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Returning fire to Ozark Highland forest ecosystems: Effects on advance regeneration

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Abstract

In mature forests of the Ozark Highlands, MO, USA, we evaluated fire effects on the survival and growth of tree seedlings and saplings (i.e., advance regeneration), and used this information to develop species-specific models that predict the probability of survival based on initial tree size and number of times burned.

A 1000 ha forest area was divided into five units that were randomly chosen to receive one, three or four dormant season surface fires during the period 1998–2001. A total of 2741 stems of advance regeneration, ranging in size up to 15 cm in basal diameter and 15 m in height, were permanently marked and measured in all the units. One and four years after initiating the burn treatments, height of survivors was measured.

Although most stems experienced shoot dieback following the first fire, survival was high (>90%) for all species as most trees produced new shoots from the living rootstock. The probability of surviving one fire was significantly related to initial stem size (basal diameter and height). With additional burning, the probability of survival increased with increasing initial tree size, and decreased as the number of burns increased. For a given initial diameter, black oak and post oak had the highest probability of survival after three or more burns (e.g., 88% for 5 cm stems), followed closely by white oak (80%), and scarlet oak (60%). For similar sized stems, flowering dogwood had low probabilities of survival (e.g., 25%), and blackgum was devastated by frequent burning (2%). Sassafras showed the greatest tolerance to burning, and more than 90% of stems survived three or more fires over a 4-year period. The probability of survival significantly decreased with increasing number of burns for most species. However, frequency of burning had less influence on the probability of survival for larger (e.g., ≥7.6 cm) diameter advance regeneration than it did for smaller stems.

One fire significantly altered the height distribution of advance regeneration, concentrating most of the stems in the smallest height class (<1 m tall). Recovery of height was slow even 4 years after a burn due to the suppression of regeneration by the overstory canopy that averaged 18 m^2/ha in basal area (69% stocking). Overall, repeated burning in the dormant season reduces understory structure and favors oak advance regeneration. Survival models can be used to plan for woodland and savanna restoration.

Keywords: Prescribed fire; Restoration; Forest regeneration; Forest structure; Oak forests; Fire ecology; Silviculture

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1. Introduction

Over the past 400 years or more, fires shaped the nature of the vegetation throughout the Ozark Highlands, United States (Ladd, 1991; Guyette and Cutter, 1991; Cutter and Guyette, 1994; Guyette et al., 2002; Guyette and Spetich, 2003). The frequency of fire differed across the Ozarks due to variations in topography and fuels, and over time because of changes in human populations and their use of fire. The net result was a mosaic of pine (*Pinus* sp.) and oak (*Quercus* sp.) savannas and woodlands, and mesic hardwood forests (Batek et al., 1999). Today, however, fire occurrence in the Ozark Highlands has been drastically reduced. For example, fires usually burn less than 20,200 ha per year throughout the 6.5 million ha Ozark Highlands in Missouri (Westin, 1992). Individual fires average less than 8 ha, and humans cause nearly all (>99%) of these fires.

Since the advent of fire suppression in the 20th century, savanna and woodland communities have developed into mature, closed-canopied forests. Tree density and stocking have increased, and vertical structure of woody species become more complex. Managers of federal and state natural resource agencies are reintroducing fire using prescribed burning to restore oak/pine savannas and woodlands, to restore glade and fen communities, to promote native biodiversity, and to return historic or *natural* disturbances to largely forested landscapes. Although managers are burning large areas (200–2800 ha) throughout the Ozark Highlands, they rely on an adaptive management approach for planning the fire regime because their ability to predict forest response to prescribed burning is limited. Managers need knowledge on how fire and forests interact to develop strategies for managing Ozark Highland forests, woodlands and savannas.

Much of our knowledge of fire effects on trees comes from a relatively small collection of studies throughout the eastern United States (Table 1). Probably the longest term fire study in North America is known as the Santee Fire Study located in the southeastern Lower Coastal Plain of South Carolina where forests have been treated by annual, biennial, or periodic prescribed winter or summer fires for 40 years (Waldrop and Lloyd, 1991). Most other fire research has evaluated a narrower range of fire treatments, and reported results often after only a single burn. Much of this research on forest responses to fire has been done in hardwood forests of the Northeast, mid-Atlantic and Southeast United States. Fewer studies have been done in the western areas of the eastern deciduous forest region of North America. Overall, results from these studies have been qualitative, descriptive, or presented in a way that limits their usefulness for modeling tree response to fire. Based on these studies we can generalize about fire effects on trees, but reliably

Table 1
Key research studies that report fire effects on hardwood regeneration and forests in the eastern United States

Fire study	Forest type	Region
Paulsell (1957)	Oak-hickory	Missouri Ozark Highland
Ferguson (1957)	Pine-hardwood	Eastern Texas
Swan (1970)	Oak-northern hardwood	South central New York state
Niering et al. (1970)	Oak-mixed hardwood	Southern New England
Shearin et al. (1972)	Mixed pine-hardwood	Upper Piedmont South Carolina
Little (1974)	Temperate forests	Northeast U.S.
Thor and Nichols (1974)	Oak-mixed hardwood	Highland Rim Tennessee
Johnson (1974)	Oak-northern hardwood	Southwestern Wisconsin
Barden and Woods (1976)	Pine-hardwood	Southern Appalachians
Teuke and Van Lear (1982)	Mixed pine-hardwood	Southern Appalachians
Harmon (1984)	Mixed hardwood	Southern Appalachians
Wendell and Smith (1986)	Oak-hickory	Central Appalachians
Reich et al. (1990)	Mixed oak	Central Wisconsin
Waldrop and Lloyd (1991)	Loblolly pine	Lower Coastal Plain South Carolina
Kruger and Reich (1997)	Oak-mesic hardwood	Southwestern Wisconsin
Brose and Van Lear (1998)	Oak-mixed hardwood	Piedmont central Virginia
Barnes and Van Lear (1998)	Oak-mixed hardwood	Upper Piedmont South Carolina

predicting forest responses to fire for specific forest types or ecoregions is problematic.

In the Ozark Highlands, we have monitored the response of forests to a set of fire treatments that differ primarily in the frequency of burning. In this paper we present the response of tree advance regeneration (as defined by Helms, 1998) after 4 years of implementing the prescribed fire treatments. Our specific objectives were to: (1) develop species-specific probability of survival models for advance regeneration experiencing one or more fires; and (2) to gain a better understanding of how fire frequency effects understory forest structure. The importance of this work is that the models can be used by managers to develop woodland and savanna restoration prescriptions that include the use of prescribed fire to control forest structure and species composition.

2. Methods

The Chilton Creek Preserve is a 2289 ha site located along the Current River in Shannon and Carter Counties, Missouri (T 28 N, R 1 W). The site lies within the Current River Hills subsection of the Ozark Highlands (Keys and Carpenter, 1995), an area characterized by rugged, steeply dissected valleys and hollows, and narrow ridges (approximately 150 m relief). The area is covered in relatively continuous oak-hickory and oak-pine woodlands and mature forests growing on excessively drained cherty clay residuum. Based on an inventory of overstory trees (with dbh $\geq$ 11.4 cm) on the set ($n = 26$) of circular 0.2-ha plots, we found that basal area averaged 18 m^2/ha (range 8.7–36.6 m^2/ha) and mean stocking was 69% (range 36–120%) (according to Gingrich, 1967).

