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Author(s): Miranda D. Redmond, Rebecca B. Wilbur, and Henry M. Wilbur

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# Recruitment and Dominance of *Quercus rubra* and *Quercus alba* in a previous Oak-Chestnut Forest from the 1980s to 2008

MIRANDA D. REDMOND<sup>1</sup>

*Department of Ecology and Evolutionary Biology, University of Colorado-Boulder, Boulder 80309*

AND

REBECCA B. WILBUR AND HENRY M. WILBUR

*Department of Biology and Mountain Lake Biological Station, University of Virginia, Charlottesville 22904*

**ABSTRACT.**—This study documents 25 y of change in the abundance of *Quercus rubra* (northern red oak) and *Quercus alba* (white oak), in a previous chestnut (*Castanea castanea*)-oak forest in the Southern Appalachians of the eastern U.S.A. Spatially explicit data from 1983–1984 and 2007–2008 of individually mapped trees on two plots in southwestern Virginia were used to examine how the basal area and density of all tree species changed, with specific attention to recruitment, growth, and mortality patterns of *Q. rubra* and *Q. alba*. Since the 1980s there has been an increase in the number of shade tolerant trees, primarily *Acer pensylvanicum* (striped maple), and a decrease in the number of shade intolerant and intermediate shade tolerant trees, including both *Q. rubra* and *Q. alba*. We found a negative correlation between *A. pensylvanicum* abundance and *Quercus* seedling abundance and a positive correlation between light availability and *Quercus* seedling abundance. Both *Q. rubra* and *Q. alba* have experienced self-thinning, and the previous oak-chestnut forest will likely become increasingly dominated by maples and other shade tolerant species.

## INTRODUCTION

Oaks have dominated many of the forests of the eastern United States for nearly 10,000 y, although their abundance and distribution has varied during this time due to different forest disturbances (Abrams, 1992). Humans have changed the nature and intensity of forest disturbances through fire ignition or suppression (Lorimer *et al.*, 2001), cattle grazing, hunting, logging, road building, and the introduction of new pathogens, insects, and plants (Abrams, 1992). In the past century, there has been a general decline in oaks throughout the eastern United States; but, in some regions, certain oak species have expanded their ranges and increased in dominance (Abrams, 2003). Oaks are an integral part of eastern U.S.A. deciduous forests; they provide nutrition for a wide range of wildlife (McShea and Healy, 2002), and the masting of oaks has a profound impact on the whole eastern deciduous biome (Wolff, 1996). Understanding how the abundance and distribution of oaks in the deciduous forests of the eastern U.S.A. has changed during discrete time intervals will enable better predictions of how well oaks will survive under future climatic and disturbance regimes.

Both human-induced and natural disturbances influence the composition of eastern deciduous forests and affect oak dominance. Periodic fires were common before Euro-american settlement and were an important disturbance that promoted oak dominance (Abrams, 1992; Lorimer, 2001). Oaks are considered to be early to middle successional species that do not survive well under a dense understory (Lorimer, 1984; Nowacki *et al.*, 1990; Crow, 1988; Burns and Honkala, 1990). Fire favors oaks compared to other hardwood

<sup>1</sup>Corresponding author: Telephone: (415) 300-6901; FAX: (303) 492-8699; e-mail: mirandaredmond@gmail.com

species due to their thick bark, sprouting ability, and rotting resistance after fire scars (Lorimer, 1984). Therefore, fires promote oak species by removing fire-sensitive competitors and maintaining light availability in the understory (Abrams, 1992; Hibbs *et al.*, 1980; Lorimer, 1984). Numerous studies have shown that fire suppression over the last century has promoted the replacement of oaks by less fire tolerant and more shade tolerant species, such as *Acer* (maples), *Betula lenta* (black birch), and *Nyssa sylvatica* (black gum) (Abrams, 1992; Abrams and Nowacki, 1992; Abrams, 1986; Host *et al.*, 1987; McCune and Cottam, 1985).

In addition to fire suppression, the introduction of chestnut blight (*Cryphonectria parasitica*), an ascomycete, in the early 1900s is an important human-induced disturbance that dramatically changed the eastern deciduous forests and oak dominance in the past century (McCormick and Platt, 1980). The chestnut blight fungus caused the virtual extinction of the dominant tree, *Castanea dentata* (American chestnut), which created large gaps in the forest canopy. Following this disturbance, studies done between the 1950s and 1980s found a large increase in abundance of several species of oak, especially *Quercus rubra* (northern red oak), and shade tolerant species such as *Acer rubrum* and *Amelanchier arborea* (service berry) in previous chestnut-oak forests (Karban, 1978; Keever, 1953; McCormick and Platt, 1980; Stephenson, 1986; Woods and Shanks, 1959).

Other abiotic and biotic factors affect oak abundance including wind, disease, drought, and herbivory (Abrams, 1992). Wind throw creates canopy gaps, which increase light availability in the understory enabling oak recruitment (Abrams, 1992). Drought favors oak recruitment and dominance because relative to other deciduous hardwood species, oaks have deep roots, xeromorphic leaves, and an ability to adjust osmotically, conferring drought tolerance (Bahari *et al.*, 1985; Abrams, 1990; Dickson and Tomlinson, 1996). Herbivory by deer, small mammals and birds is an important biotic factor that can negatively influence oak growth and recruitment (Stange and Shea, 1998; Rooney, 2003; Russel, 2001). The abundance of deer has increased throughout the eastern United States since the chestnut blight pandemic due to hunting regulations and changes in land use (McShea and Healy, 2002), and studies have shown that deer negatively affect the abundance of oak seedlings and saplings (Stange and Shea, 1998; Rooney, 2003; Russel, 2001). Defoliation by gypsy moth (*Lymantria dispar* L.) is another important biotic factor that negatively affects oak abundance through mortality (Fajvan and Wood, 1996). Gypsy moths prefer oaks compared to other hardwood species and allow oaks to be replaced by genera such as *Acer* (Fajvan and Wood, 1996). Since forests are dynamic and are affected by a suite of factors, it is useful to clearly document how these forests have changed through discrete time intervals to understand better the drivers of forest change.

