measured in 1997 (pre-burn), and remeasured in 1998, 2001 and 2007 as the prescribed burn treatments proceeded. Mortality and changes in average and aggregate total height between 1997 and 2007 were analyzed for fourteen selected tree species.

Over a ten-year period prescribed burning reduced stem density, mean height and aggregate height by 57%, 36% and 67%, respectively. However, individual tree species responded differently to the repeated burns. Oaks exhibited moderate mortality (36–54%) compared to hickories, sassafras and winged elm, all of which experienced relatively low mortality (18–35%). Flowering dogwood, shortleaf pine, blackgum and other minor species incurred higher mortality (60–76%). Oaks generally had slightly lower reductions in mean height and aggregate height than associated species with the exception of shortleaf pine, but the differences were mostly non-significant. Repeated burning tended to favor the white oak species (white oak, post oak, chinkapin oak) more than the red oak species (black oak, scarlet oak), although the differences were minor. Shortleaf pine was the only species to show increases in mean height following the ten-year period of prescribed burning.

Effects of repeated burns on mortality of advance reproduction changed with stem size (e.g., basal diameter, total height). A logistic model quantified mortality changes as a function of the ratio between total stem height and the square of stem basal diameter. Based on this model, fourteen species were classified into four groups characterized by model intercept and slope: group 1: high intercept and high slope (shortleaf pine, flowering dogwood); group 2: high intercept and low slope (blackgum, other minor species); group 3: low intercept and low slope (sassafras, winged elm, black and pignut hickories); and group 4: low intercept and high slope (oaks, mockernut hickory). Species in groups 3 and 4 are more resistant to repeated fires than those in groups 1 and 2 as indicated by their lower mortality, particularly for stems with larger basal diameters. Among species in groups 3 and 4, oaks will likely be favored over the long term because of their conservative reproduction strategies as suggested by the significance of the regression coefficients for slope. If large advance reproduction is present, shortleaf pine will likely survive repeated low intensity fires and maintain its height and competitive position due to its ability to avoid shoot dieback.

1. Introduction

The widespread mature oak (*Quercus* L.)-dominated forests in the Ozark Highlands of Missouri and Arkansas, as elsewhere in the eastern United States, are generally believed to have originated during a time of varied and frequent disturbances followed by a long period (70+ years) of fire suppression (Abrams, 1992; Anderson et al., 1999). Extensive logging, woods burning, grazing, farming, and other natural and anthropogenic disturbances were common at the turn of the twentieth century. Historically, the Ozark Highlands of Missouri had been dominated by a forest-woodland-savanna-glade mosaic, involving a mix of cover types maintained by frequent, primarily human-caused fires (Guyette

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and Cutter, 1991; Cutter and Guyette, 1994; Nigh and Schroeder, 2002; Nelson, 2005). However, fire suppression and the widespread use of high-grade cutting or selection harvesting of the forest overstory have resulted in large, contiguous blocks of high-density mature oak-hickory (*Quercus-Carya*) forests. These dense forests periodically experience health problems such as oak decline and mortality, and failure of oak reproduction. Also, shifts in species composition often occur when forests are regenerated (Johnson et al., 2009).

Advance reproduction is composed of the seedlings or saplings present in the understory of a mature forest, and is a dominant mode of regeneration for oaks and other hardwoods in the Ozark Highlands and other forest regions in Eastern North America (Johnson et al., 2009). The ability to persist in the understory by vegetative sprouting following disturbances or stresses causing shoot mortality is species dependent. Development of adequate levels of large advance reproduction is a key to successful oak regeneration. In many forest stands the presence of oak advance reproduction is insufficient to sustain current levels of oak stocking in the future overstory.

Currently, the application of prescribed fire is increasing in oak forest management in Eastern North America (Johnson, 1974; Barnes and Van Lear, 1998; Signell et al., 2005; Alexander et al., 2008; Iverson et al., 2008). Most oaks are considered early- to mid-successional species, and many mature oak-dominated forests are being successionally replaced by more shade-tolerant species (Abrams, 1992; Lorimer, 1993; Johnson et al., 2009). Oak seedlings and saplings currently account for less than 20% of all advance reproduction in oak-hickory forests of the Missouri Ozark Highlands, even though oak is considered to be better adapted to climate and site factors than most associated species (Yao, 2010). Failures of oak regeneration in the Missouri Ozark Highlands are believed to be related to long-term fire suppression (Hartman and Heumann, 2003), increasing forest overstory density (Larsen et al., 1997), and selective cutting of timber which retains high levels of overstory stocking. Studies have shown that fire can improve the competitive status of oak seedlings by reducing competition from more fire sensitive species, and by creating more favorable seedbed conditions for oak seedling establishment, i.e., reducing overly thick litter layers (Hutchinson et al., 2005; Iverson et al., 2008). The reported benefits of fire to oak regeneration have been mixed where oak seedlings are small in size and the regeneration of a competing species such as red maple (*Acer rubrum* L.) is abundant. Alexander et al. (2008) and Green et al. (2010) have shown that multiple and frequent low intensity fires reduce red maple seedling densities but survivors grow faster than the oak in the low light of a forest understory. The fires in these studies also caused moderate to high mortality in small oak seedlings depending on the species. Hutchinson et al. (2005) concluded that up to four frequent prescribed fires did not improve oak regeneration consistently in mixed-oak forests in Ohio.