The Chilton Creek watershed was divided into five management units of approximately 200 ha each (Table 2). The burn units are similar in soils, geology and forest conditions, and unit boundaries were determined based on fire control considerations. All units were burned in the spring of 1998 to initiate the process of restoring fire. Thereafter, units were burned during the dormant season (usually in March or April) on a randomly selected 1–4 year return interval basis, with the exception of the Kelly North management unit, which was burned annually (Table 2). The range of fire treatments were based on historical fire regimes in the study area that have been documented by Guyette et al. (2002) who reported mean fire intervals of 3.6 and 4.1 years just west of Chilton Creek during the historic period 1700–1820, which predates most European settlement in the area.

We randomly located and permanently marked 26 sampling points throughout the burn units (Table 2). We selected individual stems of advance regeneration from within a 25.2-m radius of each sampling point. To the extent that stems were available for each species, we allocated the sample equally among the 26 sampling points. At each sampling point, stems were selected to represent the range of basal diameters that existed in the forest understory by species, i.e., the sample included equal proportions of stems that were small, medium and large in basal diameter. Each stem was permanently marked with wire stake and metal numbered tag, and located by azimuth and distance from the sampling point.

Initial stem measurements were done in the fall of 1997, before the first burn. We recorded species, stem basal diameter 2.5 cm above the ground, diameter breast height (dbh) and height on 2741 stems that were distributed among the five management units (Table 3). Overall, the basal diameter of all stems

Table 2
Schedule of prescribed burns conducted at Chilton Creek during the dormant season in each of the management units burn unit attributes and sample size in each unit is also presented

Burn unit	Dormant season fire				Hectares	Stems (n)	Plots (n)	Aspect	Slope (%)	
	1998	1999	2000	2001					Average	Range
Kelly South	×		×	×	163	363	7	N & Ridge	15	4–28
Kelly North	×	×	×	×	244	542	6	S	20	12–33
Chilton South	×	×	×		293	1123	7	N	22	17–25
Chilton North	×				188	358	3	S	32	25–36
Chilton East	×				103	355	3	S	22	8–32

Table 3
Pre-burn seedling and sapling mean basal diameter (BD) and mean total height (HT), and post-burn fire damage after one, three or four springtime prescribed burns

Species	Sample size	BD (cm)	HT (m)	Mortality (%)		Shoot dieback with sprouts (%)		Total damage (%)	
				1 burn	3+ burns	1 burn	3+ burns	1 burn	3+ burns
Chinkapin oak	106	1.5	1.4	8	17	76	74	84	91
Sassafras	286	2.0	2.2	0	9	79	84	79	93
White ash	65	2.3	2.0	20	25	61	70	81	95
Black oak	224	2.3	2.3	10	28	70	69	80	97
Scarlet oak	156	2.5	2.2	10	44	65	53	75	97
Hickory	723	3.0	2.7	3	17	94	70	97	87
Post oak	180	3.0	2.4	9	21	64	74	73	95
Blackgum	240	3.3	3.0	3	50	49	38	52	88
White oak	346	3.5	3.3	5	22	52	63	57	85
Flowering dogwood	316	3.6	3.1	19	52	36	38	55	90
Blackjack oak	56	4.3	2.9	4	41	80	59	84	100
Shortleaf pine	74	4.8	3.5	38	39	18	39	56	78

Mortality is complete death of the individual (i.e., root and shoot). Shoot dieback is death of the aerial portion of the tree only, i.e., the rootstock is alive. Total damage is the sum of mortality and shoot dieback.

ranged between 0.25 and 15 cm, and heights varied from 0.03 to 15 m. In the fall of 1998 and 2001, we inventoried all stems, counted the number of sprouts and measured the height of the tallest sprout for surviving trees that had experienced shoot dieback due to the fires.

Each prescribed fire event was characterized using standard measures of fire behavior, fuels, and atmospheric conditions. Fuel loading was estimated before each burn using the methods of Brown (1974) and Brown et al. (1982). Two permanent 15-m transects were installed near each of the 26 sampling points (Table 2). Fuels were inventoried 1 month before any burn. Average total fuel loads ranged from 9.6 to 13.2 mt/ha for any given burn year, and herbaceous/litter fuels accounted for much (40–60%) of the total tonnage. More detailed information on fuels in this study has been reported by Hartman (2004).

Weather conditions before each burn were recorded onsite using a belt weather kit or Kestrel 3000 weather meters. Weather during the burn was recorded at the National Park Service station located 6 km from the study area. Air temperatures during most burns were between 16 and 24 °C, winds were generally less than 7 km/h, and relative humidity ranged from 33 to 44%.

During each burn, we estimated flame length, rate-of-spread and flaming front temperature. Flame length was measured with passive flame height sensor arrays. We installed one array at each of the main sampling points in units to be burned. The array consisted of 20 lengths of cotton string soaked in flame retardant that were suspended from wires positioned 3 m above the fuel bed. Visual measurements of flame angles were used to convert flame height to flame length according to Ryan (1981) and Finney and Martin (1992). Visual estimates of flame lengths were also made during the burns by observers. Flame lengths were highly variable but often were in the range of 0.3–0.9 m.

Rate-of-spread was determined by: (1) direct observation of the fire on three sampling points of those being burned using a stopwatch to time the movement of the flaming front over a known distance; and (2) on all main sampling points scheduled for burning by using arrays (nine per sampling point) of modified clock assemblies that were buried in the soil along a transect (Grabner, 1996). Rates-of-spread were also variable but the fire front usually moved at a rate of 59–317 m/h. Fire temperature along the flame front was measured using temperature sensitive paints applied to aluminum tags that were suspended from nine gauge steel rods (Cole et al., 1992). Tags were hung at the fuel surface, and at 0.3 and 0.6 m heights above the fuel surface on each rod. Nine rods were installed about each of the main sampling points in burn units. Temperatures were highest at the fuel surface (ground level), reaching 121–316 °C.

For each species, we used logistic regression (Allison, 1999) to model the probability of survival in

1998 (after one burn) based on initial basal diameter, initial height, and the interaction between basal diameter and height. Similarly, we modeled the probability that a stem of advance regeneration would be alive in 2001 (4 years after burn treatments were begun) based on initial stem size and number of times the regeneration was burned. All logistic regression models presented in this paper were highly significant ($\alpha = 0.05$) for the test of the global null hypothesis that all β_i are equal to zero using the likelihood ratio ($-2 \log L$) statistic (Allison, 1999).

We used an information-theoretic approach to modeling the probability of survival for advance regeneration that had experienced prescribed burning (Burnham and Anderson, 2002). The set of a priori models for each species were ranked using Akaike's Information Criterion, AIC, and were adjusted for small sample sizes (AIC_c) when necessary. AIC values were used to compute the ΔAIC and Akaike weight (w_i) for each model. These statistics (i.e., ΔAIC and w_i) were used to identify models that performed well, and for estimating the support a model had for being the best. Models with a lower ΔAIC and a greater w_i have more support for being the better models of those being compared. In all comparisons for a species, we included the null (intercept only) model. The Hosmer and Lemeshow (2000) goodness-of-fit test was run on each model evaluated. In our analyses of fire effects on the height structure on advance regeneration, we used Chi-square analyses to test if pre- and post-burn height distributions were significantly different for all oak species combined and for flowering dogwood. Significance was determined at the $\alpha = 0.05$ level.