In this study, we remapped individual stems on two plots first mapped in the early 1980s in an oak forest on Salt Pond Mountain, Giles County, Virginia to understand how the abundances of the two dominant canopy species, *Quercus alba* (white oak) and *Q. rubra*, have changed. Stephenson (1986) compared data of a chestnut-oak stand on Salt Pond Mountain from 1930 to the forest composition in five nearby sites in 1982. He found *Q. rubra* increased in abundance to become the dominant canopy species, but he also found an increase in *Q. alba* and more shade tolerant species. The increase in dominance of *Q. rubra* seen by Stephenson (1986) and others following the death of *Castanea dentata* may be a temporary mid-successional transition. Studies done in Vermont, Illinois, and Wisconsin found *Q. rubra* to be a pioneer species that, after initial dominance, is replaced by shade tolerant species (Marks, 1942; Peet and Loucks, 1977; Jokela and Sawtelle, 1985). Oak seedlings require a high light level to survive and grow, and they have poor survival beneath understory trees

(Lorimer, 1984; Crow, 1988; Lorimer *et al.*, 1994). Numerous studies have shown more shade tolerant trees, such as *Acer* spp., have increased (Lorimer, 1984; Abrams, 1992; Nowacki and Abrams, 2008). One such species, *A. pensylvanicum* (striped maple) is well adapted to live under heavy shade and has broad leaves, which creates a dense shade inhibiting *Q. rubra* and *Q. alba* regeneration (Hibbs *et al.*, 1980). As the forest matures, it is unclear whether *Q. rubra* and *Q. alba* will be able to maintain their dominance in the eastern deciduous forests (Nowacki and Abrams, 2008).

The purpose of this study was to understand how the abundances of the two dominant species, *Quercus rubra* and *Q. alba*, in a previous chestnut-oak forest in the Southern Appalachians have changed in the last 25 y and to predict better how the forest composition will change in the future. This study does not include a discussion of potential impacts of climate change on oaks as those have been discussed recently by Iverson *et al.* (2008). The questions specifically addressed were: (1) How has woody stem composition and diversity changed in the past 25 y? (2) How do *Q. rubra* and *Q. alba* differ in their recruitment, growth, and mortality patterns? (3) Are the abundances of *Q. rubra* and *Q. alba* seedlings correlated with the abundance of the dominant understory tree, *Acer pensylvanicum*, and light availability?

## METHODS

### STUDY AREA

This study was conducted on two plots previously mapped in 1983–1984 near Mountain Lake Biological Station at 1160 m elevation in the Valley and Ridge Physiographic Province in Giles County Virginia, USA, 37°22'N, 80°31'W. The first plot, referred to as MLBS, is a 0.5 ha plot at the Mountain Lake Biological Station. The second plot, referred to as TS, is a 3 ha plot about 1 km to the northwest on private land. The most abundant canopy trees on both plots are *Quercus rubra* and *Q. alba*. The most abundant understory trees in the plots are *Acer pensylvanicum* and *A. rubrum*. For about 140 y both plots have been owned by the same family, and the land use has been similar on both plots. Between 1870 and 1929, there was some selective cutting, grazing, and evidence of ground fires at both sites. However, since 1929 there has been no cutting, grazing, or ground fires at either site. The diameter distributions of tree species in 1983–1984 suggest both plots consisted of a multi-aged stand in 1983–1984 (Tables 1 and 2). Both plots have many trees that date to the late 1700s, mid 1800s, as well as many to the early to mid 1900s (HM Wilbur, unpublished).

There are few differences between the MLBS and TS plots in soil properties, slope, aspect, or canopy closure. Both plots are on a sandy to pebbly loam derived from sandstones (Swecker *et al.*, 1985). The soils are 1 m deep as coluvium on fractured bedrock and are generally well drained with low water holding capacity (11–12 cm) (Swecker *et al.*, 1985). They are highly acidic and nutrient poor (Swecker *et al.*, 1985). The slope on both plots never exceeds 4°, and both have high canopy closure (data are means  $\pm$  SE and were measured using a spherical densitometer; TS = 96.8%  $\pm$  0.14, n = 300; MLBS = 95.1%  $\pm$  0.15, n = 250). The daily temperature in Jan. has a mean low of -9 C and a mean high of 2 C and in Aug. has a mean low of 12 C and a mean high of 23 C (<http://ncdc.noaa.gov>). The frost-free season averages 146 d, during which the total rainfall is about 900 mm (<http://ncdc.noaa.gov>). High winds, ice, and snow are common in the winter (<http://ncdc.noaa.gov>). Hurricane damage is infrequent on the two study areas (Hazel, 1954; Camille, 1969; Hugo, 1989).

### FIELD METHODS

All trees in both plots that were  $\geq 1.4$  m tall were identified individually and mapped in 1983 (TS) and 1984 (MLBS). In 2007 (MLBS) and 2008 (TS), we re-sampled the entire

TABLE 1.—Basal area per hectare (BA/ha) and stems per hectare (stems/ha) and  $\pm$  one standard error of each species in 1983 and 2008 on the TS plot. Species with a total basal area  $<1\%$  in both 1983 and 2008 constitute the “other” row and include *Betula lenta*, *Crataegus* sp., *Prunus serotina*, *Hamamelis virginiana*, *Ilex montana*, *Nyssa sylvatica*, *Kalmia latifolia*, *Rhododendron calendulaceum*, *Sassafras albidum* and *Vaccinium corymbosum*. Species diversity and species evenness calculations in terms of basal area and stem density in 1983 and 2008. \*Note that *Quercus rubra* has been combined with *Quercus velutina* due to the difficulty in distinguishing the two species. Standard errors are computed from the 24 subplots