The use of prescribed fire in combination with appropriate timber management practices to sustain oak by promoting the accumulation of large oak advance reproduction is a preferred approach to reversing successional trends towards oak's competitors. However, our knowledge of long-term effects of fire on oak forest regeneration, in particular advance reproduction, is limited (Hutchinson et al., 2005). Few studies of forest responses to fire have been carried out in the western portions of the eastern deciduous forests of North America (Dey and Hartman, 2005). In 1996, the Nature Conservancy initiated the Chilton Creek Prescribed Burning Project (CCPBP) to understand the effects of different fire regimes on forest structure and composition with an overall goal of promoting the diversity of native species and restoring oak woodlands in the Ozark Highlands. This project provided a good opportunity to study the response of advance reproduction to repeated prescribed fires in the Ozark forests. Specifically, our study compares the effects of annual and periodic burning conducted at low intensities on survival and growth of advance reproduction (Hartman and Heumann, 2003). Dey and Hartman (2005) previously evaluated the short-term (1998–2001) effects of fire on advance reproduction using the CCPBP data, and developed species-specific logistic regression models for estimating tree survival probability based on initial tree size and burning frequency. They found that the probability of surviving a single fire was significantly related to initial stem basal diameter and height. What is unclear, however, is whether these parameters are still significantly correlated with tree mortality following a longer-term sequence of prescribed burning treatments.

The primary objective of this study was to evaluate the response of advance reproduction of major tree species following 10 years (1998–2007) of prescribed burning. Specifically, our goals were to: (1) test whether individual species responded differently to prescribed fire in terms of mortality and height development; and (2) develop species-specific logistic models to estimate mortality as a function of initial stem size, and compare differences among species following repeated prescribed fires.

2. Materials and methods

2.1. Study site

The CCPBP was conducted on a 1000 ha site located along the Current River in Shannon and Carter counties, Missouri (Fig. 1). The study site is in the Current-Black River Breaks land type association with narrow ridges and steep sideslopes (Nigh and Schroeder, 2002). Local relief ranges from 90 to 140 m. Valleys are narrow and sinuous. Soils are loess, hillslope sediments, or gravelly alluvium (Meinert et al., 1997). Frequent, low-intensity fires with a mean fire interval of about four years prevailed in this area before extensive European settlement (Batek et al., 1999; Guyette et al., 2002; Guyette and Spetich, 2003). Currently, the area is covered predominantly by relatively continuous oak-hickory and oak-pine forests originating following large-scale timber exploitation that occurred from the 1880s to the 1930s. These forests have experienced fire suppression over the past 70+ years.

2.2. Experimental design and vegetation inventory

The CCPBP includes five prescribed burn sites (Chilton North, Chilton South, Chilton East, Kelly North, and Kelly South) of approximately 200 ha each (Fig. 1). Kelly North has been burned annually during the dormant season (March or April) while the other units have been burned on a random schedule with a mean fire return interval of 4 years (Table 1). All sites were burned in the spring of 1998 to initiate the prescribed burning experiment. Prior to burning, a total of 250 0.2-ha permanent plots were randomly allocated across the five burn sites and these plots were measured in 1998, 1999, 2001 and 2007 to study oak forest structure and compositional change as the burning treatments continue. Fire has been shown to have significantly reduced understory stem density, but had little effects on overstory (Ma, 2010) (Fig. 2). Additional details on the CCPBP's experimental design and vegetation inventory are covered by Hartman and Heumann (2003) and Dey and Hartman (2005).

To monitor the response of advance regeneration ($\leqslant$15.0 cm initial basal diameter) to the prescribed burning treatments, 26 permanent plots were randomly located throughout the five burn sites (Table 1). Individual stems of advance regeneration were sampled from within a 25.2-m radius (0.2 ha) plot around each sampling point. Each stem was permanently marked with a wire stake and

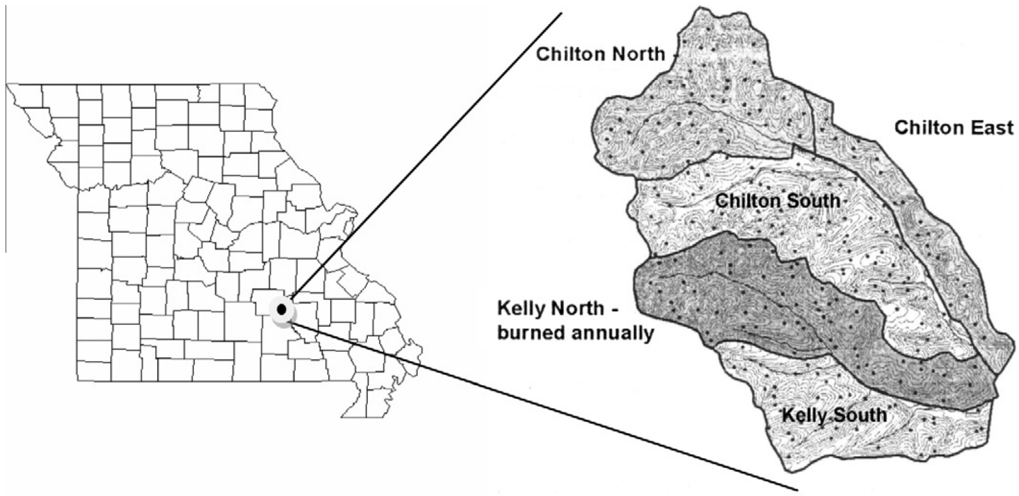

Fig. 1. Map of Chilton Creek burning sites (totaling 1000 ha) and 250 permanent vegetation monitoring plots (labeled by black dots). A subsample (n = 26) of these permanent plots were used in this study.

Table 1
Burning schedule and stems of advance reproduction sampled in the five burning sites at Chilton Creek.

Burning sites	Aspect	Slope (%)	Number of plots	Number of stems	Year of burns
Kelly South	North & ridge	15 (4–28)	7	363	1998, 2000, 2001, 2004
Kelly North	South	20 (12–33)	6	542	1998–2007
Chilton South	North	22 (17–25)	7	1123	1998–2000, 2003, 2007
Chilton North	South	32 (25–36)	3	358	1998, 2002, 2004, 2007
Chilton East	South	22 (8–32)	3	355	1998, 2002, 2003, 2006

Fig. 2. A sequence of photos taken in 2006 showing (left) unburned oak-hickory forest, (center) forest in the Kelly South burn unit that has been burned four times, the last burn was in 2004, and (right) forest in Kelly North burn unit that has been burned every year since 1998.

numbered metal tag. Approximately 3000 stems of various sizes were marked within the 26 plots. Species, basal diameter 2.5 cm above the ground, total height, diameter at breast height (if existing), status (live or dead), and sprout condition (the number of sprouts and the height of the tallest sprout) was recorded or measured for each stem. Initial stem measurements were conducted in the fall of 1997, before the first burn. Stems were measured again in 1998, 1999, 2001 and 2007 as the prescribed burning treatments progressed. For this study statistical analyses of the response of advance reproduction to prescribed fire were based on the measurement of these 3000 permanently marked stems between 1997 (pre-burn) and 2007 (post-burn).