3. Results and discussion

3.1. 1998 fire damage—after one burn

Total fire damage (sum of mortality and shoot dieback) was high (>50% of stems) for all species after one dormant season fire (Table 3). White oak (*Quercus alba* L.), blackgum (*Nyssa sylvatica* Marsh.) and shortleaf pine (*Pinus echinata* Mill.) had the lowest overall amount of fire damage. Most of the fire damage to advance regeneration occurred via death of the seedling shoot. Usually these seedlings responded by sprouting during the following summer. In general, seedlings have the greatest capacity to produce sprouts after shoot dieback from dormant season fires (i.e., before bud break and leaf out) because carbohydrate reserves in the root system are at seasonally high levels (Kozlowski et al., 1991). Summer fires cause lower rates of sprouting and increased mortality of rootstocks because, in part: (1) ambient temperatures are higher and fuel moisture lower so fires can burn with greater intensity, and hence fires are more lethal; (2) plants are physiologically more active, and thus are more sensitive to high temperatures; and (3) carbohydrate reserves in the roots are relatively low (Kozlowski et al., 1991; Whelan, 1995; DeBano et al., 1998).

After one spring fire, we observed a wide range in percent of trees that experienced shoot dieback among the species. Flowering dogwood (*Cornus florida* L.) and blackgum experienced the least amount of shoot dieback (i.e., 36–49%, respectively), whereas most (79%) sassafras (*Sassafras albidum* (Nutt.) Nees) stems died back (Table 3). The high proportion of shoot dieback is not unexpected because of the relatively small stem size, i.e., average basal diameters ranged between 1 and 5 cm depending upon species. In addition, low intensity surface fires can kill the above ground portions of most hardwood stems that are less than about 12 cm in diameter (Reich et al., 1990; Waldrop and Lloyd, 1991; Barnes and Van Lear, 1998).

In this study, the range in mortality was narrow among the hardwood species, and pine seedlings were most likely to die after one spring fire. After one spring burn, mortality was low (i.e., <5%) in hickory (Carya), blackgum, sassafras, chinkapin oak (*Quercus muehlenbergii* Engelm.), and blackjack oak (*Quercus marilandica* Muenchh.) (Table 3). Sassafras had the lowest mortality (0.3%), whereas more than one-third of shortleaf pine died. White oak, post oak (*Quercus stellata* Wangenh.), black oak (*Quercus velutina* Lam.), and scarlet oak (*Quercus coccinea* Muenchh.) experienced relatively moderate levels of mortality (i.e., 5–10%).

Ferguson (1957) reported that 15% of post oak and southern red oak (*Quercus falcata* var. *falcata* Michx.) stems (<11 cm in diameter) died after a prescribed winter surface fire in an immature southern pine stand in the Upper Coastal Plain of Texas. Also, he found that mortality of similarly sized sweetgum (*Liqui-*

dambar styraciflua L.) was 14%. Brose and Van Lear (1998) reported that burning in the winter, spring or summer after a shelterwood harvest in central Virginia caused 10–55% mortality in white oak, black oak, scarlet oak and northern red oak (*Quercus rubra* L.) regeneration. Their levels of oak mortality were higher than we observed in this study because their oak regeneration consisted mostly of smaller seedlings that were less than 3.0 m tall.

It has been widely reported that mortality is often higher for younger and smaller stems (Ferguson, 1957; Niering et al., 1970; Reich et al., 1990; Waldrop and Lloyd, 1991; Brose and Van Lear, 1998). A spring fire in a southwestern Wisconsin oak-northern hardwood stand killed 58% of all 1-year-old northern red oak seedlings (Johnson, 1974); and in southern Ontario, Dey and Parker (1996) observed 70% mortality in 1-year-old northern red oak seedlings, but only 30% mortality for seedlings that were at least 3 years old.

Others have shown that mortality of hardwood regeneration after one prescribed fire varies by species. For example, seedlings and saplings of species such as sugar maple (*Acer saccharum* March.), yellow-poplar (*Liriodendron tulipifera* L.), black

Table 4
Ranking and comparison of probability of survival models for advance regeneration one growing season after a spring burn in 1998 on the Chilton Creek Preserve

Model	White oak					Black oak					Scarlet oak				
	log *L*	*K*	AIC	ΔAIC	w_i	log *L*	*K*	AIC	ΔAIC	w_i	log *L*	*K*	AIC_c	ΔAIC_c	w_i
BD HT BDHT	107.0	4	115.1	2.4	0.14	131.0	4	139.0	0.0	0.88	[a]	[a]	[a]	[a]	[a]
BD HT	107.8	3	113.8	1.1	0.28	137.4	3	143.4	4.4	0.10	85.5	3	91.7	2.1	0.17
HT	111.8	2	115.8	3.1	0.10	145.1	2	149.1	10.1	0.00	85.5	2	89.6	0.0	0.49
BD	108.6	2	112.7	0.0	0.48	142.8	2	146.8	7.8	0.02	86.2	2	90.3	0.7	0.34
NULL	141.5	1	143.5	30.8	0.00	148.2	1	150.2	11.2	0.00	103.2	1	105.2	15.6	0.00

Model	Blackjack oak					Chinkapin oak					Post oak				
	log *L*	*K*	AIC_c	ΔAIC_c	w_i	log *L*	*K*	AIC_c	ΔAIC_c	w_i	log *L*	*K*	AIC	ΔAIC	w_i
BD HT BDHT	[a]	[a]	[a]	[a]	[a]	30.2	4	38.6	2.1	0.15	[a]	[a]	[a]	[a]	[a]
BD HT	10.4	3	16.9	2.1	0.21	30.3	3	36.5	0.0	0.43	80.8	3	86.8	1.5	0.20
HT	10.6	2	14.8	0.0	0.58	36.4	2	40.5	4.0	0.06	81.3	2	85.3	0.0	0.41
BD	13.3	2	17.5	2.7	0.15	32.9	2	37.0	0.5	0.34	81.4	2	85.4	0.1	0.39
NULL	17.2	1	19.3	4.5	0.06	40.4	1	42.4	5.9	0.02	108.0	1	110.0	24.8	0.00

Model	Hickory					Blackgum					Flowering dogwood				
	log *L*	*K*	AIC	ΔAIC	w_i	log *L*	*K*	AIC	ΔAIC	w_i	log *L*	*K*	AIC	ΔAIC	w_i
BD HT BDHT	178.5	4	186.5	3.6	0.06	41.2	4	49.2	0.0	0.62	236.0	4	244.0	0.0	0.94
BD HT	178.9	3	184.9	2.0	0.14	45.0	3	51.0	1.8	0.25	244.0	3	250.0	6.0	0.05
HT	178.2	2	182.9	0.0	0.37	48.9	2	52.9	3.7	0.10	248.0	2	252.0	8.0	0.02
BD	179.4	2	183.3	0.4	0.30	51.9	2	55.9	6.7	0.02	257.8	2	261.8	17.8	0.00
NULL	182.9	1	184.9	2.0	0.14	56.1	1	58.1	8.9	0.01	289.0	1	291.0	47.0	0.00

Model	White ash					Shortleaf pine				
	log *L*	*K*	AIC_c	ΔAIC_c	w_i	log *L*	*K*	AIC_c	ΔAIC_c	w_i
BD HT BDHT	[a]	[a]	[a]	[a]	[a]	82.1	4	90.7	4.2	0.06
BD HT	38.1	3	44.5	1.8	0.26	82.2	3	88.5	2.1	0.19
HT	41.9	2	46.1	3.4	0.11	83.9	2	88.1	1.6	0.23
BD	38.5	2	42.7	0.0	0.63	82.3	2	86.5	0.0	0.52
NULL	52.3	1	54.4	11.7	0.00	97.1	1	99.2	12.7	0.00

Number of parameters (*K*) in each model includes the intercept and each independent variable. Models with lower ΔAIC_c or ΔAIC, and greater w_i have more support for being the better models (Burnham and Anderson, 2002).

