

TREE SURVIVORSHIP IN AN OAK-HICKORY FOREST IN SOUTHEAST MISSOURI, USA UNDER A LONG-TERM REGIME OF ANNUAL AND PERIODIC CONTROLLED BURNING

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Abstract: Fire significantly altered survivorship in southeastern Missouri forests burned at annual and four-year (periodic) intervals since 1949 and 1951. In the ANOVA model tested, treatment, species, pretreatment diameter and the interaction between species and pretreatment diameter were highly significantly related to survivorship. Overall survivorship and survivorship of hickories (*Carya* spp.) and red oak group species, including scarlet oak (*Quercus coccinea* Muenchh.), black oak (*Quercus velutina* Lam.), southern red oak (*Quercus falcata* Michx.), was greatest in control plots, less in annually burned and least in periodically burned plots. In contrast, the survivorship of post oak (*Quercus stellata*, Wangenh.) did not significantly differ among fire regimes. General fire survivorship rankings were post oak > red oak species > hickory. Logistic regression indicated that survivorship was significantly and positively correlated with diameter at breast height for post oak and red oak group species, but not for hickories. This relationship of DBH with survivorship was apparently attributable more to self-thinning and differential life-span of trees rather than fire treatment effects. However, survivorship of red oak species was more sensitive to burning regime at smaller pretreatment DBH. When using fire to maintain or increase the abundance of red oak species of oak-hickory forests, age, species life-span, stage of stand development and other environmental stresses should be considered.

INTRODUCTION

The role of fire in oak-hickory forests in the Eastern Deciduous Forest of North America varies across regions. These regional differences are due, in part, to differences in fire behavior which are strongly influenced by topography and fuel type (Pyne 1984). In addition, variation in climate, species composition of the forest itself, soil type and composition of the surrounding vegetation also contribute to regional differences in fire response of oak-hickory forests (Pyne 1984).

In the southeastern U.S., frequent low intensity fires favor the dominance of southern pines, such as shortleaf (*Pinus echinata* Mill.), longleaf (*Pinus palustris* Mill.) and slash pine (*Pinus elliottii* Engelm.) over species of oaks (Garren 1943). In this region oak-hickory forests exist in areas protected from fire, such as in ravines (Garren 1943). Oaks are better adapted to fire than associated hickory species (Harlow and others 1991). As a result of these differential responses and the frequency of fire in this region, oak species can co-exist with pine better than hickories, forming oak-pine forests over much of the southeastern United States (Braun 1950).

Fire helps to maintain the composition of oak-hickory forests through selective mortality, or by creating conditions which alter growth rates of surviving trees (Curtis 1959, Bazzaz 1979, Crow 1988). However, fire also may kill and damage oaks (Stickel 1935). Fire may have both short- and long-term effects on tree mortality. The immediate danger fire poses is high temperature. Cells are killed between 50 and 64°C depending on cellular water content and species (Byram 1958, Hare 1961, Levitt 1980, Rouse 1986). Longer term risks posed by fire result from cambial injury and associated increased susceptibility of the stem to insect attack and diseases (Hedgecock 1926, Johnson 1974, McCarthy and Sims 1935, Stickel 1935, Stickel and Marco 1936).

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Fuel loading and moisture content determine both the maximum temperatures reached and duration of elevated temperatures during a fire (Byram 1958, Pyne 1984, Smith 1986, Vines 1968). In controlled burns at University Forest, southeastern Missouri, periodic burns, conducted every four years since about 1950, were more intense and caused greater mortality by 1964 than annual burns because of the accumulation of a deeper and more continuous litter layer in plots burned periodically (Paulsell 1957, Scowcroft 1966).

Many plant characteristics influence survival and growth after fire. Differential development of these characteristics explains much of the variation among species in post-fire survival and growth (Hare 1961, Kimmins 1987). Thick bark can insulate vital tissues, such as the cambium, which would otherwise be killed by high temperatures (Hare 1961, Vines 1968). Sufficient starch reserves and an ability to resprout allow some trees to survive despite experiencing topkill after fire (Johnson 1974, Kozlowski and others 1991, Little 1974, Malanson and Trabaud 1988). Thus, larger diameter trees may survive fire better than small diameter trees because they have thicker bark and greater starch reserves and because there is a lower probability that complete girdling will occur (Greene and Shilling 1987, Maslen 1988, McCarthy and Sims 1935, Paulsell 1957, Stickel 1935).