2.3. Data analysis

Oak forests in the Ozark Highlands may include a mixture of up to 50 tree species. This makes it statistically difficult to analyze fire effects on each individual species due to small sample sizes (<30 stems) for many of the tree species. Therefore, thirteen individual species (>70 stems) and one composite group consisting of minor species were selected for analysis. Mortality and changes in total height of the advance reproduction following 10 years of burning treatments were analyzed for these species (groups).

To test for treatment effects on mortality and changes in total height among tree species (groups), all stems of advance reproduc-

Table 2
Pre- and post-burn mean total height, relative change of mean and aggregative total height, and mortality by species in the study sites.*

Species	Pre-burn mean height (m) in 1997	Post-burn mean height (m) in 2007	Relative change of mean height	Relative change of aggregate height	Mean mortality in 2007 (%)
Mockernut hickory (*Carya tomentosa*)	2.28 (0.07)	0.80 (0.05)	-0.72^{bcd}	-0.65^{d}	18.92^{a}
Winged elm (*Ulmus alata*)	1.70 (0.25)	0.97 (0.12)	-0.55^{ab}	-0.43^{bcd}	22.35^{a}
Black hickory (*Carya texana*)	2.08 (0.05)	0.96 (0.14)	-0.67^{abcd}	-0.53^{cd}	27.67^{ab}
Sassafras (*Sassafras albidum*)	2.18 (0.11)	0.57 (0.01)	-0.81^{cd}	-0.73^{d}	28.37^{ab}
Pignut hickory (*Carya glabra*)	3.25 (0.02)	1.94 (0.23)	-0.61^{abcd}	-0.40^{bcd}	34.77^{bc}
Post oak (*Quercus stellata*)	2.28 (0.07)	1.45 (0.17)	-0.59^{abc}	-0.36^{bcd}	36.13^{bc}
White oak (*Quercus alba*)	3.28 (0.18)	1.77 (0.40)	-0.67^{abcd}	-0.47^{bcd}	36.81^{bc}
Chinkapin oak (*Quercus muehlenbergii*)	1.41 (0.11)	1.25 (0.44)	-0.45^{a}	-0.14^{b}	37.74^{bc}
Black oak (*Quercus velutina*)	2.30 (0.24)	0.62 (0.11)	-0.84^{d}	-0.72^{d}	44.00^{cd}
Scarlet oak (*Quercus coccinea*)	2.16 (0.39)	1.15 (0.78)	-0.79^{bcd}	-0.52^{cd}	53.99^{de}
Blackgum (*Nyssa sylvatica*)	2.93 (0.01)	2.18 (0.46)	-0.69^{abcd}	-0.26^{bc}	59.84^{ef}
Other species	1.67 (0.19)	0.89 (0.27)	-0.79^{bcd}	-0.48^{bcd}	60.06^{ef}
Shortleaf pine (*Pinus echinata*)	3.55 (0.15)	6.25 (0.49)	-0.47^{a}	0.79^{a}	68.92^{fg}
Flowering dogwood (*Cornus florida*)	2.93 (0.14)	2.25 (0.09)	-0.82^{cd}	-0.23^{bc}	75.79^{g}

* The number in parentheses is the standard error of pre- and post-burn mean stem height. Same letters represent no significant difference among species (groups) at $p = 0.05$ based on Fisher's LSD test.

tion from the five burning sites were randomly divided into two groups with at least 30 stems of each tree species included in each group. Thus, the means and variances of mortality and changes in total height could be calculated for each individual species and tested for statistical significance. For each species, mortality ten years following initiation of the prescribed burning treatments in 1998 was calculated as the ratio of the number of live stems in 2007 to the initial number in 1997:

$$\text{Mortality}_{ij} = \frac{m_{ij}}{n_{ij}} \tag{1}$$

Relative aggregate height (*RAH*) change was calculated as:

$$RAH_{ij} = \frac{\sum_{k=1}^{m_{ij}} \text{Height}_k - \sum_{j=1}^{n_{ij}} \text{Height}_k}{\sum_{k=1}^{n_{ij}} \text{Height}_k} \tag{2}$$

Relative mean height (*RMH*) change, used to evaluate height growth differences among species, was calculated as:

$$RMH_{ij} = \frac{\frac{1}{m_{ij}} \sum_{k=1}^{m_{ij}} \text{Height}_k - \frac{1}{n_{ij}} \sum_{j=1}^{n_{ij}} \text{Height}_k}{\frac{1}{n_{ij}} \sum_{k=1}^{n_{ij}} \text{Height}_k} \tag{3}$$

where m_{ij} and n_{ij} are the stem number in 2007 (post-burn) and 1997 (pre-burn) for species i in group j ($i = 1,2,\ldots, 14$; $j = 1,2$). *RAH*, *RMH* and the arcsine square root of mortality were tested using analysis of variance (ANOVA), and Fisher's protected least significance difference (LSD) test was conducted to compare species difference at the significance level of 0.05.

A logistic regression was employed to develop mortality models for the fourteen selected species (groups) using initial stem basal diameter and total height in 1997. After testing different combinations of total height and basal diameter, a morphological variable – the ratio of total height to the square of basal diameter (*HBR*) – was found as the best estimator of the probability of mortality across most species based on the Hosmer–Lemeshow goodness-of-fit test. This test assesses whether the rate of an observed event matches the expected event rate in subgroups identified as the deciles of the fitted risk values of the model population. Models for which expected and observed event rates in subgroups are similar are deemed well-calibrated, as indicated by having larger p values (e.g., >0.05). The logistic regression model for a given tree species i was,

$$p_i = \frac{1}{1 + e^{-(\beta_{i0} + \beta_{i1} * HBR_i)}} \tag{4}$$

where HBR_i = total height/(basal diameter)^2 for species i.