[a] Maximum likelihood estimate may not exist for this model. Validity of model fit is questionable. These models were not considered in the comparison and ranking of models.

birch (*Betula lenta* L.), and red maple (*Acer rubrum* L.) are more likely to die after a low intensity surface fire than are stems of oak and hickory species (Niering et al., 1970; Kruger and Reich, 1997; Reich et al., 1990; Brose and Van Lear, 1998). Differences in mortality among species are more dramatic in the smaller size classes of regeneration. But the consensus among researchers of fire in eastern hardwood forests is that one fire seldom causes major shifts in species composition (Johnson, 1974; McGee, 1979; Wendell and Smith, 1986; Van Lear, 1991; Van Lear and Waldrop, 1991).

In this study, initial basal diameter and height of advance regeneration were significantly ($\alpha = 0.05$)

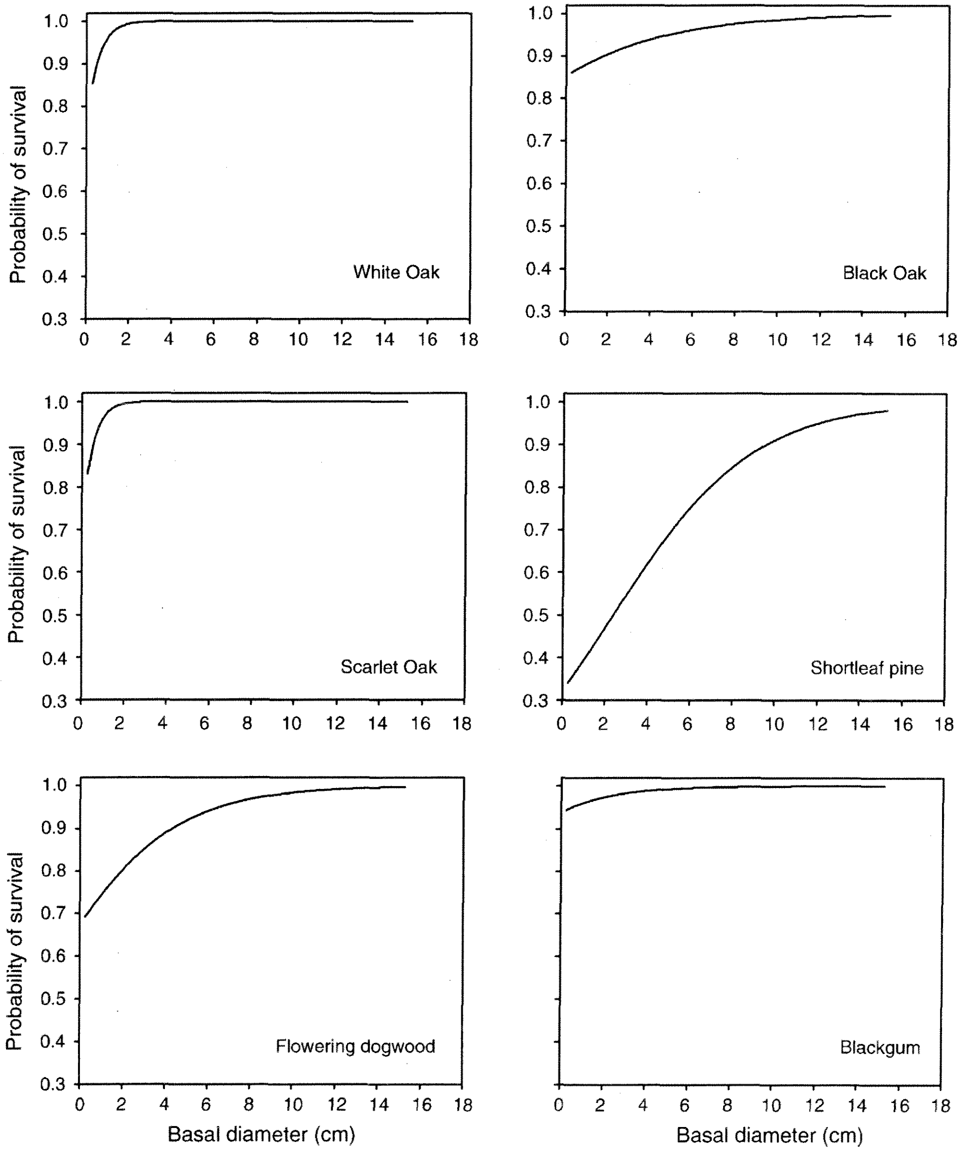

Fig. 1. The probability that advance regeneration will be alive one growing season after a dormant season prescribed fire based on the initial basal diameter and species. All logistic models shown were significant ($\alpha = 0.05$) and had at least moderate support according to the Akaike weight (w_i) in Table 4. These plots of survival probabilities are derived from equations presented in Tables 5 and 6 by species.

related to the probability of survival 1 year after a dormant season fire, regardless of species, based on logistic regression analyses. The full model used to predict the probability of survival after one burn, which included initial basal diameter and height, and their interaction, had strong support for being one of the best models for flowering dogwood ($w_i = 0.94$) and for black oak ($w_i = 0.88$) (Table 4). The full model had moderate support ($w_i = 0.62$) in explaining blackgum's response to a prescribed burn. For the other species, subset models that contained initial basal diameter, initial height or a combination of the two variables had moderate support for being in the set of best survival models (w_i varying from 0.25 to 0.63). For all species, there was no support ($w_i = 0$) for the null hypothesis model (intercept only model). The Hosmer Lemeshow (2000) goodness-of-fit test on the full model showed a good fit of the model for all species except black oak.

We found that the probability of survival increased rapidly with increasing basal diameter for most species (Fig. 1). Small diameter shortleaf pine advance regeneration had the lowest survival probabilities compared to similarly sized hardwood seedlings. The probability of surviving one spring burn was very high for advance regeneration of the oak species and blackgum, even for seedlings with small (i.e., <2 cm) basal diameters. Survival of sassafras advance regeneration was so high that we could not derive a meaningful logistic regression model. Estimates of survival probabilities based on height of advance regeneration were similar to the basal diameter models in that taller trees have higher survival probabilities among the species other than sassafras. Logistic regression parameters for the set of best survival models are presented by species in Tables 5 and 6.

