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ABSTRACT: Poor regeneration of some species of oaks (*Quercus* spp.) within undisturbed closed-canopy forests is common throughout much of the eastern United States. Oak regeneration failure is often inferred from negatively skewed size-class distributions, but evidence of replacement by non-oaks requires investigation of changes in composition and size distributions. I examined how tree species composition and the log-transformed diameter distributions of oaks and non-oaks changed between 1999 and 2013 in an old-growth forest on the University of Mississippi campus. There was a general weak trend towards replacement of oaks by non-oaks. Oaks showed nonskewed or negatively skewed diameter distributions in 1999 and 2013. Diameter distributions of southern red oak (*Quercus falcata*) became significantly more negatively skewed, and the abundance of this species declined. However, there was no significant change in skewness of diameter distributions of the more fire-tolerant but longer-lived post oak (*Q. stellata*) and no significant decline in its abundance. Diameter distributions of trees of mockernut hickory (*Carya tomentosa*) became significantly more positively skewed, as it increased in abundance due to high recruitment and survival. In contrast, there was no significant change in diameter distributions in sweetgum (*Liquidambar styraciflua*) despite high recruitment, due to significant mortality of medium-sized trees of sweetgum. In addition to differences in fire tolerance between oaks and non-oaks, this study shows that differences in survival and longevity are important predictors of future species composition and that fire tolerance is not synonymous with early-successional status.

Index terms: fire suppression, oak regeneration, size frequency distribution, tree longevity

INTRODUCTION

The failure of some species of oaks (*Quercus* L. spp.) to regenerate within closed-canopy forests is common throughout much of the eastern United States (Abrams 1992). In the absence of stand-reducing disturbances or the combination of stand-reducing disturbances and fire, the long-term persistence of oaks is jeopardized for two reasons. First, although oaks in closed-canopy stands are sometimes capable of accumulating significant numbers of seeds and seedlings (Johnson et al. 2009), these seedlings are unable to grow when heavily shaded by a dense midstory (Lorimer et al. 1994). Second, densities of oaks are expected to decline as a result of mortality of older individuals (Greenberg et al. 2011). If the rate of recruitment is not sufficient to compensate for losses associated with mortality, oaks may eventually disappear from stands they currently dominate (Nowacki and Abrams 2008).

Some issues that remain unclear regarding oak loss are; (1) the rate at which oaks are expected to decline, (2) which species of oaks are most likely to be displaced, and (3) which non-oak species are most likely to replace oaks. Although there is considerable evidence that sapling and small tree recruitment is generally much lower for oaks than most non-oaks in mature forests protected from disturbance (Abrams 1992; Lorimer 1993), the rate (and even the occurrence) of displacement of oaks potentially depends on differences in tree mortality rates of oaks and non-oaks (Meadows and Hodges 1997; Ward et al. 1999). The recruitment advantage that non-oaks have over oaks may not translate into future dominance of the stand by the former if oaks are more long-lived or exhibit lower mortality after recruitment than do non-oaks. To the extent that longevity varies more among oak species and among non-oak species than between oaks and non-oaks, there may not be a general displacement of oaks by non-oaks. Rather, there may be a shift to dominance by longer-lived oaks and non-oak species. Predictions of successional trajectories require continued monitoring of changes in the relative abundances and size structure of oaks and non-oaks in undisturbed forests.

The main objective of this study was to compare composition and diameter distributions of oaks and non-oaks in 1999 and 2013 to determine if there is evidence of replacement of oaks by non-oaks in a mature upland oak-dominated forest long protected from fire. Previous long-term studies of natural stand development of undisturbed forests with oaks have revealed decreasing positive skew (or increasing negative skew) of diameter distributions of oaks in mixed forests over time (Schnur 1937; Christensen 1977; Ward et al. 1999). Hence, I examined changes in diameter distributions to infer replacement of oaks