3. Results

After a decade of prescribed fire, significant differences in mortality ($p < 0.0001$), relative aggregate height change ($p = 0.0186$), and relative mean height change ($p = 0.0003$) were observed among the fourteen selected species. Fisher's protected LSD test showed that oaks generally experienced levels of mortality (36–54%) that were intermediate relative to associated tree species. Pignut hickory (*Carya glabra* Mill.), black hickory (*Carya texana* Buckley), mockernut hickory (*Carya tomentosa* (Poir.) Nutt.), sassafras (*Sassafras albidum* (Nutt.) Nees) and winged elm (*Ulmus alata* Michx.) experienced relatively low mortality (19–35%), while flowering dogwood (*Cornus florida* L.), shortleaf pine (*Pinus echinata* Mill.), blackgum (*Nyssa sylvatica* Marsh.) and other minor species had the highest mortality, ranging from 60% to 76% (Table 2 and Fig. 3). Among the oaks, scarlet oak (*Quercus coccinea* Muenchh.) exhibited higher mortality than white oak (*Quercus alba* L.), post oak (*Quercus stellata* Wangenh.) and chinkapin oak (*Quercus muehlenbergii* Engelm.), although the difference between scarlet oak and black oak (*Quercus velutina* Lam.) was not statistically significant (Table 2).

Height development of flowering dogwood, black oak, scarlet oak, sassafras, and other minor species were most strongly affected by the burning treatments, with aggregate height reductions ranging from 79% to 84% (Table 2). The remainder of the species exhibited varying degrees of reduction (45–72%) in aggregate height. Chinkapin oak and shortleaf pine had the lowest reductions (45% and 47%, respectively) and were significantly different from most of the other species. Moreover, shortleaf pine was the only species in which average height of surviving stems in 2007 was greater than in 1997. For the other species, reductions in mean height ranged from 14% to 73% (Table 2).

Exploratory analyses indicated that as the number of prescribed fires increased, species, initial total stem height and stem basal diameter became increasingly important determinants of mortality and height growth, whereas burning treatment (annual burn vs. periodic burn), slope, aspect, and overstory stocking were not

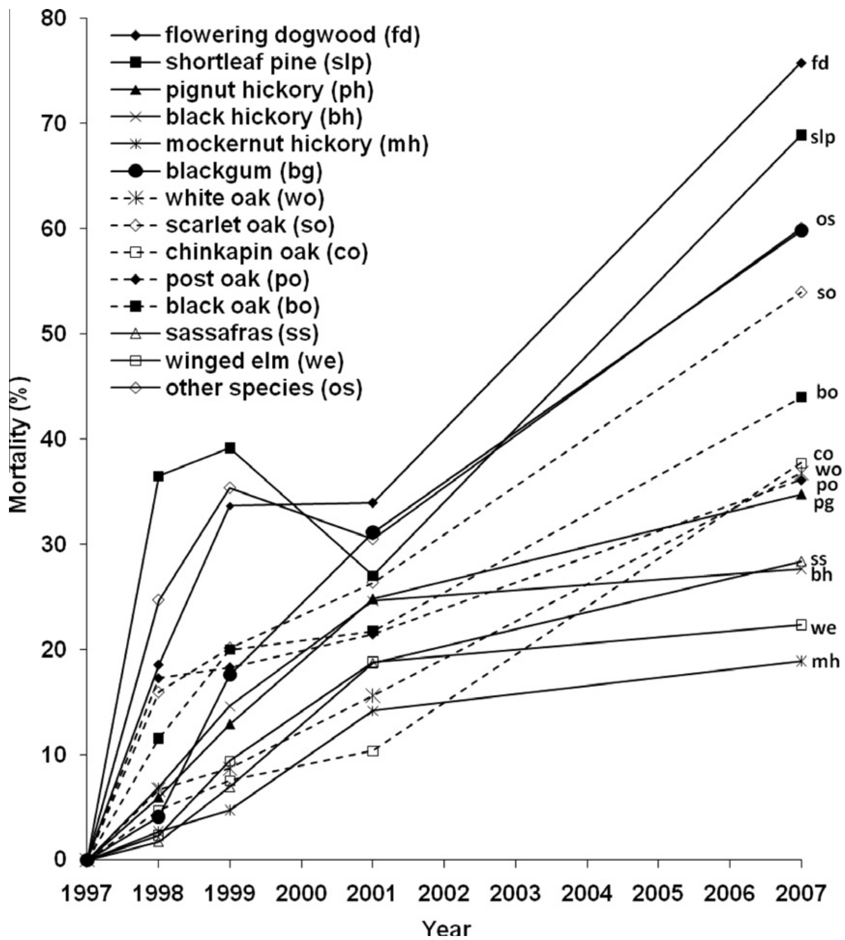

Fig. 3. Change in mortality by inventory year in Chilton creek burning sites.

Table 3
Estimated parameters (standard errors) for logistic regression of stem mortality in 2007 as a function of *HBR* by species.