Previous field studies and observations have shown that species can be ranked according to fire tolerance. Hickory species are noted for their sensitivity to fire due to their thin bark. Fire sensitivity of oak species varies according to bark thickness, susceptibility to decay and ability to sprout. *Quercus coccinea* and *Q. falcata* both have thin bark and low resistance to decay after being wounded, making them quite sensitive to fire (Belanger 1990, Johnson 1990, Harlow and others 1991). Although more fire resistant because they have thicker bark, fire scars create entry points for decay organisms in both *Q. alba* and in *Q. velutina* (Sander 1990, Rogers 1990). Other oak species, such as *Q. stellata* and *Q. marilandica* survive fire better because they possess thick bark and can sprout after top-kill to form scrub thickets on sites subject to frequent fires (Harlow and others 1991, Stransky 1990, Vines 1968).

White oak group species (Subgenus *Leucobalanus*) generally live longer than red oak group species (Subgenus *Erythrobalanus*, Harlow and others 1991). Hence in young or near mature forests, white oak group species should have inherently lower mortality rates than red oak group species and, other factors held constant, should thus have greater survivorship. These differential fire and life history traits suggest that species differences in survivorship should be observed in the oak-hickory forests of southeastern Missouri.

Specific hypotheses addressed in this paper focused on factors affecting fire survivorship in these forests that have been subjected to three different long-term burning regimes: (1) annual and periodic burning decrease survivorship, (2) periodic burns reduce survivorship more than annual burns, (3) survivorship increases with DBH, and (4) fire survivorship differs among species.

METHODS

Experimental Design

In 1949 and 1951 two replicates of burning treatments were established about one mile apart from each other at the University State Forest in Wapapello, Missouri (36° 55' N, 90° 15' W). Replicate 1 had a site index of 65 on a Typic Fragiudalf while Replicate 2 had a site index of 56 on a Typic Fragiudult (Godsey 1988). Prior to establishment of the two study sites, fire had been excluded since 1930 and there had been no grazing permitted for 15 years. Each replicate contained two unburned control plots, two annually burned plots and two periodically burned plots for a total of six plots randomly arranged in a two by three grid. Each plot was 40 m by 40 m with 10.1 m buffer strips between plots. The burning schedule was staggered between replicates. Treatment of burn plots began in 1949 in replicate 1 and in 1951 in Replicate 2. Prescribed fire was conducted every four years after treatments began in periodically burned plots. Burning was conducted in the spring between March to May. The dates of the spring burns were chosen so that conditions in the late afternoon, when the burns were conducted, fell within moderate to high fire danger conditions (Paulsell 1957). The dates of prescribed burning always coincided with the occurrence of local fires (Paulsell 1957).

Stand Characteristics

Experimental plots had initial basal areas prior to treatment ranging from 12.49 to 15.25 m²/ha in Replicate 1 and from 15.56 to 17.34 m²/ha in Replicate 2. By 1984 total basal area, including ingrowth, had increased for all plots. Species of oak and hickory were predominant in tree-sized individuals (≥ 4.06 cm DBH). Hickories reported at the sites include shagbark hickory (*Carya ovata* (Mill.) K. Koch), mockernut hickory (*Carya tomentosa* (Poir.) Nutt.) and black hickory (*Carya texana* Buckl.). Hickory basal area ranged from 1.82 to 6.07 m²/ha. Measurements of all species of hickory were pooled in this study. White oak group species were *Quercus alba*, ranging in basal area from 0.00 to 1.18 m²/ha before treatments, and *Quercus stellata* ranging in basal area from 2.79 to 10.00 m²/ha in plots before treatment. Red oak group species were *Quercus falcata*, *Q. coccinea*, *Q. marilandica* and *Q. velutina* ranging in basal area before treatment from 3.59 to 8.15 m²/ha. Other trees on the plots were flowering dogwood (*Cornus florida* L.), common persimmon (*Diospyros virginiana* L.), ash (*Fraxinus* spp.), plum (*Prunus* spp.), sassafras (*Sassafras albidum* (Nutt.) Nees) and winged elm (*Ulmus alata* Michx.). Data from these last species were eliminated before calculations (see below).