by non-oaks in an undisturbed, old-growth upland oak-dominated forest that historically (in the early 1800s) experienced frequent fires (Brewer 2001). I tested the following hypotheses: (1) oaks decreased in abundance, whereas non-oaks increased in abundance between 1999 and 2013; (2) the two most abundant non-oak species, *Liquidambar styraciflua* L. (sweetgum) and *Carya tomentosa* (Poir.) Nutt. (mockernut hickory), showed more positively skewed diameter distributions than did oaks and maintained these positively skewed distributions, consistent with either lower small tree mortality or higher recruitment in the former; and (3) diameter distributions of the two most abundant oak species, *Quercus stellata* Wangenh. (post oak) and *Q. falcata* Michx. (southern red oak) became more negatively skewed over time as a result of growth of survivors, mortality of the largest individuals, and lower recruitment into small tree size classes from saplings than observed for sweetgum or hickory. Support for all three hypotheses would provide evidence in support of general replacement of oaks by non-oaks in this old-growth forest.

METHODS

Study Site

This study was conducted in two old-growth remnant fragments of an upland oak-dominated forest on the University of Mississippi campus: Bailey Woods and Jackson Strip (Brewer 2001). Bailey Woods (34°21'31.43"N; 89°31'32.36"W), on the eastern border of the campus, covers approximately 20 ha; part of Bailey Woods is a National Historic Landmark and the former estate of the late novelist, William Faulkner. The remaining part of Bailey Woods has been owned by the university since the date of its charter in 1844 (Sansing 1999). The university was built on forested land in 1848 (Sansing 1999). Aerial photographs of Bailey Woods, and personal interviews with long-time residents of Oxford and relatives of Faulkner, indicate that a mature deciduous forest existed as early as the late 1930s and has retained this appearance since (Brewer 2001). The oldest trees aged to over 150 years old

(in 1999) in this forest were white oaks (*Quercus alba* L.) and post oaks (*Q. stellata*) with diameters greater than 1.1 m at 1.5 m (hereafter, diameter). There is clear evidence, however, of some human-caused disturbance within a small portion of the interior of the forest. Aerial photographs revealed that some selective logging was done to create a dirt road, which has been abandoned since the 1950s, and these areas were excluded from sampling in the current study. Up until Faulkner's death in 1962, the understory of the forest had experienced some grazing by dairy cows (Lawrence and Hise 1993). Fires have not occurred within the interior of the forest, however, for at least 80 years and according to long-time residents of Oxford, much longer. Since 1973, there has been no significant human disturbance of the forest, although residential development adjacent to Bailey Woods continues today.

Jackson Strip (34°22'8.32"N; 89°32'34.03" W), on the northern border of the campus, is a narrow strip of woods (from 50- to 200-m wide by ~ 500-m long) that occurs along a major road in Oxford (Jackson Avenue) and has been owned by the university since 1844. Like Bailey Woods, aerial photographs show these woods were mature in the 1930s (in contrast to the surrounding landscape not owned by the university) and were contiguous with Bailey Woods at that time. Some post oaks located at the edge of the forest, which were cut in the late 1990s to widen Jackson Avenue, were over 120 years old. Bailey Woods and Jackson Strip are as old as any upland oak forest I have been able to locate in northcentral Mississippi.

The University of Mississippi—Oxford Campus is located on an east–west oriented ridge in between the Little Tallahatchie River to the north and the Yocona River to the south in a physiographic region recognized in Mississippi as the north central plateau of the interior coastal plain. Both Bailey Woods and Jackson Strip occurred on uplands containing Smithdale sandy (Typic Hapludult) soils underlain by a reddish sand and clay of Eocene origin (Hilgard 1860; Lowe 1921; Morris 1981). Neither occurred on a major floodplain or terrace, which in the early 1800s were

the primary locations of mesic and hydric forests in Lafayette County, and in which fire-sensitive tree species (e.g., American beech (*Fagus grandifolia* Ehrh.) and sweetgum) codominated.

In the early 1800s, before extensive logging and fire exclusion, open, self-replacing stands of fire-tolerant tree species such as black oak (*Quercus velutina* Lam.), blackjack oak (*Q. marilandica* Munchh.), post oak, and southern red oak dominated the upland landscape of this region (Surrette et al. 2008). As a result of fire exclusion in the 20th century, second-growth stands developed, which are now dominated in the overstory by a mixture of some of the upland oak species (but not blackjack oak), some species historically common in floodplains (e.g., sweetgum), and some species that were common in both uplands and floodplains historically (e.g., white oak, mockernut hickory; Surrette et al. 2008). Species historically indicative of poorly drained or moderately well-drained floodplains (and occasionally occurring in uplands as trees) in this region (e.g., sweetgum and winged elem (*Ulmus alata* Michx.)) now dominate the subcanopy (Surrette et al. 2008).