Species	Number of dead/total stems	Intercept	*HBR*	*P* value*
Flowering dogwood (*Cornus florida*)	240/317	0.792 (0.161)	0.320 (0.111)	0.071
Shortleaf pine (*Pinus echinata*)	50/73	−0.041 (0.368)	2.699 (1.216)	0.333
Pignut hickory (*Carya glabra*)	105/302	−0.760 (0.148)	0.153 (0.097)	0.184
Black hickory (*Carya texana*)	36/130	−1.008 (0.268)	0.056 (0.207)	0.239
Mockernut hickory (*Carya tomentosa*)	56/295	−1.758 (0.237)	0.411 (0.235)	0.079
Blackgum (*Nyssa sylvatica*)	146/244	0.367 (0.156)	0.042 (0.085)	0.201
White oak (*Quercus alba*)	127/345	−0.725 (0.143)	0.135 (0.063)	0.044
Scarlet oak (*Quercus coccinea*)	88/163	−0.153 (0.217)	0.162 (0.081)	0.434
Chinkapin oak (*Quercus muehlenbergii*)	40/106	−1.175 (0.316)	0.348 (0.127)	0.133
Post oak (*Quercus stellata*)	69/191	−1.083 (0.210)	0.350 (0.095)	0.148
Black oak (*Quercus velutina*)	99/225	−0.888 (0.212)	0.462 (0.118)	0.003
Sassafras (*Sassafras albidum*)	82/289	−1.012 (0.163)	0.048 (0.054)	0.640
Winged elm (*Ulmus alata*)	19/85	−1.305 (0.309)	0.044 (0.120)	0.807
Other species	194/326	0.146 (0.140)	0.106 (0.040)	0.768

* The *p* values are for Hosmer and Lemeshow's goodness-of-fit tests with $p > 0.05$ representing a good fit.

statistically significant by 2007. The simple logistic regression models developed for the fourteen species using the morphological variable *HBR* adequately depicted the impact of initial stem size on mortality of advance reproduction for most species based on the Hosmer–Lemeshow goodness-of-fit test (Table 3 and Fig. 4). The test statistic indicated that 12 of the 14 models had significant fits (i.e., $p > 0.05$) (Table 3). Interestingly, for several of the major associated species such as hickories (pignut, black, mockernut), blackgum, sassafras and winged elm, the estimated coefficients for *HBR* were not statistically significant, indicating mortality was less affected by the ratio. However, for the oaks, shortleaf pine, flowering dogwood, and the minor species as a whole, the HBR ratio was a significant determinant of mortality (Table 3). For these species, *HBR* consistently performed better than initial basal diameter, total height, or a combination of both variables included in the model. In the logistic regression models, oaks, hickories, sassafras and winged elm had relatively low intercepts (<0.4) compared to shortleaf pine, flowering dogwood, blackgum and other minor species, suggesting relatively lower mortality in these species as the ratio of stem height to the square of stem basal diameter decreases.

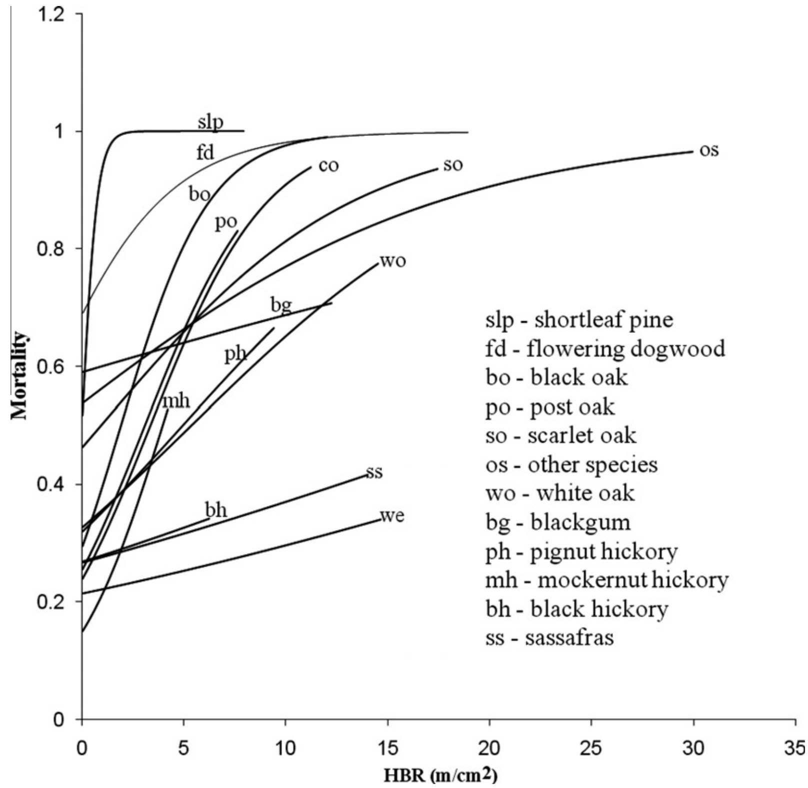

Fig. 4. Relationship between mortality and the ratio of total stem height to the squared stem basal diameter (*HBR*) by species following a ten-year period of burning treatments.

Except for shortleaf pine, the slope of the logistic curves for oaks was steeper than for other associate species, suggesting that oak mortality was more strongly affected by the HBR ratio.

4. Discussion

Dey and Hartman (2005) reported survival probabilities for major oaks and several competitor species following one to four burns (1998–2001) on the study site. They used a logistic regression to quantify the relationship between survival probability and initial basal diameter, initial height, and number of burns by species. As the burning treatments have continued, however, the number of burns has had only a marginal effect, statistically, on mortality and was therefore not included in the logistic regression model used in this analysis covering a ten-year period. The lack of significance for number of burns may be due, in part, to the fact that all treatment sites except for Kelly North, the annually burned site, have had a similar number of burns (Table 1). By 2007, of the four periodically burned sites, three (Chilton North, Chilton East, Kelly South) had been burned four times and one (Chilton South) had been burned five times (Table 1). Over time, as the prescribed burning sequence continues, the number of burns on each of these sites will approach the goal of a four-year fire return interval and thus the treatment effects would be expected to become more similar. Also contributing to the limited influence of number of burns is that repeated burning has greatly reduced fuel loading, leaving the sites with relatively low fuel loads, which subsequently result in low fire intensity (Hartman and Heumann, 2003). Finally, the more vulnerable of the larger stems of advance reproduction have been eliminated along with the smaller- sized seedlings that had low potential to resprout and build root reserves during the fire-free intervals. Advance reproduction in this study was growing under a moderate to high density overstory (>16 m^2/ha of basal area on average), which limits the amount of light reaching the forest floor and the ability of seedlings, especially those of low shade tolerance, to produce new biomass between fires. Similarly, Alexander et al. (2008) found that most of the mortality in small (basal diameter <8 mm; total height <75 cm) oak seedlings occurred after a single low intensity spring fire in eastern Kentucky oak-hickory forests; and that two additional fires over the following three years only increased mortality slightly in red (black oak, northern red (*Q. rubra* L.), and scarlet oak) and white (white oak, chestnut oak (*Q. prinus* L.), and chinkapin oak (*Q. muehlenbergii* Engelm.) oak groups. Both Alexander et al. (2008) and Green et al. (2010) found higher mortality in white oak group species (35–60%) than red oak group species (15–25%) after two to three frequent fires. We found the opposite result in this study; red oak species' mortality was nominally higher (54% for scarlet oak, 44% for black oak) than white oak species (36–38% for white, post, and chinkapin oak) after as many as 10 annual burns. The trees in our study included a much broader range in stem diameters and tree heights than the Kentucky fire studies.