In other studies, tree stem diameter has been positively correlated to survival after burning because

Table 5
1998 Survival models[a] for oak species after one spring prescribed burn (logistic regression model parameter estimates are presented with their standard errors in parenthesis)

Species models	Intercept	Basal diameter (BD)	Height (HT)	Diameter-height interaction (BDHT)
White oak				
BD	1.2657 (0.367)	0.1967 (0.074)		
BD + HT	1.1014 (0.420)	0.3646 (0.210)	−1.3544 (1.454)	
BD + HT + BDHT	1.0097 (0.433)	0.3829 (0.209)	−1.1494 (1.378)	−0.014 (0.007)
HT	1.5599 (0.315)		1.4680 (0.555)	
Post oak				
HT	0.7477 (0.481)		4.1286 (2.306)	
BD	0.6986 (0.476)	0.2603 (0.132)		
BD + HT	0.6702 (0.495)	0.0977 (0.190)	2.8309 (3.414)	
Chinkapin oak				
BD + HT	0.1871 (1.018)	1.2004 (0.620)	−4.9925 (3.111)	
BD	0.9407 (0.952)	0.4513 (0.279)		
BD + HT + BDHT	0.1171 (1.106)	1.1944 (0.622)	−4.5294 (4.260)	−0.0329 (0.201)
Black oak				
BD + HT + BDHT	1.1807 (0.324)	0.1935 (0.080)	−0.6802 (0.599)	−0.00813 (0.0034)
Scarlet oak				
HT	1.1436 (0.407)		2.7993 (1.898)	
BD	1.0312 (0.443)	0.2188 (0.131)		
BD + HT	1.1575 (0.470)	−0.0168 (0.290)	2.9915 (3.855)	
Blackjack oak				
HT	−0.1287 (1.556)		14.1243 (9.944)	
BD + HT	0.2749 (1.571)	−0.2237 (0.388)	17.1016 (12.088)	
BD	0.8925 (1.975)	0.3686 (0.484)		

[a] Where models are of the form: $P = [1 + \exp[-(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_n X_n)]]^{-1}$ and P, probability of a stem of advance regeneration being alive 1 year after a spring (dormant season) prescribed burn, the β_i are the regression coefficients and the X_i are the independent variables BD, HT, BDHT used in the model. BD, basal diameter (mm) at 2.54 cm above groundline; HT, total height (m).

Table 6
1998 survival models[a] for non-oak species after one spring prescribed burn (logistic regression model parameter estimates are presented with their standard errors in parenthesis)

Species models	Intercept	Basal diameter (BD)	Height (HT)	Diameter–height interaction (BDHT)
Flowering dogwood				
BD + HT + BDHT	0.1085 (0.238)	0.00614 (0.026)	1.0696 (0.307)	−0.00765 (0.002)
Shortleaf pine				
BD	−0.7379 (0.432)	0.0308 (0.009)		
HT	−0.7701 (0.454)		0.4169 (0.128)	
BD + HT	−0.7314 (0.454)	0.0320 (0.027)	−0.0174 (0.374)	
Hickory				
HT	3.1287 (0.296)		0.2098 (0.120)	
White ash				
BD	−0.3602 (0.747)	0.2051 (0.089)		
BD + HT	−0.4294 (0.764)	0.3103 (0.187)	−0.9491 (1.396)	
HT	0.2373 (0.618)		1.3665 (0.646)	
Blackgum				
BD + HT + BDHT	3.8195 (1.108)	−0.3881 (0.190)	1.6684 (1.416)	0.12 (0.094)
BD + HT	2.3855 (0.520)	−0.159 (0.081)	2.8455 (1.304)	

[a] Where models are of the form: $P = [1 + \exp[-(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_n X_n)]]^{-1}$ and P, probability of a stem of advance regeneration being alive 1 year after a spring (dormant season) prescribed burn, the β_i are the regression coefficients and the X_i are the independent variables BD, HT, BDHT used in the model. BD, basal diameter (mm) at 2.54 cm above groundline; HT, total height (m).

it is directly related to bark thickness and tree height, and hence to a tree's ability to resist heat injury to the cambium or to the crown (Hare, 1965; Loomis, 1973; Hengst and Dawson, 1994; Regelbrugge and Smith, 1994; Guyette and Stambaugh, 2004). Also, basal diameter has been positively correlated with size of root system (Canadell and Roda, 1991; Dey and Parker, 1997), therefore, larger diameter advance regeneration has greater energy reserves in the roots to support growth of sprouts after death of the parent shoot due to burning.

4. 2001 fire damage—after one, three or four burns

After three or four burns, total fire damage (mortality plus shoot dieback) was high for all species, and was often greater than it was after one burn (Table 3). For stems that experienced more than one burn, a higher proportion of the damage was due to mortality and less of the damage was shoot dieback. Mortality after three or more burns increased notably in scarlet oak, blackjack oak, flowering dogwood, and blackgum. For example, mortality of flowering dogwood advance regeneration increased from 19% after one fire to 52% after three fires, while mortality of blackgum increased from 3 to 50% (Table 3). Moderate increases in mortality were seen in the other species as they experienced repeated burning. Sassafras showed the greatest tolerance to frequent burning, with more than 90% of the stems surviving, even for small diameter trees (e.g., 0.25 cm).

After three or four burns, the white oak group species (white, post, chinkapin), hickory species and white ash (*Fraxinus americana* L.) had relatively low mortality (ranging from 14 to 22%), whereas half of the blackgum and flowering dogwood advance regeneration died. Black oak suffered relatively moderate levels of mortality (28%), and blackjack oak and scarlet oak were the most fire sensitive of the oak species (41–44% mortality, respectively).

Differences in mortality among oak species were reported by Paulsell (1957), who found that mortality (of stems ≥4 cm dbh) was highest for scarlet oak and southern red oak, moderate for black oak and least for post oak and hickory after eight annual spring burns in a mature Missouri Ozark Highland forest. Waldrop and Lloyd (1991) also reported differential mortality among species that were subjected to prescribed burning treatments over a period of 40 years in loblolly pine forests of the South Carolina Lower Coastal Plain. Prescribed surface fires of low intensity were set annually, biennially, or periodically (every 3–7 years) in either the winter or summer. In the annual summer fire treatment, which represented the most severe fire regime, they found that sweetgum advance regeneration was eliminated after 8 years of burning, but it took 20 years to eradicate the oak species (e.g., southern red oak, post oak, water oak (*Quercus nigra* L.) and willow oak (*Quercus phellos* L.)), at which time the hardwood understory was practically eliminated. They concluded that the oak species were among the most persistent in all burning treatments.

In general, oak and hickory seedlings and saplings are more tolerant of fire than many of their common associates such as sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), sweetgum and yellow-poplar (*Liriodendron tulipifera* L.) in forests of

Table 7
Ranking and comparison of probability of survival models for advance regeneration one growing season (Fall 2001) after different burning treatments on the Chilton Creek Preserve

Model	White oak					Black oak					Scarlet oak				
	log *L*	*K*	AIC	ΔAIC	w_i	log *L*	*K*	AIC	ΔAIC	w_i	log *L*	*K*	AIC_c	ΔAIC_c	w_i
BD HT BDHT NB	304.6	5	314.6	0.1	0.32	224.6	5	234.6	0	0.65					
BD HT NB	308.0	4	316.0	1.4	0.16						185.0	4	193.0	2.1	0.14
HT NB	310.7	3	316.7	2.1	0.12						185.0	3	191.0	0	0.40
BD NB	308.6	3	314.6	0.0	0.34						185.6	3	191.6	0.6	0.29
NB															
BD HT BDHT						229.0	4	237.0	2.3	0.20					