Twin springs species	1983		2008	
	BA/ha	Stems/ha	BA/ha	Stems/ha
<i>Quercus rubra</i> *	12.2 $\pm$ 1.0	211.9 $\pm$ 18.0	13.1 $\pm$ 0.4	135 $\pm$ 11.9
<i>Acer rubrum</i>	6.5 $\pm$ 0.7	434.5 $\pm$ 53.9	7.7 $\pm$ 0.8	248.1 $\pm$ 25.8
<i>Quercus alba</i>	8.2 $\pm$ 0.8	186.7 $\pm$ 21.5	6.2 $\pm$ 0.7	77.4 $\pm$ 11.9
<i>Quercus prinus</i>	3.7 $\pm$ 0.6	71.8 $\pm$ 14.4	3.5 $\pm$ 0.6	37.7 $\pm$ 9.9
<i>Amelanchier arborea</i>	1.5 $\pm$ 0.2	251.4 $\pm$ 25.1	1.3 $\pm$ 0.2	123.1 $\pm$ 23.8
<i>Acer pensylvanicum</i>	0.4 $\pm$ 0.1	983.9 $\pm$ 125.7	1.8 $\pm$ 0.1	1252.5 $\pm$ 55.6
<i>Magnolia acuminata</i>	0.2 $\pm$ 0.1	18 $\pm$ 7.2	0.5 $\pm$ 0.2	13.9 $\pm$ 6.0
<i>Tsuga canadensis</i>	0.1 $\pm$ 0.1	14.4 $\pm$ 3.6	0.4 $\pm$ 0.1	15.9 $\pm$ 9.9
<i>Carya</i> sp.	0.5 $\pm$ 0.1	28.7 $\pm$ 3.6	0.4 $\pm$ 0.1	13.9 $\pm$ 4.0
<i>Castanea dentata</i>	0.9 $\pm$ 0.1	869 $\pm$ 100.5	0.1 $\pm$ 0.1	33.7 $\pm$ 7.9
<i>Robinia pseudoacacia</i>	1.1 $\pm$ 0.2	86.2 $\pm$ 14.4	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
Other	0.5 $\pm$ 0.1	434.5 $\pm$ 89.8	0.1 $\pm$ 0.1	31.8 $\pm$ 15.9
Total per hectare	35.8 m <sup>2</sup> $\pm$ 0.3	3591 $\pm$ 5.53	35.1 m <sup>2</sup> $\pm$ 0.45	1985 $\pm$ 3.08
Species Diversity (H')	1.832 $\pm$ 0.037	2.180 $\pm$ 0.053	1.719 $\pm$ 0.040	1.380 $\pm$ 0.063
Species evenness (J')	0.602 $\pm$ 0.012	0.716 $\pm$ 0.019	0.565 $\pm$ 0.015	0.453 $\pm$ 0.026

MLBS plot and half of the TS plot by matching individual trees in the first survey with current living trees, snags, and logs. To sample the TS plot, we subdivided the plot into 12 sections and further subdivided each section into four 25 m  $\times$  25 m subplots. We randomly selected two diagonally opposing subplots in each section to sample. In both plots, all trees, excluding *Acer pensylvanicum*, on the 1983–1984 maps were relocated and their DBH (diameter at breast height, 1.4 m) and condition (alive, dying, snag (standing dead tree), or log) were recorded. The *A. pensylvanicum* trees on the 1983–1984 maps were not relocated due to their high density in the understory in 2007–2008, which made distinguishing trees surviving since 1983 from recruits difficult. All recruits of other species (trees not present in 1983 and  $\geq 1.4$  m. tall in 2007–2008) were identified and their DBH, condition, and location were recorded.

In Jun. 2008, we subdivided one subplot in each section of the TS plot into 25 5 m  $\times$  5 m quadrats ( $n = 300$ ) and subdivided the MLBS plot into 250 5 m  $\times$  5 m quadrats to obtain *Acer pensylvanicum* stem density and basal area estimates and to understand the relationship between *Quercus* juvenile abundance, *A. pensylvanicum* abundance, and light availability. We recorded the total number and the DBH of all *A. pensylvanicum*  $\geq 1.4$  m. tall, the number of *Q. rubra*, *Q. alba*, *Q. prinus*, and *Q. velutina* juveniles, and percent canopy closure using a convex spherical densitometer for four counts in each quadrat on both plots. We divided juveniles into three categories: true seedlings, *i.e.*, trees that germinated in 2008; herb layer juveniles, *i.e.*, trees  $\leq 25$  cm in height; and shrub layer juveniles, *i.e.*, trees 25 cm to 1.4 m. Herb layer juveniles, also known as seedling sprouts, are a common life stage among *Q. rubra* and *Q. alba* in dense shade environments (Lorimer, 1993; Johnson *et al.*, 2002), in which growth is allocated to root development rather than shoot development (Crow, 1988;

TABLE 2.—Basal area per hectare (BA/ha) and stems per hectare (stems/ha) of each species in 1983 and 2008 on the MLBS plot. Species with a total basal area <0.5% in both 1984 and 2007 constitute the “other” row and include *Betula lenta*, *Prunus serotina*, *Rhododendron calendulaceum*, and *Vaccinium corymbosum*. No standard error is given since the entire plot was surveyed in both 1984 and 2007. \*Note that *Quercus rubra* has been combined with *Quercus velutina* due to the difficulty in distinguishing the two species

MLBS species	1984		2007	
	BA/ha	Stems/ha	BA/ha	Stems/ha
<i>Quercus rubra</i> *	20.0	593.4	23.1	370.9
<i>Acer pensylvanicum</i>	0.0	144.6	2.1	796.3
<i>Quercus alba</i>	2.7	310.0	1.9	221.8
<i>Acer rubrum</i>	0.8	132.8	1.8	487.9
<i>Robinia pseudoacacia</i>	0.9	29.5	0.4	12.1
<i>Carya</i> sp.	0.5	53.1	0.3	28.2
<i>Castanea dentata</i>	0.8	1275.3	0.0	46.4
<i>Amelanchier arborea</i>	0.2	64.9	0.3	32.3
Other	0.1	348.3	0.1	20.2
Total per hectare	26.1 m <sup>2</sup>	2952	30.1 m <sup>2</sup>	2016
Species Diversity (H')	0.913	1.695	0.907	1.562
Species evenness (J')	0.367	0.682	0.365	0.629

Dickson, 1991). While herb layer juveniles and true seedlings were often the same size, they were distinguished because true seedlings still obtained nutrients from the acorn and lacked a woody stem, unlike herb layer juveniles.