Considering the high correlation between basal diameter and total height, the morphological variable *HBR* was employed to evaluate the impact of initial stem size on mortality under repeated burn treatments. This variable was found to be significantly related to tree mortality rate and resulted in better model fits for most species than attained with models that included initial basal diameter, total height, and their interactions for most of the species (Table 3). *HBR* is a synthetic parameter derived by combining total height and basal diameter. Basal diameter has been shown to be highly correlated with the size of root systems, especially in oak species (Canadell and Roda, 1991; Dey and Parker, 1997), and thus *HBR* essentially represents the allocation of biomass/carbohydrate between above- and below-ground tree components (high *HBR*

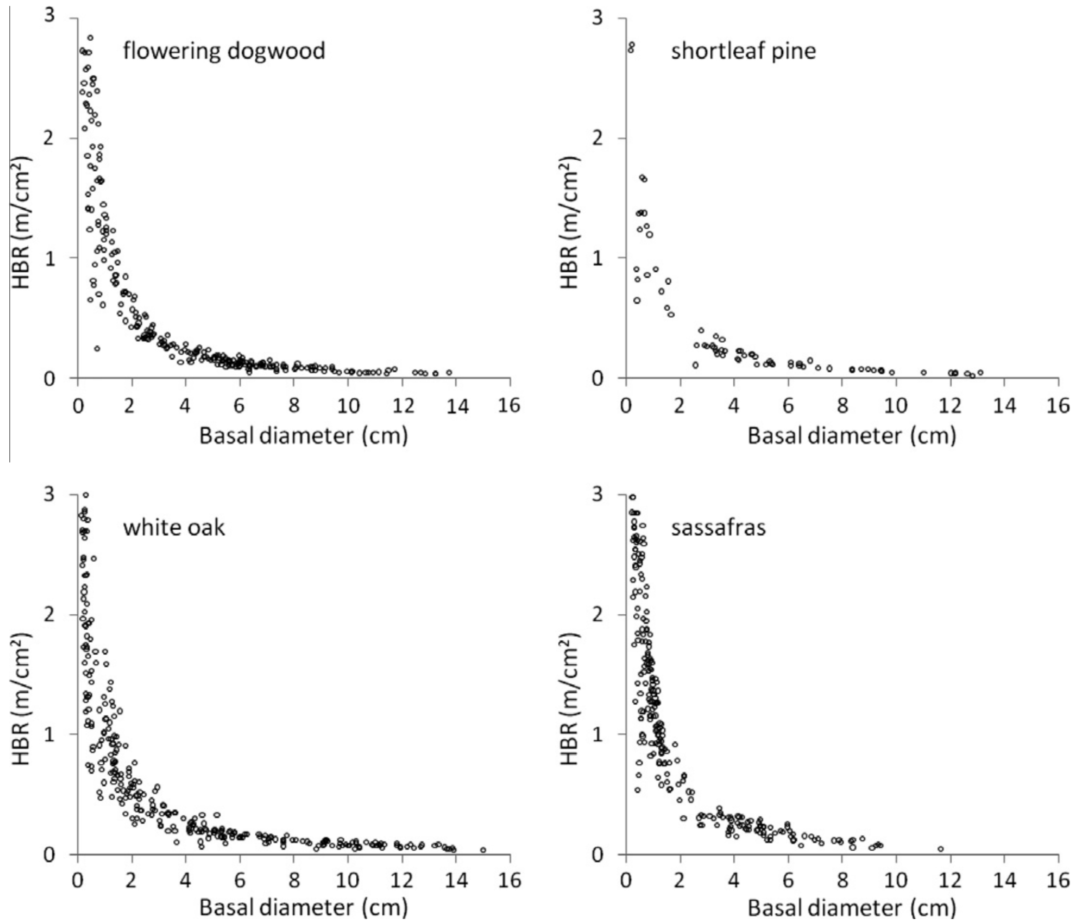

Fig. 5. Relationship between the ratio of total height to the squared basal diameter (*HBR*) and basal diameter for four selected species. The data points with *HBR* > 3 (around the 90% quantile of *HBR*) were not plotted so as to clearly show the inflection point of the change of *HBR* with basal diameter.

indicating lower relative belowground allocation, or vice versa). To gain a greater intuitive understanding of this parameter, its correlation with stem basal diameter was plotted using the data from this study. Regardless of species, there appears to be a threshold value of basal diameter (approximately 3 cm) that marks a change in the rate that *HBR* decreases with increases in basal diameter. When basal diameter is smaller than 3 cm, *HBR* tends to be relatively large and decreases dramatically with increases in basal diameter. Once basal diameter exceeds 3 cm, *HBR* decreases at a much slower rate with the change, eventually approaching zero with further increases in basal diameter (Fig. 5). High *HBR* values are associated with trees having smaller basal diameters, while near-zero *HBR* values occur when basal diameters exceed approximately 13 cm.