Model	Blackjack oak					Chinkapin oak					Post oak				
	log *L*	*K*	AIC_c	ΔAIC_c	w_i	log *L*	*K*	AIC_c	ΔAIC_c	w_i	log *L*	*K*	AIC	ΔAIC	w_i
BD HT NB						58.0	4	66.0	2.8	0.10	158.1	4	166.1	2.0	0.08
BD NB						58.5	3	64.5	1.1	0.24	158.2	3	164.2	0	0.22
HT NB						58.9	3	64.9	1.5	0.20	158.3	3	164.3	0.1	0.21
NB	65.0	2	69.0	0.8	0.36	59.5	2	63.5	0	0.42					
BD HT											160.6	3	166.6	2.4	0.07
BD	64.2	2	68.2	0	0.54						160.7	2	164.7	0.4	0.18
HT	64.4	2	68.4	0.2	0.48						160.8	2	164.8	0.5	0.17
INTERCEPT	68.8	1	70.8	2.4	0.16										

Model	Hickory					Blackgum					Flowering dogwood				
	log *L*	*K*	AIC	ΔAIC	w_i	log *L*	*K*	AIC	ΔAIC	w_i	log *L*	*K*	AIC	ΔAIC	w_i
BD HT BDHT NB	541.2	5	551.3	0	0.99	242.3	5	252.3	0	0.99	405.1	5	415.1	0	0.46
BD HT NB											408.3	4	416.3	1.14	0.26
HT NB											410.5	3	416.6	1.28	0.24

Model	White ash					Shortleaf pine				
	log *L*	*K*	AIC_c	ΔAIC_c	w_i	log *L*	*K*	AIC_c	ΔAIC_c	w_i
BD HT BDHT NB	24.7	5	34.7	0.9	0.30					
BD HT NB	27.8	4	35.8	1.67	0.20					
BD NB	28.4	3	34.4	0	0.47	95.5	3	101.5	1.87	0.14
HT NB						96.2	3	102.2	2.57	0.10
BD HT						95.8	3	101.8	2.17	0.12
BD						95.8	2	99.8	0	0.34
HT						96.3	2	100.3	0.5	0.27

Number of parameters (*K*) in each model includes the intercept and each independent variable. Models with lower ΔAIC_c or ΔAIC, and greater w_i have more support for being the better models (Burnham and Anderson, 2002). Models with $\Delta AIC > 3.0$ and $w_i < 0.06$ are not presented.

the eastern United States (Swan, 1970; Little, 1974; Reich et al., 1990; Kruger and Reich, 1997; Brose and Van Lear, 1998; Barnes and Van Lear, 1998). Although the regeneration of some species such as yellow-poplar can be reduced by several frequent fires, and the competitiveness of oak regeneration is improved by periodic burning, it takes long term and relatively frequent, if not annual, burning to effect a significant shift in tree species composition in the regeneration layer of a forest (Waldrop and Lloyd, 1991; Van Lear and Waldrop, 1991).

We found that for most species, the probability of surviving one or more dormant season burns was significantly ($p < 0.05$) related to initial basal diameter, initial height, and number of burns. The full logistic model, which included initial basal diameter and height, their interaction and the number of burns, had strong support for being the best model ($w_i = 0.99$) for blackgum and hickory, and moderate support (w_i ranging from 0.32 to 0.65) for black oak, flowering dogwood and white oak (Table 7). The model with initial basal diameter and number of burns as independent variables had moderate support (w_i varying from 0.22 to 0.47) for white ash, post oak, chinkapin oak, scarlet oak and white oak. For blackjack oak, the model with initial basal diameter ($w_i = 0.54$) or the number of burns ($w_i = 0.36$) as independent variables had the most support in predicting survival of advance regeneration. The model with number of burns as the only independent variable also had moderate support ($w_i = 0.42$) for predicting survival in chinkapin oak. Survival of sassafras advance regeneration was high enough, even after four consecutive burns (i.e., 91%), that all models tested were statistically insignificant

Table 8
2001 survival models[a] for oak species—logistic regression parameter estimates presented with their standard errors in parenthesis

Species models	Intercept	Basal diameter (BD)	Height (HT)	Diameter–height interaction (BDHT)	Number of burns (NB)
White oak					
BD + NB	2.2044 (0.445)	0.0141 (0.005)			−0.4023 (0.157)
BD + HT + BDHT + NB	2.1519 (0.456)	0.0382 (0.018)	−0.0123 (0.191)	−0.00229 (0.001)	−0.4629 (0.164)
BD + HT + NB	2.2133 (0.448)	0.0271 (0.017)	−0.1404 (0.176)		−0.3993 (0.158)
HT + NB	2.2049 (0.443)		0.1324 (0.050)		−0.3875 (0.156)
Post oak					
BD + NB	2.1294 (0.775)	0.0206 (0.008)			−0.3278 (0.223)
HT + NB	2.1531 (0.772)		0.2586 (0.101)		−0.3291 (0.222)
BD	1.0776 (0.245)	0.019 (0.0079)			
HT	1.0959 (0.240)		0.2376 (0.099)		
Chinkapin oak					
NB	4.6308 (1.352)				−0.7392 (0.358)
BD + NB	4.5343 (1.358)	0.0139 (0.019)			−0.7746 (0.360)
HT + NB	4.5065 (1.369)		0.1159 (0.216)		−0.7519 (0.358)
BD + HT + NB	4.8447 (1.458)	0.0564 (0.068)	−0.5243 (0.753)		−0.844 (0.377)
Black oak					
BD + HT + BDHT + NB	1.9561 (0.659)	0.0443 (0.022)	0.0549 (0.211)	−0.0049 (0.002)	−0.3782 (0.194)
BD + HT + BDHT	0.7691 (0.230)	0.0413 (0.022)	0.1841 (0.200)	−0.00576 (0.002)	
Scarlet oak					
HT + NB	2.0878 (0.712)		0.1465 (0.071)		−0.5733 (0.218)
BD + NB	2.1474 (0.711)	0.012 (0.006)			−0.5883 (0.218)
BD + HT + NB	2.0782 (0.711)	−0.0052 (0.022)	0.205 (0.264)		−0.5692 (0.218)
Blackjack oak					
BD	1.4831 (0.456)	0.0135 (0.006)			
HT	1.4444 (0.446)		0.1884 (0.092)		
NB	2.424 (1.014)				−0.4783 (0.274)

[a] Where models are of the form: $P = [1 + \exp[-(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_n X_n)]]^{-1}$ and P, probability of a stem of advance regeneration being alive 1 year after a spring (dormant season) prescribed burn; BD, basal diameter (mm) at 2.54 cm above groundline; HT, total height (m); NB, number of burns.