Initial Tree Species Composition of Bailey Woods and Jackson Strip

To determine tree species composition and potential stand replacement dynamics in Bailey Woods, three transects (140 to 260-m long) were oriented from the edge of the woods into the interior in mid-April, 1996. Later (in 1999), two additional transects were established atop ridges in the forest. Transects were placed so as to provide a representative sample of the forest as a whole and to examine differences associated with slope position and aspect. One transect was located parallel to a northfacing slope. A second transect was located perpendicular to a gentle southfacing slope and descending into a hollow. A third transect was located perpendicular to a southfacing slope, descending into a hollow, and then ascending a ridge within the interior of the woods. A fourth transect was located within the interior of the forest atop a ridge, and two additional points

were located haphazardly atop another ridge. Altogether, 36 sampling points were placed within Bailey Woods.

In Jackson Strip, a single (140-m) transect was oriented lengthwise >20 m from any edge. Approximately one-half of the length of the transect (containing three points) was located atop a ridge and the other half (containing four points) was located along an east-facing slope and associated hollow.

Within each transect, I sampled tree species composition using a plotless (point-centered quarter) method (Cottam and Curtis 1956). Points were placed at 20-m intervals within each transect. Within each quarter, I located the two closest woody stems (taller than 1.5 m and ≥10 cm in diameter) and measured the diameter, the distance from the point to each stem, and identified the stem to species. Not all points contained eight trees due to errors in sampling. These errors included sampling the same tree twice in two nearby points and accidental tagging of dead trees by student workers during spring censuses before leaf flush. I permanently tagged all stems for subsequent verification of their identity and to permit a repeat census in the future. Altogether, I encountered 287 stems at Bailey Woods and 56 stems at Jackson Strip.

Resampling of Trees

Beginning in the summer of 2012 and continuing into the spring and summer of 2013, I revisited all points, relocated all live trees (and when possible all dead trees), and measured diameter at the tag (or 1.5 m above ground level in cases where the tags were lost). Because the point-centered quarter method is not appropriate for measuring tree recruitment, I quantified recruitment using the following approach. First, in 1999, I established a 100-m^2 circular pivot plot at each point to quantify sapling densities. All saplings were permanently marked with numbered aluminum tags. I quantified recruitment of these saplings into the small tree class in 2013. Measurements of point-to-tree

distances in 1999 indicated that the total area initially sampled in Bailey Woods and Jackson Strip was approximately equivalent to 1.2 ha, or 286 m^2 per point. Hence, I extended the circular pivot plots initially established to quantify sapling recruitment to encompass an area of 300 m^2. I estimated recruitment into the small tree class beyond the first 100 m^2 by counting, identifying, and marking all previously nontagged live stems between 10 and 14 cm in diameter. I assumed that all nontagged stems greater than 14 cm in diameter were present as tree-sized individuals in 1999. The upper bound of 14 cm was consistent with observations of the sizes of recruits in the 100-m^2 sapling plots established in 1999.

Changes in Species Composition

I analyzed changes in tree species composition statistically by calculating differences in total density for each species and then using Wilcoxon signed rank tests to determine if the differences were statistically significant (using species as observations). I conducted separate one-tailed signed rank tests for all non-oaks combined and for all oaks combined to specifically test the hypotheses that non-oaks as a group increased and oaks as a group decreased. I converted the W statistic associated with each signed rank test to a z score and then to a chi-square statistic with one degree of freedom. Because independent chi-square statistics are additive (Steel and Torrie 1980), I summed the resulting chi-square values for non-oaks and oaks, assuming the direction of change was opposite and independent for oaks and non-oaks, and assessed the statistical significance of the resulting chi-square statistic with two df. A significant chi-square resulting from an increase in non-oaks and a decrease in oaks provided support for the hypothesis of replacement of oaks by non-oaks. I did the calculations associated with the Wilcoxon signed rank tests using a spreadsheet and then used R (version 2.14.1; The R Foundation for Statistical Computing, 2011) to convert the resulting W statistics to z scores and chi-square values and to evaluate statistical significance of summed chi-square values.