The logistic regression models developed using *HBR* adequately quantified the impact of initial stem size on the mortality of advance regeneration for most of the species examined (Table 3 and Fig. 4). Thus, the resultant logistic regression models could be used to predict the mortality of existing advance reproduction prior to the application of multiple fires. Upon examining the models, we tentatively classified the species into four groups based on their relative slopes and intercepts in the logistic models (Fig. 4). These groupings were group 1: species with low intercepts and low slopes representative of black and pignut hickories, sassafras and winged elm; group 2: species with low intercepts and high slopes typical of various oaks and mockernut hickory; group 3: species with high intercepts and slopes such as shortleaf pine and flowering dogwood; and group 4: species with high intercepts but low slopes such as blackgum and other minor species as a whole.

These groupings may represent different functional strategies for tolerating (e.g., vegetative sprouting in species such as oaks, hickories, sassafras and winged elm) or avoiding (e.g., thick bark in species such as shortleaf pine) fire mortality; or indicate a lack of ability to persist in environments of multiple and frequent fires, i.e., the most fire sensitive and inherently vulnerable species such as flowering dogwood (Dey and Jensen, 2002). As illustrated in Fig. 4, the intercept values represent mortality rates of trees with relatively large basal diameters where *HBR* approaches zero. The slopes reflect the change in fire-induced mortality rates with increasing *HBR* (i.e., decreased basal diameter). Species with low slopes and low intercepts, such as hickories, are more resistant to fire-induced mortality, whereas species with high slopes and high intercepts, such as shortleaf pine, are vulnerable to fire (Fig. 4). Most oak species have low intercepts and relatively high slopes indicating that oaks with larger basal diameter will have lower mortality rates but advance reproduction in the smaller size classes is moderately sensitive to fire-induced mortality.

Oaks have a conservative and effective strategy to persisting in a frequent fire environment. They preferentially allocate biomass to their root systems (Dey and Jensen, 2002; Johnson et al., 2009), which does two things: (1) the belowground plant tissues are insulated from the fire's heat and thus more likely to survive the fire, and (2) the belowground carbohydrate stores provide energy to fuel rapid growth of new vegetative shoots following top-kill. Oak seedlings and saplings, particularly those with larger root systems, have an inherent ability to produce sprouts after death of the shoot, which again helps explain why the *HBR* was statistically significant for all oak species in the logistic models. The opposite might be true for species where *HBR* was not significant (Table 3). Flowering dogwood, blackgum, and other minor species have high intercepts but low slopes indicating that these species would have higher mortality rates even for the trees with relatively larger diameters.

Advance reproduction of oaks and hickories were relatively favored by repeated, low-intensity surface fires compared to dogwood, shortleaf pine, blackgum and the other species group, indicating they would be more likely to persist under the forest canopy where fires occur frequently such as in woodland restoration projects, or in regeneration prescriptions designed to increase oak regeneration potential (Fig. 3). Ensuring adequate light at the forest floor by mechanical reduction of overstory density in combination with prescribed burning would also favor the growth of oak and increase its probability of surviving future fires.

Aggregate height, which is a composite measure of regeneration abundance and height development that factors in both mortality and height growth (Fei and Steiner, 2008), was another variable used to compare species response to fire. Although shortleaf pine experienced relatively high mortality under repeated burning, surviving trees maintained an advantageous position over most other species due to lower rates of topkill as illustrated by its significantly higher relative change in mean height (Table 2). By 2007, repeated fires had killed two-thirds of the shortleaf pine advance reproduction on the study sites, but the mean height of surviving stems was over 6 m, nearly double the pre-burn mean height.

Shortleaf pine has several traits that give it the ability to survive fire at certain life stages. Sprouting from the base following top-kill, a trait commonly regarded as an adaptation to fire, was observed in shortleaf pine (Fig. 3). New pine germinants have little ability to sprout after even a low intensity fire. But with increasing age and size, pine seedlings commonly sprout after being top killed by fire. Also, Shortleaf pine typically develops thick bark early in its development (seedlings and saplings), which provides resistance to frequent low intensity ground fire (Guldin, 1986). Shortleaf pine has been classified as both a fire resilient species (McCune, 1988) and a fire resistant or adapted species (e.g., Lawson, 1990). However, any factor slowing the growth of shortleaf pine, such as overstory shade, delays the development of its fire adapted traits and reduces its probability of survival.

A closer examination of the fate of individual shortleaf pines in 1998, 1999, 2001 and 2007 revealed that nearly 20% of surviving stems had larger pre-treatment basal diameters (4–13 cm) and no visible damage from the fires. However, post-treatment stems of deciduous species consisted predominantly of sprouts as the tops were killed or partially damaged by fire. Roughly 26% of shortleaf pine stems (mainly in the small basal diameter classes) were permanently killed after the first burn (1998), while the percentage of stems experiencing complete mortality for most of the deciduous species was less than 10%. The average pre-burn basal diameter of shortleaf pine still alive as of the most recent inventory (2007) was 7.3 cm, which is nearly double that of shortleaf pine stems that have died since treatments began. The initial mean basal diameters of surviving shortleaf pine stems in 2007 tended to be larger than those of dead stems for any of the deciduous species, but the differences were not statistically significant. This explains why mean height of surviving shortleaf pine increased, while mean height of all other species decreased following ten-years of burning treatments.

Advance reproduction of shortleaf pine appears to have survived repeated burns through a combination of large initial basal diameter and thick bark. Therefore, our results suggest that larger advance reproduction (e.g., >4–5 cm basal diameter) must be present before commencement of burning or longer fire intervals (e.g., every 15 years according to Stambaugh et al. (2007)) would be required to regenerate shortleaf pine using repeated burns. The time required for pine to reach fire resistant sizes will be delayed by retaining a hardwood canopy as pine is intolerant of shade and requires nearly full sunlight for rapid growth (Lawson, 1990).