#### DATA ANALYSIS

The spatially explicit historical data and current data allowed documentation of forest composition change from 1983–1984 to the present for basal area (m<sup>2</sup> per ha) and density (number of stems per ha) of all tree species. On both plots, we used the measure of abundance and DBH of *Acer pensylvanicum* from the quadrats to estimate the current total density and basal area. *Quercus velutina* (black oak) and *Q. rubra* are both part of the red oak section (Lobatae), are known to hybridize with each other (Nixon, 2008), and can be difficult to distinguish without acorns or young leaves. Therefore, we combined the data from these two species when estimating the change in forest composition and oak mortality patterns. We evaluated species diversity for both plots in 1983–1984 and 2007–2008 using the Shannon-Wiener index of diversity ( $H' = -\sum p_i \ln p_i$ ), where  $p_i$  is the proportion of total basal area (or stem density) per hectare of species  $i$ , and  $\ln$  is the natural logarithm. We calculated a separate measurement of species evenness,  $J' = H'/H'_{\max}$ , since  $H'$  alone confounds species richness (the number of species in a sample) and species evenness (Elliot *et al.*, 2002). For both the species diversity and species evenness, two calculations were made: one based on basal area per hectare and the other based on stem density per hectare of each species.

The spatially explicit historical data and current data enabled us to analyze how growth and mortality patterns of *Quercus rubra* and *Q. alba* vary for the two species, among size classes, and plots. To analyze the data, we divided the oak trees  $\geq 1.4$  m tall into three size classes: small tree (DBH 0–5 cm), subcanopy (5.1–20 cm), and canopy (>20 cm). These size classes were similar to other *Quercus* studies that related DBH to canopy strata level in the eastern deciduous forests (*e.g.*, McDonald *et al.*, 2003). We calculated species mortality rates by plot and size classes of *Q. rubra* and *Q. alba*, and used a Pearson chi-squared statistic to test

for differences. We calculated the mean and standard error of growth rate of *Q. rubra* and *Q. alba* in each size class and at each plot. Data on true seedlings and herb layer juveniles, were pooled within *Q. prinus* and *Q. alba*, both in the white oak group (section *Quercus*), and within *Q. velutina* and *Q. rubra*, both in the same red oak group (section *Lobatae*), due to the difficulty in identifying seedlings within the same subgenus. A Wilcoxon test used the data gathered from the  $5 \times 5$  m quadrats to determine if the abundance of white oak and red oak juveniles were significantly different between the plots and between the two subgenera. We did a correlation analysis to see if there was a correlation of number of white oak and red oak juveniles with the abundance of *Acer pensylvanicum* and light availability. Additionally, we did a correlation analysis of *A. pensylvanicum* abundance and light availability. All statistical analyses were done using JMP (version 8, SAS institute, Cary, North Carolina, U.S.A.) with  $\alpha = 0.05$  for significance.

## RESULTS

### PLOT DIFFERENCES IN 1983–1984

The forest composition of the two plots differed when initial measurements were made in 1983 and 1984. The diversity ( $H'$ ) of basal area of tree species was twice as great, and evenness ( $H'/H_{\max}$ ) was 64% greater, respectively on the TS plot than on the MLBS plot (Tables 1 and 2). *Quercus rubra* had the greatest basal area in both plots and was especially dominant in the MLBS plot (Tables 1 and 2). *Acer pensylvanicum* and *Castanea dentata* had the greatest number of stems in the TS plot (27% and 23% respectively). *Castanea dentata* was the most abundant species (44%), and *A. pensylvanicum* was not very abundant (<5%) in the MLBS plot (Tables 1 and 2).

### CHANGES IN FOREST COMPOSITION

Species diversity and evenness of stem density decreased by 37% in the TS plot and decreased by 8% in the MLBS plot from 1983–1984 to 2007–2008 (Tables 1 and 2). Diversity and evenness of basal area exhibited similar trends (Tables 1 and 2). Self-thinning occurred on both plots; the total numbers of stems decreased by 32% on the MLBS plot and by 44% on the TS plot (Tables 1 and 2). The overall basal area decreased by 2% on the TS plot and increased by 15% on the MLBS plot (Tables 1 and 2). The average basal area of an individual tree increased by 69% in the TS plot ( $100 \text{ cm}^2$  to  $177 \text{ cm}^2$ ) and by 77% in the MLBS plot ( $88 \text{ cm}^2$  to  $149 \text{ cm}^2$ ) from 1983–1984 to 2007–2008.

*Quercus rubra* remained the dominant species by basal area on both plots in 2007–2008 (37% and 77% at TS and MLBS, respectively). In 1983–1984, *Castanea dentata* as stump sprouts had the greatest number of stems on the MLBS plot (43%), and *Acer pensylvanicum* and *C. dentata* had nearly equal numbers of stems on the TS plot (27% and 23% respectively) (Tables 1 and 2). In 2007–2008, however, *A. pensylvanicum* had the most stems (63.1% on TS and 39.5% on MLBS), and *C. dentata* contributed less than 3% of stems (Tables 1 and 2).