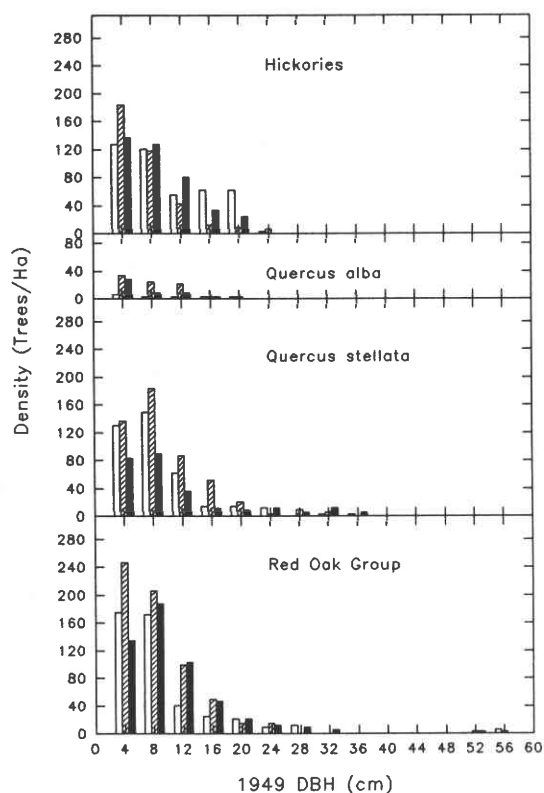
In the original inventory, a j-shaped DBH distribution was observed in all plots, as was shown when plots were grouped by treatment for each replicate (Figure 1). Replicate 1 plots had a greater density of red oak group species, but fewer *Q. alba* or *Q. stellata* trees than Replicate 2. In addition, Replicate 1 plots had fewer hickories than replicate 2.

Statistical Analysis

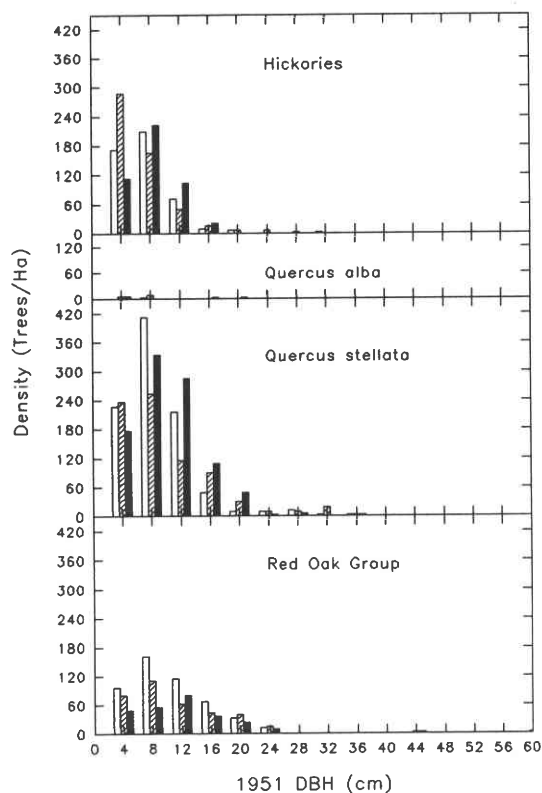
Only individuals of the 1949 (1951) cohort were included in the analysis. In contrast with Godsey (1988) who analyzed plot frequencies, mean percent survivorship was calculated by plot, in 4 cm pretreatment diameter classes for each species. Separation by size was performed to increase the sensitivity of the statistical analyses (see below). Trees in diameter classes larger than 20 cm DBH were removed before analysis in order to ensure that there were observations for every species and pretreatment diameter class combination in all plots. No hickories larger than 20 cm were observed on the plots before treatments were started. In addition, observations of large oaks were not consistent among large diameter classes and were generally a small proportion of the cohort (Figure 1). Because the number of white oak trees and trees of "other species" were low, plot survivorship means of these species categories also were removed from the analysis.

Mean survivorship of each plot for each species group and diameter class combination was then arcsin transformed before analysis of variance to normalize error as described by Box and Cox (1964). Least square means of transformed 1984 survivorship were calculated by employing a nested ANOVA model with pretreatment diameter as a covariate and using the SAS General Linear Models procedure (Table 1). Least square means were then back-transformed into percentages.