Repeated burns have been suggested as a means to improve the competitive status of advance oak reproduction before regeneration harvesting, particularly on good sites where competition from shade tolerant species and fast growing pioneer species such as yellow-poplar (*Liriodendron tulipifera* L.) is more intense (e.g., Sander, 1988; Van Lear and Waldrop, 1989; Waldrop et al., 1992; Van Lear and Watt, 1993). However, the benefits of fire to oaks have been found, in numerous studies, to vary depending on multiple factors including site condition (e.g., xeric vs. mesic), fuel characteristics, fire frequency and intensity, size or age of advance reproduction of both oaks and competitors, and overstory density (Moser et al., 1996; Johnson et al., 2009; Brose et al., 2006; Brose, 2008). In our study, no distinct competitive advantage for oak species was evident relative to associated species in terms of stem mortality, and changes in mean total height and aggregate total height between pre- and post-burn treatments under the prescribed burn treatments (Table 2). In neighboring unburned Missouri Ozark Forest Ecosystem Project (MOFEP) study sites, the overall proportion of advance reproduction of oak species has continually decreased from 14% to 11% due to vigorous regeneration of nonoak species and oak mortality from 1995 to 2006 (Yao, 2010). Overall mortality of advance oak reproduction averaged 19% when expressed on a ten-year basis (Yao, 2010). Compared to the unburned MOFEP sites, the prescribed burn treatments in our study increased mortality of oak advance reproduction by approximately 2–3 times over a ten-year period. However, the potential benefit of prescribed burning for oaks lies in its reducing the relative decline of oak advance reproduction by inducing greater mortality in non-oak competitors, as reported in recent studies in upland oak forests (e.g., Alexander et al., 2008; Green et al., 2010).

The Chilton Creek study area belongs to the "intrinsic oak accumulator systems" (xeric oak forests) (Johnson et al., 2009). Total overstory basal areas were around 16 m^2 ha^{-1} and stem densities (>12 cm dbh) averaged around 350 trees ha^{-1}, among which oaks accounted for approximately 80% (Ma, 2010). Ten-years of repeated surface fires reduced understory density by 50–75%, but overstory densities remained constant or increased slightly (Dey and Fan, 2009). Low light levels combined with advance regeneration of competing species with similar size and sprouting capacities have resulted in oaks as a group failing to attain clear dominance over nonoak species following repeated fires. Larsen et al. (1997) reported that, in the Missouri Ozarks, the probability of having large oak advance reproduction >0.8 m tall present decreased significantly when overstory density exceeded 14 m^2/ha. A longer period of burning treatments, if conducted during the dormant season, coupled with partial overstory removal may be needed for oaks to outcompete other species as has been shown in other studies (e.g., Waldrop et al., 1992). However, Brose and Van Lear (1998) and Brose (2010) have demonstrated in more mesic forests that even a single prescribed fire, if conducted during the growing season and at relatively high intensity, can improve the competitive status of oak regeneration after a partial harvest. It remains to be seen if this would also hold true in the Missouri Ozarks.

Among the oaks, the white oak species (i.e., white, post, and chinkapin oak) tended to outperform the red oak species (black and scarlet oak) with respect to rates of survival and height growth although the differences were marginal (Table 2 and Fig. 4). This could be related to differences in species attributes such as shade tolerance, potential growth rates, sprouting ability, etc.; but might also vary with fire regimes and the duration of the prescribed treatments (Fig. 3). A wide array of factors will need to be scrutinized when comparing species responses to fire and evaluating their relative competitive status (Huddle and Pallardy, 1996).

5. Conclusions

Ten-years of repeated burning reduced stem density of advance reproduction by 57% under fully-stocked oak-hickory forests in the Ozarks of Missouri. Reductions varied by tree species and stem size. For example, flowering dogwood and shortleaf pine stem densities were reduced by 76% and 70%, respectively, and were significantly higher than most of other species. Stem densities of blackgum and other minor species were reduced by 60%. However, 20% or less of the advance reproduction of winged elm and mockernut hickory were killed by fire. Oaks, hickories (other than mockernut hickory) and sassafras exhibited mortality rates ranging from 28 to 54%. Reductions in mean stem heights varied from 14% to 73% among deciduous species including oaks, although the differences among species were generally not statistically significant. Unlike the deciduous species, the mean height of surviving shortleaf pine increased by 80% over the ten-year period of prescribed burning treatments due to the ability of pines (e.g., >8 cm dbh) to avoid being topkilled. Repeated top-killing of sprouts as well as low light levels under the main forest canopy contributed to height reduction of deciduous species, but the thicker bark of the largest shortleaf pine advance reproduction, particularly for those in the sapling size class, reduced topkill from repeated low-intensity surface fires and contributed to the net height increase of surviving stems. When considering both mortality and height growth (i.e., aggregate height), repeated fires reduced the abundance of all species to varying degrees.

The effects on advance reproduction of periodic versus annual prescribed burns, as well as the effects of site and stand conditions, were no longer important after ten-years of prescribed burning in this study. Ten years after the initiation of burning treatments, initial stem size (basal diameter, total height) has become the most significant determinant of a species response to repeated burns. *HBR*, the ratio of stem height to the square of its basal diameter, was found to be significantly related to the rate of tree mortality for most of the species. Logistic regression models of mortality revealed species differences in response to repeated fires. Oaks, hickories, sassafras and winged elm had lower mortality and were more fire-resistant, but oak mortality was significantly related to *HBR*. Oaks employ a more conservative growth strategy by allocating more carbohydrates to the belowground root system. Flowering dogwood, shortleaf pine, blackgum and the minor species collectively were less resistant to fires and suffered higher mortality. However, it is likely that under current management approaches which consist of prescribed burning only, shortleaf pine will eventually out-compete the other species and enter into the main forest canopy due to its faster height growth which will allow it to better take advantage of canopy gaps as overstory trees die. Oaks and hickories will remain a major component of advance reproduction, but may not advance to the main canopy under conditions of high overstory stocking and frequent burning that topkills smaller diameter trees. A sufficient fire-free period is required for seedlings and saplings to recruit into the overstory.

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