The majority of species on both plots experienced greater mortality than recruitment, and many species declined in numbers and basal area by >50% (Figs. 1, 2). All *Vaccinium corymbosum* stems died on the TS plot ( $n = 248$ ) and on the MLBS plot ( $n = 16$ ). On the TS plot, all stems of *Crataegus* sp. ( $n = 2$ ), *Sassafras albidum* ( $n = 23$ ), and *Robinia pseudoacacia* ( $n = 129$ ) also died. *Rhododendron calendulaceum* declined in numbers by 94% on the MLBS plot ( $n = 326$ ) and by 99% on the TS plot ( $n = 202$ ).

Only three species, *Acer pensylvanicum*, *Tsuga canadensis*, and *Amelanchier arborea* had recruitment into the tree size class on the TS plot (Fig. 1 and Table 3). Six species, *A.*



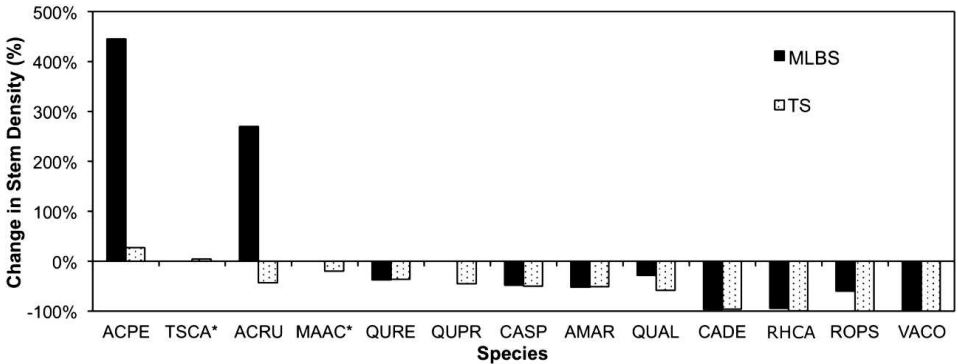


FIG. 1.—Percent change in stem density from 1983–1984 to 2007–2008 of each species on the MLBS plot and TS plot. Species with a total basal area or stem density that were <1% in 1983–1984 and 2007–2008 in both plots are not listed and include *Betula lenta* and *Prunus serotina* on both plots, and *Crataegus* sp., *Hamamelis virginiana*, *Ilex montana*, *Nyssa salvatica*, *Kalmia latifolia*, and *Sassafras albidum* on the Twin Springs plot. Species codes are the first two letters of the genus followed by the first two letters of the species (i.e., *Quercus alba* is QUAL) except QURE that includes *Quercus rubra* and *Quercus velutina* (see Tables 1 and 2). \*Note that species with an asterisk are present on the TS plot, but not on the MLBS plot

*pensylvanicum*, *A. rubrum*, *Quercus alba*, *A. arborea*, *Q. rubra*, and *Robinia pseudoacacia*, had recruitment into the tree size class on the MLBS plot (Table 3).

#### RECRUITMENT, GROWTH, AND MORTALITY PATTERNS OF QUERCUS RUBRA AND QUERCUS ALBA

Mortality exceeded recruitment for *Quercus rubra* and *Q. alba* on both plots as evidenced by their decline in stem density (Tables 1 and 2). There was no oak recruitment on the TS plot. On the MLBS plot there was low *Q. alba* recruitment and even less *Q. rubra* recruitment (Table 3). Size classes of *Q. rubra* and *Q. alba* significantly differed in mortality on each plot (Fig. 3). Small trees of *Q. rubra* and *Q. alba* experienced greater mortality than subcanopy trees, which experienced greater mortality than canopy trees ( $\chi^2$  tests,  $P < 0.0006$ ; Fig. 3). Among canopy trees, mortality of *Q. alba* was significantly greater than that of *Q. rubra* only on the TS plot ( $\chi^2_1 = 9.82$ ,  $P = 0.002$ ; Fig. 3). Among subcanopy trees on both plots, *Q. alba* mortality was significantly greater than *Q. rubra* (MLBS  $\chi^2_1 = 4.57$ ,  $P = 0.03$ ; TS  $\chi^2_1 = 7.39$ ,  $P = 0.006$ ; Fig. 3). Among small trees, mortality was significantly greater on the TS plot than on the MLBS plot only for *Q. alba* trees (Fig. 3).

Among canopy trees, *Quercus rubra* had greater relative growth rates (RGR) ( $RGR = (DBH_2 - DBH_1)/DBH_1$ ) than *Q. alba* (Fig. 4). Small trees of *Q. alba* had greater RGR than subcanopy trees, which had a greater RGR than canopy trees (Fig. 4).

The combination of recruitment, growth, and mortality patterns of *Quercus rubra* and *Q. alba* caused the DBH distribution of *Q. rubra* and *Q. alba* to shift to the right and down on both plots, showing that there had been more mortality than recruitment, and that the trees that survived had grown (Fig. 5). On both plots, there was a decline in numbers of *Q. rubra* and *Q. alba* in the smaller size classes (Fig. 5).

#### QUERCUS SEEDLING ABUNDANCE, ACER PENSYLVANICUM ABUNDANCE, AND LIGHT AVAILABILITY

There was an interaction between species and plot in the abundances of true seedlings and herb layer juveniles. For both of these age classes, *Quercus alba* was less abundant than *Q. rubra* on the MLBS plot, but the reverse was true on the TS plot (Fig. 6). There were fewer