In a second model, logistic regression (Harrell 1986) was used to develop functions describing the probability of an individual of a species or species group (hickory, post oak or red oak) surviving from 1949 (or 1951) until 1984 using the binary data of individual survivorship with DBH treated as a continuous independent variable. Pretreatment DBH was included as both linear and squared terms in logistic regression because a curvilinear relationship between survivorship and DBH² has been observed for other species of oak (McCarthy and Sims 1935). The Wald-Chi square values calculated for each logistic curve were used to determine the significance of DBH and DBH² coefficients for all combinations of species groups and treatments for which both sufficient numbers of observations were present and convergence was achieved in the logistic regression. Significant differences are reported at $p \leq 0.05$ unless otherwise noted.



A.



B.

Figure 1: A - Density-diameter relationship in 1949 in Replicate 1 of species of hickory, white oak and red oak. B - Density-diameter relationship in 1951 in Replicate 2 of species of hickory, white oak and red oak. Open bars - control plots; cross hatched bars - annually burned plots; solid bars - in periodically burned plots. In Replicate 1, total densities were 1544 trees/ha in control plots, 1601 trees/ha in annually burned plots, and 1147 trees/ha in periodically burned plots. Density-diameter relationship Open bars - control plots; cross hatched bars - annually burned plots; solid bars - in periodically burned plots. In Replicate 2, total densities were 1872 trees/ha in control plots, 1631 trees/ha in annually burned plots, and 1616 trees/ha in periodically burned plots.

Table 1: Effects and their associated p-values from the ANOVA model used to calculate least square means of transformed 1984 plot survivorship.

Effect	Degrees of freedom	Associated p-value
DBH	4	<0.01
Species	2	<0.01
Species*DBH	8	<0.01
Treatment	2	<0.01
Treatment*DBH	8	0.43
Species*Treatment	4	0.22
Species*Treatment*DBH	16	0.63
Error	44	(Replicate*Species*Treatment*DBH)

RESULTS

Statistical and Logistic Regression Models

In the complete ANOVA model, effects of pretreatment diameter, species, treatment, and the interaction between species and pretreatment diameter all were highly significant ($p \leq 0.001$, Table 1). Neither the interactions between treatment and pretreatment diameter, nor the interaction between species, treatment and pretreatment diameter were significant. Although the F-test of the interaction between species and treatment was not significant ($p = 0.22$, Table 1) statistically significant differences existed between least square means (Table 2).

Except for the DBH² term for post oak on control plots, all terms of the logistic regression models (intercept, DBH and DBH²) were highly significant ($p \leq 0.01$) for post oak and red oak group trees in all treatments. In contrast, only the intercept term was significant in all logistic regression models for hickory species. In periodically burned plots DBH and DBH² approached statistical significance in relation to survivorship of species of hickory ($p = 0.071$ and 0.084 , respectively).

Species Differences in Survivorship

Both the effects of species and the interaction between species and pretreatment diameter were highly significant in the ANOVA model tested (Table 1). Differences among species in percent survivorship in all treatments were significant. Post oak showed the highest mean survivorship (55.6%), red oak species showed the next highest mean survivorship (26.1%) and the hickories showed the lowest mean survivorship (4.8%). The effect of burning regime was highly significant with mean survivorship in control plots (37.9%) being significantly greater than those in either annually burned plots (24.7%) or periodically burned plots (16.2%) (Table 2).

Although the interaction between species and treatment was not significant ($p = 0.22$, Table 1), there were differences among species/groups in response to fire regime. For example, both hickories and red oak species exhibited significant reductions in survivorship in periodically burned plots compared with control plots (Table 2). In addition, the survivorship of hickories in periodically burned plots was significantly lower than that of either control plots or annually burned plots (Table 2). In contrast, post oak showed no significant decrease in percent survivorship in annually burned or periodically burned plots compared with control plots.

The 1984 diameter distribution illustrated two ongoing population processes in the experimental plots. First, as the cohorts are followed through time, the form of the distribution based on the total number of living individuals changed from a j-shaped into a bell-shaped curve, reflecting stem exclusion resulting from competition (cf. Figures 1 and 2). Second, growth of hickories was slower than that of either post oak or the red oak group species. The largest diameter of hickories was 28 cm in Replicate 1 and 20 cm in Replicate 2 (Figure 2). In contrast, the largest diameter of post oak was 52 cm in Replicate 1 and 44 cm in Replicate 2. Likewise, the largest diameter of the red oak group was 48 cm in Replicate 1 and 44 cm in Replicate 2. Peaks of the diameter distributions appeared to be shifted among treatments. However, it was not possible to ascertain whether this shift in diameter distribution was due to the treatments or to differences in pretreatment size-class distributions among plots (cf. Figures 1 and 2).