Changes in Diameter Distributions of Trees

To ensure adequate sample sizes, I restricted my statistical analyses of diameter distributions to the four most abundant tree species at Bailey Woods and Jackson Strip (combined), two of which were upland oaks (post oak and southern red oak) and two of which were not (mockernut hickory and sweetgum). I calculated skewness (using R) for all four species' diameter distributions in 1999 and 2013. I used separate randomization tests for each of the four species to determine whether the magnitude and direction of skewness changed significantly between 1999 and 2013 (using a spreadsheet and a macro function). I restricted the randomization by randomly shuffling the year of measurement of diameter for each stem. In addition, I randomly shuffled the diameters of recruits and individuals that died between 1999 and 2013 between years. I derived P values from 1000 randomized pseudoreplicates and counted the number of randomized pseudoreplicates in which the randomized differences in skewness between 1999 and 2013 exceeded the observed difference. In cases of borderline statistical significance, I calculated 10,000 pseudoreplicates. I used 0.05 (50 of 1000 (or 500 of 10,000) pseudoreplicates) as the cutoff for statistical significance.

Size-Related Mortality

I used nominal logistic models to examine relationships between mortality and diameter in the two most abundant species that showed significant mortality (southern red oak and sweetgum). To consider the possibility that mortality did not increase or decrease monotonically with diameter, I divided the sample of trees for each species into quartiles and then included diameter quartile as either an ordinal or unordered nominal predictor variable in the analyses. I conducted the analyses of mortality using a nominal logistic model procedure in JMP (version 5.0.1; SAS Corporation, 2002).

RESULTS

Changes in Tree Species Composition

The four most abundant species at Bailey Woods and Jackson Strip combined in both 1999 and 2013 were sweetgum, southern red oak, post oak, and mockernut hickory (Table 1). The rank order of these four species, however, changed between 1999 and 2013 as a result of declines in southern red oak and increases in mockernut hickory (Table 1). Sweetgum was the most abundant species in 1999 and 2013. In contrast, southern red oak had the greatest total basal area in 1999 and 2013, despite its decline in abundance (Table 1). Some species that were not present in 1999 were present in 2013. These species included blue beech (*Carpinus carolinianus* Walter (one recruit)), yellow poplar (*Liriodendron tulipifera* L. (one recruit)), and southern magnolia (*Magnolia grandiflora* L. (seven recruits)). No species were lost entirely from the samples at Bailey Woods or Jackson Strip.

In terms of counts, there was a trend towards a general (but not statistically significant) increase in non-oaks (median increase per species = 1; $W = 34$; $\chi^2 = 2.40$; $P = 0.12$) and a general decrease in oaks (median decrease per species = 1; $W = 15$; $\chi^2 = 3.42$; $P = 0.06$), resulting in a shift in favor of non-oaks that approached statistical significance ($\chi^2 = 5.83$, df = 2, $P = 0.054$). Alhough most non-oaks (especially mockernut hickory and winged elm) increased, some non-oaks showed substantial declines (e.g., flowering dogwood (*Cornus florida* L.), 14 to 5, and eastern redcedar (*Juniperus virginiana* L.), 23 to 16). Five of the seven species of oaks examined declined in abundance. One species, scarlet oak (*Quercus coccinea* Münchh.), increased by a single individual, and another species, white oak, remained the same. In contrast, among non-oaks, nine species increased, four decreased, and the densities of three species remained the same (Table 1). A chi-square test of independence indicated that oaks and non-oaks differed significantly with respect to the

Table 1. Counts and basal area of all woody stems greater than 10 cm in diameter at 1.5-m height in 1999 and 2013 within two mature upland oak-dominated forests (Bailey Woods and Jackson Strip) on the University of Mississippi campus in Oxford, Mississippi.