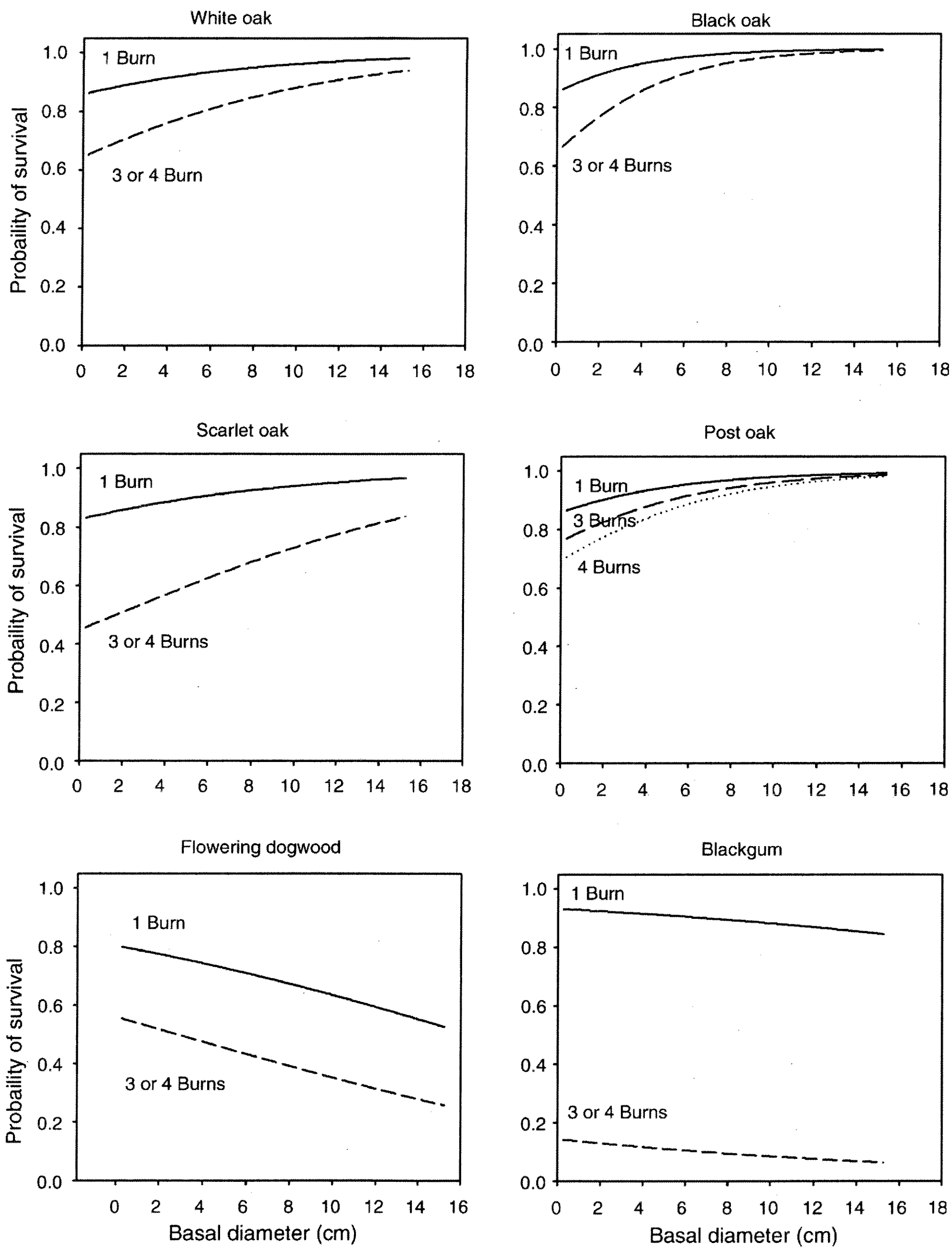

Fig. 2. The probability that advance regeneration will be alive one growing season after four consecutive dormant season burns, 2 years after three burns, or 4 years after a dormant season prescribed fire based on the initial basal diameter, initial height and species. For models that include initial height, results are presented for trees with height held constant at 3 m, i.e., black oak, blackgum and flowering dogwood. All logistic models shown were significant ($\alpha = 0.05$) and had at least moderate support according to the Akaike weight (w_i) in Table 7. These plots of survival probabilities are derived from equations presented in Tables 8 and 9 by species.

($p > 0.05$). For all species, except blackjack oak, there was no support ($w_i = 0$) for the null hypothesis model (intercept only model). The Hosmer Lemeshow goodness-of-fit test (Hosmer and Lemeshow, 2000) on the full model showed a good fit of the model for all species except scarlet oak and hickory.

The probability of survival increased with increasing initial basal diameter for all oak species in this study (Table 8, Fig. 2). In contrast, survival probabilities declined with increasing stem diameter in hickory, blackgum and flowering dogwood species regardless of tree height or number of burns (Table 9, Fig. 2). In these species, tall trees had a higher probability of surviving than did short trees of the same basal diameter, regardless of the number of fires. In flowering dogwood, the effect of height on survival was most pronounced in smaller diameter trees, whereas the opposite was observed in blackgum and black oak advance regeneration.

We observed that survival for all species was greatly reduced after three or four fires (Fig. 2). In many cases, survival rates were 20–30% lower after four fires than after one. Differences in survival between trees subjected to one or four burns were greatest for small diameter trees, but survival probabilities converged at larger basal diameters (e.g., 7.6 cm and larger trees). In general, multiple burns lowered survival in flowering dogwood and blackgum more than in most of the oaks, with the exception of scarlet oak and blackjack oak. Survival in scarlet oak was reduced by nearly 40% for small diameter advance regeneration, but it improved with increasing basal diameter, though not to the extent that was seen in other oak species.

4.1. Recovery of height and understory woody structure

The effect of fire and time since the last fire on the height of sprouts from advance regeneration that experienced shoot dieback was similar among the species. We compared pre- and post-burn height distributions in the single burn and four burn treatments for oak species combined and for flowering dogwood, a major competitor of oak regeneration in the Ozark Highlands (Dey et al., 1996). Four growing seasons after a burn, the post-burn height distribution of oaks was significantly ($p < 0.0001$) different than

Table 9
2001 survival models[a] for non-oak species—logistic regression parameter estimates presented with their standard errors in parenthesis

Species models	Intercept	Basal diameter (BD)	Height (HT)	Diameter–height interaction (BDHT)	Number of Burns (NB)
Flowering dogwood					
BD + HT + BDHT + NB	0.3799 (0.390)	−0.00006 (0.014)	0.4618 (0.16)	−0.00278 (0.002)	−0.3875 (0.126)
BD + HT + NB	0.5374 (0.378)	−0.0164 (0.011)	0.4193 (0.16)		−0.3694 (0.124)
HT + NB	0.6203 (0.373)		0.1997 (0.05)		−0.3813 (0.124)
Shortleaf pine					
BD	−0.626 (0.401)	0.0169 (0.007)			
HT	−0.6829 (0.432)		0.2464 (0.11)		
BD + NB	−0.5234 (0.445)	0.0191 (0.008)			−0.1271 (0.242)
BD + HT	−0.6558 (0.433)	0.0135 (0.019)	0.0542 (0.29)		
Hickory					
BD + HT + BDHT + NB	3.5338 (0.410)	−0.055 (0.013)	0.2199 (0.14)	0.0048 (0.002)	−0.4663 (0.123)
White ash					
BD + NB	3.1255 (1.922)	0.2627 (0.095)			−1.3936 (0.534)
BD + HT + BDHT + NB					
BD + HT + NB	3.2371 (2.024)	0.3853 (0.200)	−1.2488 (1.65)		−1.4334 (0.556)
Blackgum					
BD + HT + BDHT + NB	4.5497 (0.941)	−0.0574 (0.032)	−0.1555 (0.28)	0.0168 (0.005)	−1.4664 (0.295)

[a] Where models are of the form: $P = [1 + \exp[-(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_n X_n)]]^{-1}$ and P, probability of a stem of advance regeneration being alive 1 year after a spring (dormant season) prescribed burn; BD, basal diameter (mm) at 2.54 cm above groundline; HT, total height (m); NB, number of burns.