Although the probability of hickory survivorship increased slightly with increasing DBH in control and annually burned plots (Figure 3), its significance is questionable because of the small numbers of surviving hickory trees in 1984. In contrast with hickory species, both post oak and the red oak group species had sizable surviving populations that had grown into larger DBH classes (cf. Figures 1 and 2). The estimated probability of survival of trees of post oak increased with DBH (Figure 3) with most trees with a pretreatment DBH 12 cm or larger surviving until 1984. Additionally, burning treatments had little effect on the relationship between DBH and the probability of survivorship in the post oak (Figure 3). Like post oak, pretreatment diameter had a noticeable effect on the probability of survivorship in the red oak group (Figure 3). However, the effect of pretreatment DBH on survivorship of red oaks differed from that of post oak in two respects.

Table 2: Percent survivorship from 1949 (1951) to 1984. Least square means with different letters are significantly different ($p \leq 0.05$).

Treatment	Species Group	% Survival in 1984
CONTROL PLOTS		
	Hickory	17.9 c
	Post Oak	57.3 ab
	Red Oak Species	40.9 b
ANNUALLY BURNED PLOTS		
	Hickory	2.4 d
	Post Oak	62.1 a
	Red Oak Species	23.0 bc
PERIODICALLY BURNED PLOTS		
	Hickory	0.5 d
	Post Oak	47.2 ab
	Red Oak Species	16.2 c

First, survivorship of red oak species showed distinct peaks at about 18 cm in both control and periodically burned plots rather than simply increasing monotonically with DBH as was observed in post oak. Second, the peak in the probability of survivorship changed with burning regime for red oak group species. Below a pretreatment DBH of 20 cm, the probability survivorship of red oaks was greatest in control plots, followed by annually burned plots, and then periodically burned plots (Figure 3). Above a pretreatment DBH of 20 cm the probability of survivorship of red oaks was greatest in periodically burned plots, less in control plots, and least in annually burned plots (Figure 3). In contrast, the relationship between DBH and estimated survivorship probability differed little among treatments in post oak.

DISCUSSION

The relationships of survivorship with burning regime and pretreatment size depended on species. Burning reduced survivorship of hickory and red oak group species in both annually burned plots and periodically burned plots, but had little effect on survivorship of post oak. Reductions in the survivorship of hickory and red oak species were greater in periodically burned plots than in annually burned plots. Overall, the hickories had low survivorship rates which were further reduced with burning; the red oak group had intermediate survivorship rates that were sensitive to both burning regime and initial tree size; the post oaks had the highest survivorship rates that were relatively insensitive to burning regime and increased monotonically with initial tree size.

Because environmental stresses interact synergistically to increase susceptibility of trees to attack by insects and disease (Houston 1987), other stresses such as drought may account for some of the variation in survivorship among species. There are reports of decline symptoms in oaks in the Missouri Ozarks, particularly in the red oak group, that have been attributed to drought stress occurring in the 1980's (Jenkins 1992). The conservative growth strategy of post oak (Harlow and others 1991) and its high drought tolerance (Ni and Pallardy 1991, 1992) may have given post oak an advantage during and/or after this period of drought. However, while the species of hickory found in the study sites are somewhat sensitive to water stress, red oak group species are noted for being drought tolerant (esp. *Q. coccinea* and *Q. falcata*) (Belanger 1990, Johnson 1990, Sander 1990).