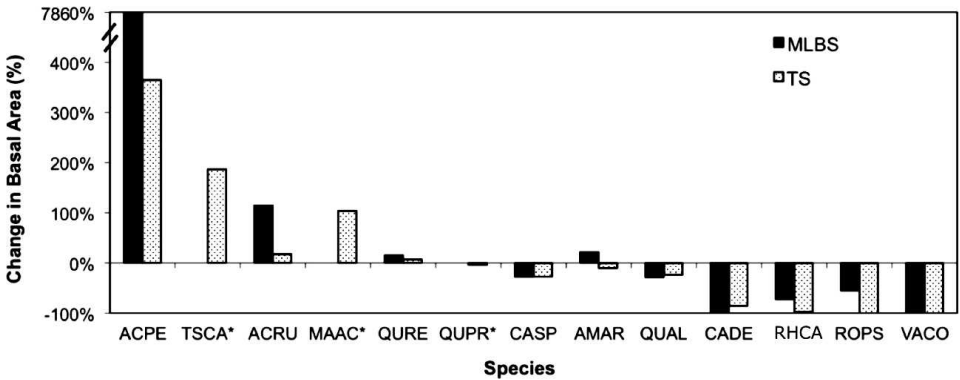


FIG. 2.—Percent change in basal area from 1983–1984 to 2007–2008 of each species on the MLBS plot and TS plot. Species with a total basal area or stem density that were less than 1% in 1983–1984 and 2007–2008 in both plots are not listed and include *Betula lenta* and *Prunus serotina* on both plots, and *Crataegus* sp., *Hamamelis virginiana*, *Ilex montana*, *Nyssa salivatica*, *Kalmia latifolia*, and *Sassafras albidum* on the Twin Springs plot. \*Note that species with an asterisk are present on the TS plot, but not on the MLBS plot. \*\*Note that the y-axis is split from 400% to 7860%. Species codes are the first two letters of the genus followed by the first two letters of the species (*i.e.*, *Quercus alba* is QUAL) except QURE that includes *Quercus rubra* and *Quercus velutina* (see Tables 1 and 2)

shrub layer juveniles than herb layer juveniles of both species on both plots (Fig. 6). On the MLBS plot, there were more shrub layer juveniles of *Q. alba* than *Q. rubra*. There was a statistically significant, weak, negative relationship between the basal area of *Acer pensylvanicum* and canopy closure in both the MLBS plot (Spearman's  $\rho = -0.23$ ,  $P = 0.0002$ ,  $n = 250$ ) and the TS plot (Spearman's  $\rho = -0.39$ ,  $P < 0.0001$ ,  $n = 300$ ). The density of true seedlings was generally uncorrelated with the basal area of *A. pensylvanicum*. The exception was a statistically significant, weak, positive relationship of *Q. alba* true seedlings on the TS plot (Spearman's  $\rho = 0.14$ ,  $P = 0.014$ ,  $n = 300$ ). The densities of herb layer juveniles of both oaks, however, were negatively correlated with *A. pensylvanicum* basal area (TS plot Spearman's  $\rho = -0.13$ ,  $P = 0.037$ ,  $n = 300$ ; MLBS plot  $\rho = -0.30$ ,  $P < 0.001$ ,  $n =$

TABLE 3.—Recruitment of all species in both the MLBS and TS plot based on number of stems per hectare. Species with no recruitment are not listed. \*Note that *Acer pensylvanicum* recruitment number is the minimum number possible recruited. Individual *A. pensylvanicum* were not relocated on the TS or MLBS map. The number of *A. pensylvanicum* recruits listed is the number alive in 2007/2008 minus the number alive in 1983. Therefore, the annual rate of recruitment would be greater than suggested by these net 23 or 25 y differences

Species	Recruitment	
	MLBS	TS
<i>Acer pensylvanicum</i> *	650*	268*
<i>Tsuga canadensis</i>	0	6
<i>Acer rubrum</i>	428	0
<i>Quercus rubra</i> + <i>Q. velutina</i>	16	0
<i>Amelanchier arborea</i>	18	0.67
<i>Quercus alba</i>	134	0
<i>Robinia pseudoacacia</i>	16	0

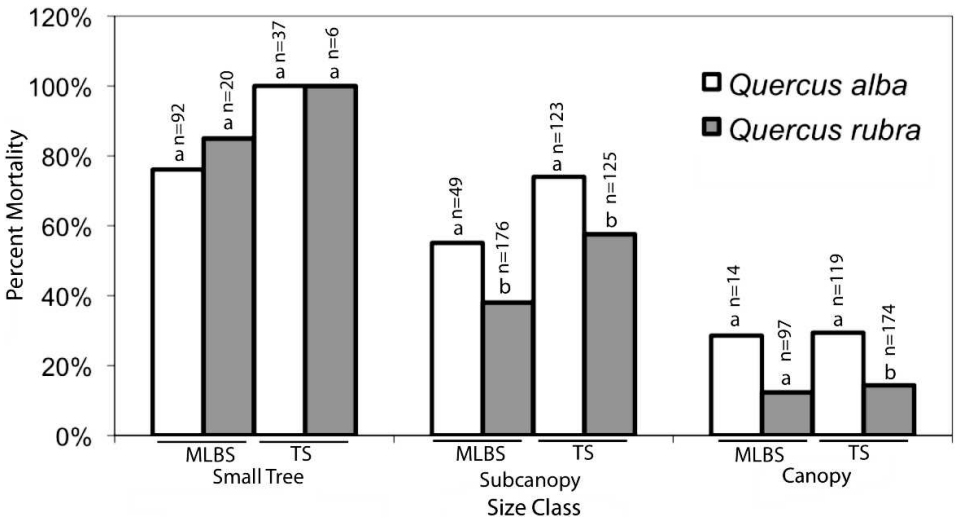


FIG. 3.—Percent mortality of *Quercus rubra* and *Q. alba* in the TS plot and the MLBS plot from 1983–1984 and 2007–2008. N shows the number of trees in the size class that were alive in 1983–1984. There were significant differences among size class within both plots and species ( $P < 0.05$ ,  $\chi^2_1$  tests), and there were significant differences in mortality among plots of *Q. alba* in the small tree size class ( $P = 0.001$ ,  $\chi^2_1$  tests) and of both *Q. alba* and *Q. rubra* in the subcanopy size class ( $P < 0.02$ ,  $\chi^2_1$  tests). Different letters indicate significant differences ( $P < 0.05$ ,  $\chi^2_1$  tests) in mortality among species within the same size class and plot