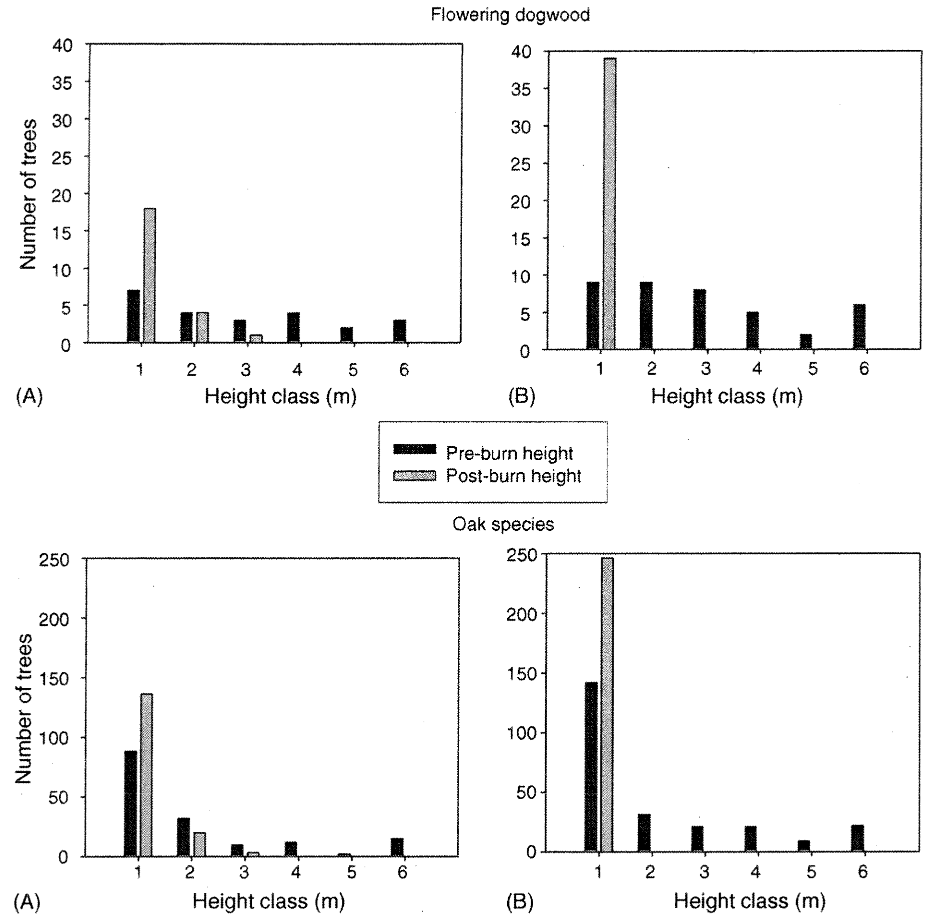

Fig. 3. Pre-and post-burn height distributions of flowering dogwood and oak advance regeneration that sprouted following shoot dieback after one, or four consecutive dormant season fires. Post-burn heights are shown: (A) 4 years after one burn; and (B) 1 year after four burns by 1 m height classes (e.g., class 1 = trees from 0 to 1 m in height, class 2 = trees from 1 to 2 m in height, etc., class 6 includes trees greater than 5 m).

the initial distribution before any burning (Fig. 3A). Densities of sprouts in the smallest height classes (<1.2 m tall) had significantly increased above initial pre-burn levels, and many of the taller height classes had no trees, 4 years following a single spring fire. After experiencing shoot dieback due to burning, the tallest oak sprouts had only grown enough in height to make it into the 3.0-m height class in 4 years since the burn, approximately 4.3 m or more shorter than the tallest pre-burn stems. This slow recovery in height after each fire may be due to sprouts growing under a forest canopy that averaged 18 m^2/ha and 69% stocking. Dey and Jensen (2002) found that overstory densities that averaged 14.2 m^2/ha inhibited the height growth of oak stump sprouts.

One year after four consecutive burns, we found that all oak stems were in the smallest height class (Fig. 3B). In this case, the tallest oak sprouts were less than 1.2 m, and most of the oak advance regeneration were less than 0.6 m tall. Similar results were seen in flowering dogwood (Fig. 3A and B) where the difference between pre- and post-burn height distributions was statistically significant ($p < 0.0008$) regardless of frequency of burns (i.e., one or four burns), or time since the last burn (i.e., 1 or 4 years).

A common result of one low intensity surface fire is to shift the size distribution of midstory and understory trees downward by reducing the density of larger trees through shoot dieback, and increasing the density of smaller stems that occurs after many of the affected trees produce multiple-stemmed sprout clumps (Paulsell, 1957; Thor and Nichols, 1974; Barnes and Van Lear, 1998). One year after a fire, sprouts from trees that suffered shoot dieback are usually less than 1 m tall. Additional annual, biennial or periodic (every 3–10 years) burning keeps trees from growing into larger size classes (Waldrop and Lloyd, 1991). In the understory of a mature hardwood forest, growth of hardwood sprouts after a burn is also inhibited by low light levels (Barnes and Van Lear, 1998; Dey and Jensen, 2002). Thus, one prescribed spring surface fire can create an open forest understory that persists for a number of years (i.e., four or more) if the advance regeneration is growing under a fully stocked hardwood forest canopy. One fire may help managers achieve the "open park-like" appearance of historic woodlands that has been so often noted in early explorer and settler journals (Williams, 1989).

5. Conclusions

One dormant season prescribed burn reduced the size distribution of advance regeneration for common hardwood species found in the Missouri Ozark Highlands. Most stems of advance regeneration less than 15 cm in basal diameter were damaged by fire causing shoot dieback and formation of sprout clumps. Mortality of advance regeneration was generally low in all hardwood species after one burn. Small shortleaf pine seedlings had high mortality rates. We found that the probability of survival was significantly related to size of advance regeneration and that there were significant differences among the species studied. Recovery of height by the hardwood sprouts is slow under a mature forest canopy. Thus, one fire can significantly modify the height structure of the woody understory in upland oak forests for up to 3 years, but it does little to alter the species composition of the advance regeneration. By virtue of reducing the diameter and height of advance regeneration, a single prescribed burn predisposes sprouts to experience more severe damage and higher rates of mortality from subsequent fires.

Three or four consecutive dormant season burns caused substantially higher mortality to advance regeneration and consequently greater levels of total fire damage. Mortality of flowering dogwood and blackgum advance regeneration increased substantially under a regime of frequent fire. Frequent burning increased mortality of oak and hickory advance regeneration, but to a lesser degree. Among the oaks, scarlet and blackjack advance regeneration were most vulnerable to repeated burning, whereas black, post and white oak were intermediate. Overall, repeated burning in the dormant season favors oak and hickory regeneration.

The survival probability models presented here can be used to formulate silvicultural prescriptions that use prescribed burning to, for example: (1) create or maintain the composition and structure of savanna, woodland and forest communities; or (2) favor the competitiveness of oak regeneration by controling competing species. Together with forest inventory data these models can facilitate an evaluation of alternative fire management strategies by estimating shifts in species composition and changes in forest structure by species. Using these models, managers can gain insight into the number and frequency of fires necessary to affect the desired forest composition and structure.

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