Species	1999		2013	
	Count	Basal Area (m² per total estimated sampled area of 1.35 ha)	Count	Basal Area (m² per total estimated sampled area of 1.35 ha)
Liquidambar styraciflua	74	2.38	75	3.09
Quercus falcata	44	6.48	36	7.28
Quercus stellata	39	5.26	38	5.52
Carya tomentosa	39	1.87	55	2.54
Juniperus virginiana	23	1.42	16	1.17
Quercus alba	18	2.41	18	2.04
Prunus serotina	17	0.36	16	0.44
Nyssa sylvatica	15	1.17	18	1.37
Cornus florida	14	0.21	5	0.09
Ulmus alata	13	0.18	23	0.31
Fagus grandifolia	12	0.88	13	1.32
Quercus velutina	10	2.12	9	2.43
Quercus nigra	5	0.48	4	0.68
Quercus marilandica	3	0.16	2	0.09
Quercus coccinea	3	0.10	4	0.18
Sassafras albidum	3	0.06	4	0.10
Acer rubrum	2	0.18	2	0.26
Morus rubra	2	0.04	1	0.02
Diospyros virginiana	1	0.02	1	0.03
Magnolia grandiflora	0		7	0.10
Liriodendron tulipifera	0		1	0.02
Carpinus caroliniana	0		1	0.01
Total	337	25.77	349	29.11

proportions of increasing vs. decreasing species ($\chi^2 = 4.55$, $P = 0.03$, df = 1).

Changes in Diameter Distributions

In 2013, the skewness of the diameter distributions of the four most abundant tree species was ranked in descending order as follows: mockernut hickory, sweetgum, post oak, and southern red oak (Figure 1). The diameter distribution of mockernut hickory was significantly more positively skewed than that of any of the other three species in 2013 ($P = 0.027$ for the comparison with sweetgum). The diameter distribution of southern red oak was significantly more negatively skewed than that of any of the other three species in 2013 ($P = 0.018$ for the comparison with post oak; Figure 1). Although skewness of the diameter distribution of sweetgum appeared to be more positive than that of post oak in 2013, the difference was not statistically significant

($P = 0.115$). The diameter distribution in mockernut hickory became significantly more positively skewed between 1999 and 2013 ($P < 0.001$; Figure 1). In contrast, the diameter distribution of southern red oak became more negatively skewed between 1999 and 2013 ($P = 0.0489$; Figure 1). The diameter distributions of sweetgum and post oak did not change significantly between 1999 and 2013 (P for test of greater negative skew = 0.428 and 0.362, respectively). The dramatic increase in the positive skew of the diameter distribution of mockernut hickory resulted from substantial recruitment (16; 41%) combined with no observed mortality of small trees. The change towards a more negatively skewed diameter distribution in southern red oak resulted from the lack of recruitment combined with mortality (eight individuals; 18%) of primarily smaller trees. The lack of change in the skewness of the diameter distributions in sweetgum and post oak

had different causes. Although there was substantial recruitment in sweetgum (12; 16%), this species also exhibited substantial mortality of small to medium sized trees (50% of individuals in the second smallest diameter quartile), resulting in very little change in the skewness of the diameter distribution. In contrast, no recruits of post oak were observed, but only one death was observed. The reduction in skewness from 0.11 to 0.04 in post oak was not statistically significant ($P = 0.362$).