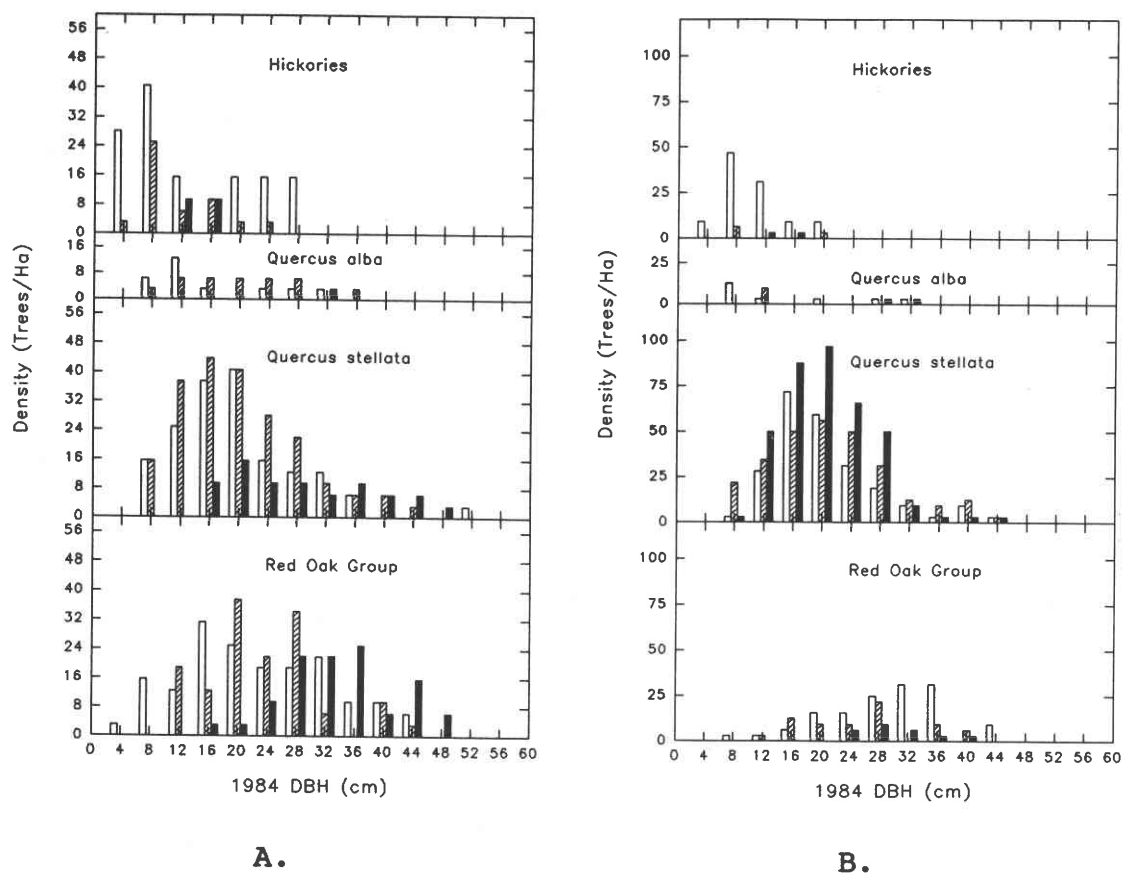


Figure 2: A - Density-diameter relationship in 1984 DBH distribution of species of hickory, white oak and red oak in Replicate 1. B - Density-diameter relationship in 1984 DBH distribution of species of hickory, white oak and red oak in Replicate 2. Open bars - control plots; cross hatched bars - annually burned plots; solid bars - in periodically burned plots.

Because forests at University Forest are between 80 and 90 years old (Jenkins 1992), the effects of differential average life-spans also may have influenced survivorship. White oak group species may live an average of 300-400 years while red oak group species generally live an average of 200 years or less (Harlow and others 1991). Logistic regressions supported the hypothesis that differential life-span accounts for at least some of the higher mortality observed in red oak species compared with post oak. Probability of post oak survivorship increased monotonically with DBH and hence showed no decline in larger, presumably older, trees. In contrast, the red oak group species in two of these burning regimes showed a distinct peak in survivorship probability with respect to DBH indicating mortality of older, larger trees as well as small trees.

As both the DBH*treatment and species*treatment*DBH interaction effects were not significant, while both DBH and species*DBH interaction were, most of the observed species difference in relationships between survivorship and DBH appeared to be the result of self-thinning and senescence-related mortality rather than the result of differential fire response. However, the logistic curves do suggest some species differences in survivorship response to fire regimes. For hickory species, DBH had little effect on survivorship. However, for red oak group species, the relationship between DBH and survivorship predicted by logistic regression differed among burning regimes. The curves suggest that survivorship of red oak group species was sensitive to burning, particularly for smaller diameter