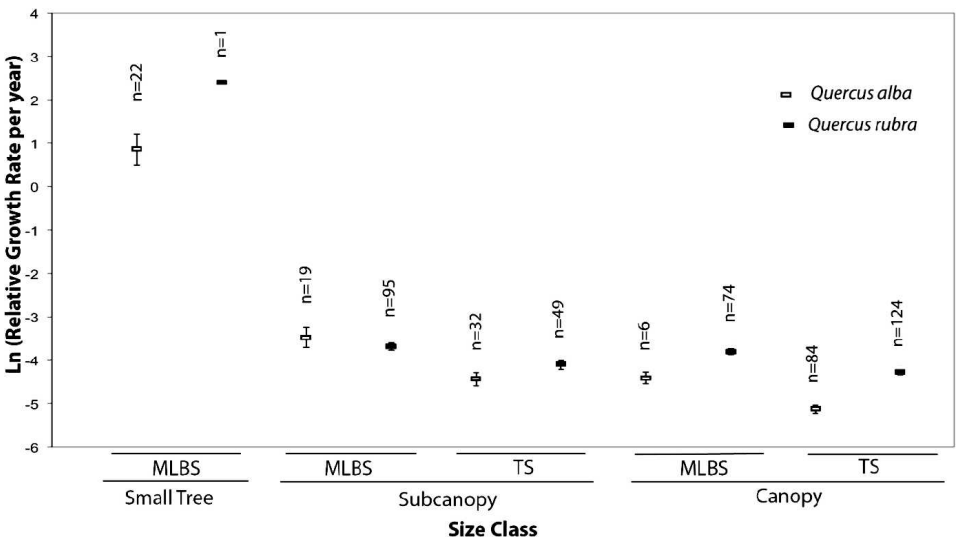


FIG. 4.—Mean and one standard error of the natural log of relative growth rate of *Quercus rubra* and *Q. alba* in the TS plot and the MLBS plot from 1983–1984 and 2007–2008. N is the number of trees in the size class that survived from 1983–1984 to 2007–2008

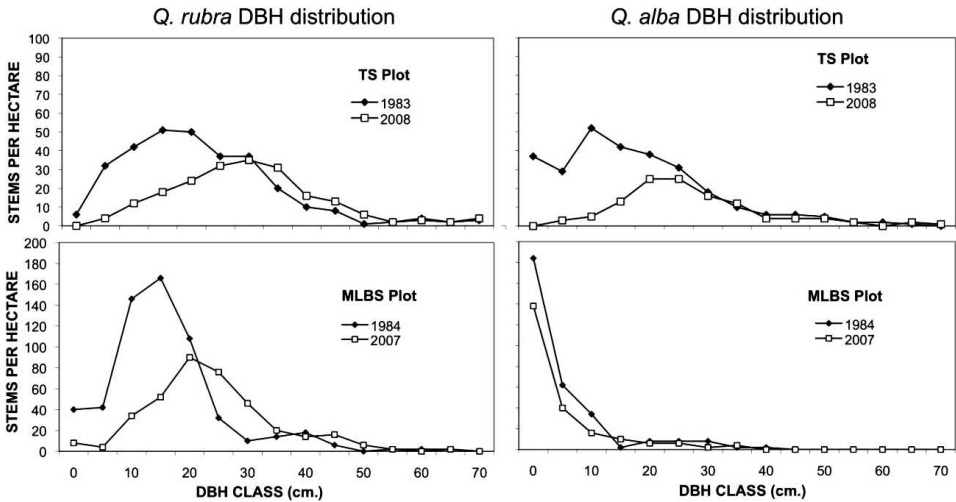


FIG. 5.—Size class distribution based on DBH (cm) of *Quercus rubra* and *Q. alba* in 1983–1984 and in 2007–2008 in the MLBS and TS plot. Upper left and upper right show the size class distribution of *Q. rubra* (left) and *Q. alba* (right) in the TS plot in 1983 and in 2008. Lower left and lower right show the size class distribution of *Q. rubra* (left) and *Q. alba* (right) in the TS plot in 1984 and in 2007

250). There were no sufficient shrub layer juveniles of either oak in the TS plot or *Q. rubra* shrub layer juveniles in the MLBS plot for a correlation analysis (Fig. 6). In the MLBS plot, there was a significant weak negative correlation with the abundance of *Q. alba* shrub layer juveniles and the basal area of *A. pensylvanicum* (Spearman's  $\rho = -0.19$ ,  $P = 0.0028$ ,  $n = 250$ ).

## DISCUSSION

Our study supported the generalization that mesic species with greater shade tolerance are increasing in abundance in the Southern Appalachians where no stand-initiating disturbances have occurred, resulting in a less oak dominated forest (Nowacki and Abrams, 2008; Figs. 1, 2). In particular, *Acer pensylvanicum* has dramatically increased in abundance in the understory, while the majority of other species have declined. There has been a lack of oak recruitment, which may be linked to the increase in *A. pensylvanicum*, the lack of stand initiating disturbance, and ungulate browsing.

### PLOT DIFFERENCES IN 1983–1984

The physical characteristics of the two plots were similar, but their forest composition and structure differed in 1983–1984, which clearly affected how the forest composition of the two plots changed over time. In 1983–1984, the TS plot may have been successional more advanced with lower light levels than the MLBS plot, because individual trees had a larger basal area and *Acer pensylvanicum* (a shade tolerant understory tree) was already more abundant in the TS plot than on the MLBS plot (Tables 1 and 2).