Size-Related Mortality

Mortality in sweetgum varied with size in a nonmonotonic fashion. Logistic regression indicated that diameter quartile (included as an unordered categorical variable) was significant (Likelihood-Ratio $\chi^2 = 21.7$; df = 3; $r^2 = 0.34$; $P < 0.001$). Mortality was greatest in the second smallest diameter quartile (50%), and lowest in the second
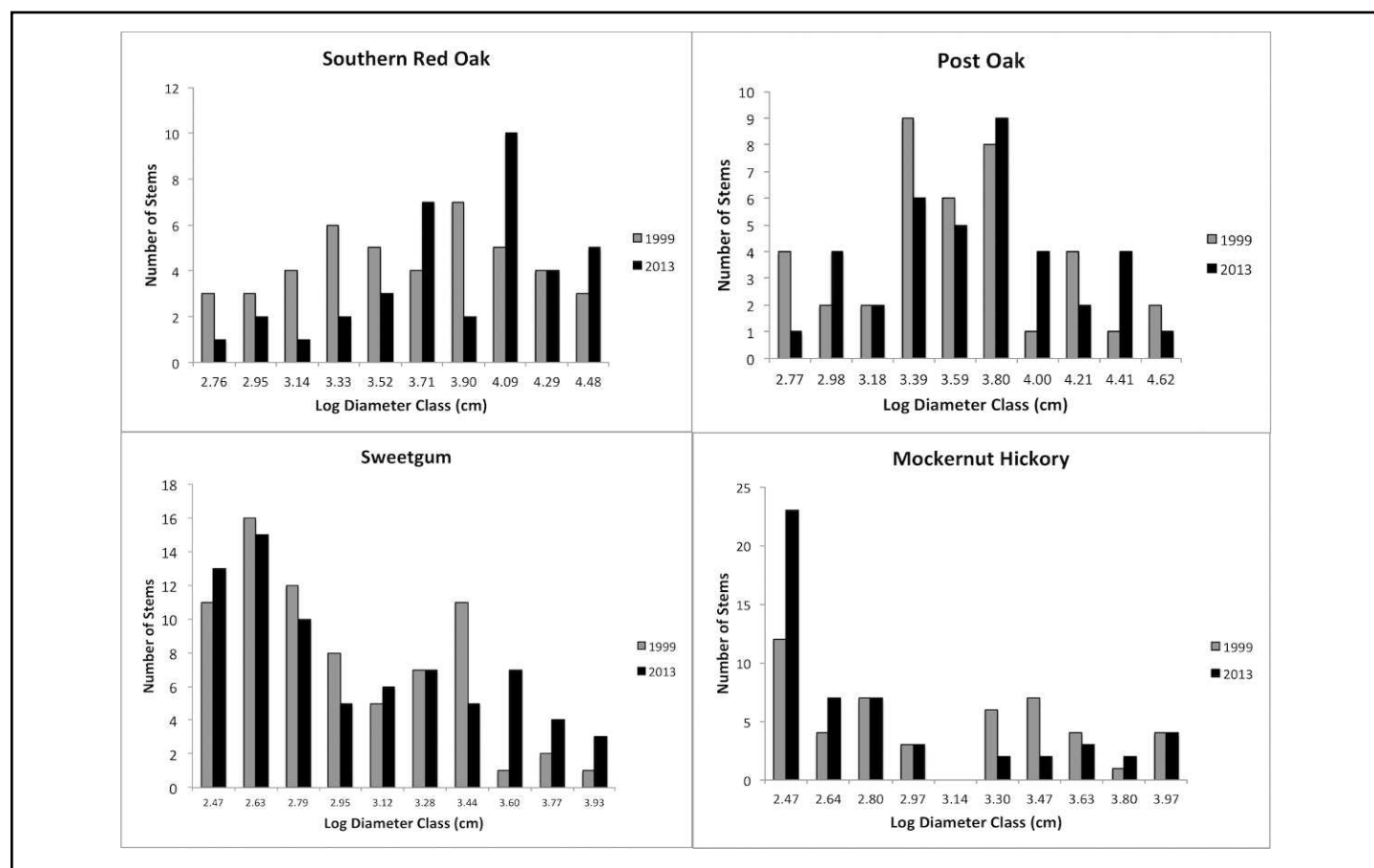

Figure 1. Frequency distribution of log diameter in ten diameter classes in 1999 and 2013 for the four most common tree species at Bailey Woods and Jackson Strip (combined).

largest quartile (0%). As with sweetgum, mortality was size-related in southern red oak. Diameter quartile (included as an ordinal variable) explained 18% of the variation in mortality (Likelihood-Ratio $\chi^2 = 7.71$; df= 3; $r^2 = 0.18$; $P = 0.05$). Mortality was negatively associated with diameter. Mortality was 36%, 27%, 0%, and 9% in the smallest to largest diameter quartiles, respectively (Likelihood-Ratio χ^2 for smallest quartile vs. larger quartiles = 2.93; df = 1; $P = 0.09$; Likelihood-Ratio χ^2 for the second smallest quartile vs. larger quartiles = 3.35; df = 1; $P = 0.07$).