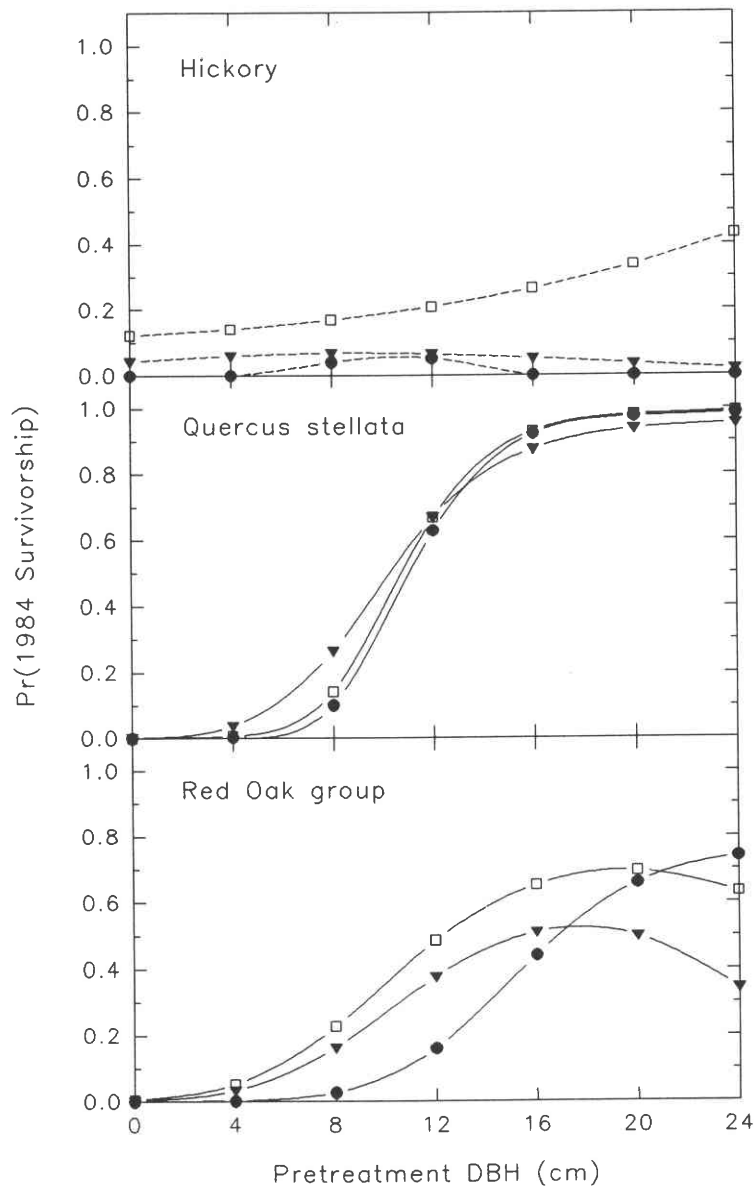


Figure 3: Probabilities of survivorship until 1984 given pretreatment DBH for hickory species, *Q. stellata* and the red oak group. Curves calculated from logistic equations using DBH and DBH² terms using all 1984 survivorship data. □ denote survivorship of control plots; ▼ denote survivorship in annually burned plots; ● denote survivorship in periodically burned plots.

trees. The considerable shade tolerance of hickory species (Graney 1990, Harlow and others 1991, Smith 1990) may account for the lack of significance of DBH terms in logistic regression for this species. Burning regime also had little effect on survivorship of post oaks which increased monotonically with DBH. These results suggest that post oak may become more important in oak-hickory forests of the Ozarks because of its longevity and/or superior fire adaptation. Red oak group species, on the other hand, appear to be somewhat more susceptible to fire and inherently shorter-lived. Thus, if a forest is reaching maturity, recruitment and protection of regeneration is important if maintenance of species, particularly short-lived species, is a management objective.

CONCLUSIONS

Annual and periodic burning regimes decreased survivorship of hickory and red oak group species, but had little impact on survivorship of post oak. Reductions in survivorship of hickory and red oak group species were greater in periodically burned plots than in annually burned plots. Survivorship increased with DBH for post oak and peaked at an intermediate DBH for the red oak group species. The relationship between DBH and survivorship appeared more likely associated with self-thinning and life-span of trees rather than with fire treatment effects. However, in red oak species there was some evidence of preferential fire mortality in small diameter trees. Results suggest that when using fire, age, species life-span, stage of stand development and other environmental stresses must be considered if maintaining or increasing the red oak component of an oak-hickory stand is an important management objective.

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