DISCUSSION

Results of this 14-year longitudinal study of an upland hardwood forest show a general but gradual replacement of oaks by non-oaks. At least some oak species are being replaced by mockernut hickory, a species currently codominating the mid- and understory with sweetgum. The current dominance of the understory by sweetgum, however, does not portend its dominance of the overstory in the long term. Although diameter distributions of mockernut hickory became increasingly positively skewed between 1999 and 2013, the same was not true of sweetgum, despite continued high recruitment in both species. The main difference between mockernut hickory and sweetgum was the much higher mortality of small to medium-sized trees in the latter species between 1999 and 2013. Hence, despite current dominance of the understory by sweetgum, mortality of recruits may prevent this species from dominating the overstory in the long term, unless there is significant mortality of overstory trees.

Although results of the current study reveal little to no recruitment into the tree size class among oaks between 1999 and 2013, a significant decline in density was only apparent for southern red oak. Declines in southern red oak resulted from the combination of significant mortality and the lack of recruitment. In contrast, despite the lack of recruitment, the very low mortality observed in post oak resulted in no significant decline in this species. These results suggest one of two possible

trajectories for post oak over time. First, post oak is undergoing an inexorable albeit very gradual decline that will ultimately lead to the loss of this species from the forest studied. The fact that no significant decline was observed in this study may simply indicate that 14 years was not long enough to observe declines in this long-lived species. Second, periodic canopy disturbances could provide opportunities for recruitment that are adequate to maintain post oak in this forest (Brewer 2001; Cannon and Brewer 2013). Such canopy disturbances of sufficient size to promote post oak tree recruitment did not occur during the study. Additional long-term monitoring of post oak will be necessary to test these alternative hypotheses.

CONCLUSIONS

Differences in tree recruitment rates between oaks and non-oaks in closed forests undoubtedly play an important role in determining long-term trajectories in composition. Nevertheless, interspecific differences in mortality rates can determine the rate at which (and even if) oaks will generally be replaced by non-oaks in forests that have experienced fire suppression. It is worth noting that post oak is generally assumed to be a more fire-tolerant and possibly less shade-tolerant tree than is southern red oak (Huddle and Pallardy 1996; Guyette et al. 2004) and was a more common component of the fire-maintained presettlement upland landscape in northern Mississippi than was southern red oak (Brewer 2001). Nevertheless, the current study indicates that, even with continued prolonged fire suppression, southern red oak is likely to be displaced long before post oak will be, in part because tree-sized individuals of post oak have higher survival probabilities and are longer lived than are those of southern red oak (Guyette et al. 2004; this study). Hence, the rate of successional replacement in the fire-suppressed forest studied here cannot be predicted solely from interspecific differences in fire tolerance.

If one accepts the premise that interspecific differences in fire tolerance, alone, do not explain patterns of succession

in forests in which fires have been suppressed, then it follows that premodern fire-maintained oak woodlands were not early-successional communities. Rather, these communities are better described as fire-climax communities (sensu Chapman 1932). Ironically, oak woodlands in north Mississippi assumed the character of modern early-successional communities only after fires were suppressed. I hypothesize that it was only after fire suppression that colonization of upland areas by offsite pioneer species such as sweetgum began. Today, Bailey Woods and Jackson Strip, despite being "old growth" forests, are transitional communities. If fire suppression is maintained (and barring any major canopy disturbances), I predict that these forests eventually will transition to an alternative, novel, quasi-equilibrium state dominated by mockernut hickory.

Ecological restoration of historical fire regimes has the potential to restore natural oak regeneration in long fire-suppressed oak-dominated forests such as those found on the University of Mississippi campus (Nowacki and Abrams 2008). Nevertheless, the forest tracts studied here are surrounded by residential development within the city of Oxford. Implementing the thinning and prescribed burning treatments necessary for effective restoration would be challenging and probably would most likely not have general support from local residents. In addition, fire suppression has been in place for so long that native groundcover vegetation diversity is extremely depauperate (Surrette and Brewer 2008). It, therefore, may be too late to effectively restore a fire-maintained oak woodland in a safe and cost-effective manner (Nowacki and Abrams 2008). Bailey Woods and Jackson Strip perhaps would best serve the purpose of unmanipulated controls against which restoration efforts in nearby forests could be compared.

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Steve Brewer is a professor of biology at the University of Mississippi. His research interests include the effects of fire and other disturbances and competition on plant diversity in pine- and oak-dominated ecosystems of the southeastern United States.

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