### FOREST COMPOSITIONAL CHANGES

Species diversity decreased on both plots, and mortality exceeded recruitment for the majority of species. *Quercus rubra* still dominated the basal area on both plots (Tables 1 and

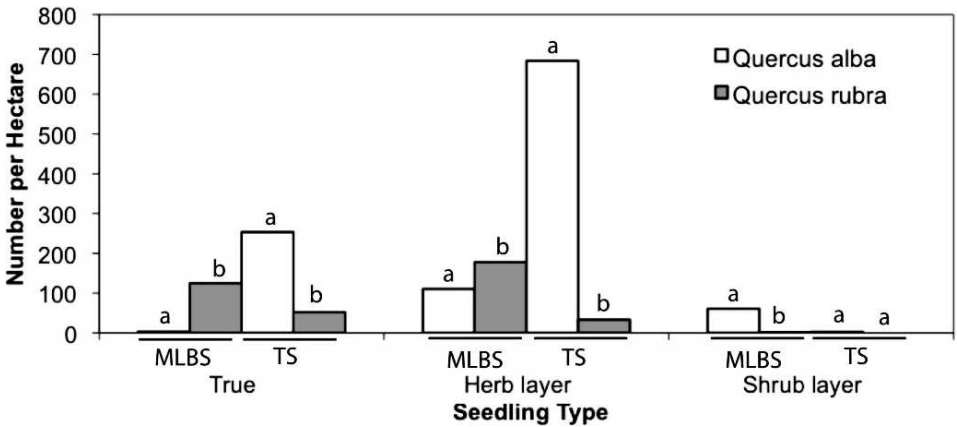


FIG. 6.—Abundance of *Quercus alba* and *Q. rubra* true, herb layer, and shrub layer juveniles per hectare in both the MLBS and TS plot. There were significant differences in seedling abundance among seedling types within both plots and species (all  $P < 0.0001$ , Wilcoxon test). Significant differences in juvenile abundance among plots (all  $P < 0.001$ , Wilcoxon test), except for *Q. rubra* shrub layer juveniles ( $P = 0.27$ , Wilcoxon test). Different letters indicate significant differences ( $P < 0.05$ , Wilcoxon test) in juvenile abundance among species within the same seedling type and plot

2), but it had decreased in numbers through self-thinning (Fig. 1). On the other hand, *Acer pensylvanicum* had increased more than any other species both in numbers and in basal area (Figs. 1, 2; Table 3), so had the greatest density among all species on both plots (Tables 1 and 2). These results supported work by Jokela and Sawtelle (1985) and Peet and Loucks (1977), who suggested that *Q. rubra* is a pioneer species that, after initial dominance, is replaced by more shade tolerant species.

Only shade tolerant species have increased in stem density since the 1980s on both plots. *Tsuga canadensis* on the TS plot and *Acer rubrum* on the MLBS plot were the only species, other than *A. pensylvanicum*, to increase in numbers (Table 3). *Tsuga canadensis* is one of the most shade tolerant species of eastern deciduous forests and can establish and persist under a closed canopy, where it receives as little as 5% of full sunlight (Graham, 1941; Baker, 1949; Hough, 1960; Goerlich and Nyland, 2000). *Acer rubrum* is also shade tolerant but only moderately so compared to *T. canadensis* and *A. pensylvanicum* (Graham, 1941; Baker, 1949). Thus, in the past 25 y there has been an increase in shade tolerant species and a decline in intermediate tolerant and shade intolerant species in the study locations.

The lack of recruitment and high mortality of shade intolerant species and intermediate shade tolerant species suggested that light availability in the understory was limiting species regeneration and survival, especially on the TS plot. Very shade intolerant species such as *Sassafras albidum* and *Robinia pseudoacacia* were no longer present on the TS plot, and on the MLBS plot, *R. pseudoacacia* declined by over 60% in stem density. *Quercus rubra*, *Q. alba*, *Amelanchier arborea*, and *Carya* spp. have intermediate shade tolerance (Baker, 1949; Minckler, 1965; Sanders, 1965; Smalley, 1965) and all declined on both plots. Given the high mortality of shade intolerant species and the low mean light levels of both plots (less than 5% of full sunlight), these findings agree with Kobe *et al.* (1995), who found that at these light levels there are large differences in survival among northern hardwood species. High mortality and no recruitment of *Vaccinium corymbosum* and *Crataegus* sp., two shade intolerant understory shrubs (Rogers, 1974; Sharps, 1974), and *Rhododendron calendulaceum*,

an intermediate shade tolerant shrub (Carey, 1994), support Abrahamson and Gohn (2004) who found dense ground cover of *Vaccinium* sp. and *R. calendulaceum* under a mixed-oak over-story but sparse ground cover beneath dense canopies of either *T. canadensis* or *A. pensylvanicum*. Furthermore, high recruitment of shade tolerant species, particularly *A. pensylvanicum*, and lack of recruitment of intermediate shade tolerant and shade intolerant species suggest that light limits species regeneration, and juveniles have not been able to survive and grow in the understory.

#### RECRUITMENT, GROWTH, AND MORTALITY PATTERNS OF QUERCUS RUBRA AND QUERCUS ALBA

The increase in basal area of *Quercus rubra*, unlike *Q. alba*, on both plots is likely due to its faster growth rate and lower mortality of subcanopy and canopy trees compared to *Q. alba* (Figs. 3, 4). However, the lack of small *Q. rubra* trees (Fig. 5), their higher mortality on the MLBS plot (Fig. 3), and their lower recruitment (Table 3) indicated that this species was less able to regenerate under a closed canopy than *Q. alba*. These life histories generate the more symmetric DBH distribution of *Q. rubra* in contrast to the inverse J-shaped DBH distribution of *Q. alba* in 1983–1984 (Fig. 5). Our results, coupled with those from other studies that have found symmetric distributions of *Q. rubra* and *Q. alba* in mixed forests in the eastern U.S. (Christensen, 1977; Orwig *et al.*, 2001; Abrahamson and Gohn, 2004), suggest that a decline of *Q. rubra* and *Q. alba* has occurred throughout their eastern range.

#### QUERCUS SEEDLING ABUNDANCE, ACER PENNSYLVANICUM ABUNDANCE, AND LIGHT AVAILABILITY

There are several possible explanations for the lack of oak recruitment: lack of acorns, inability of the acorns to germinate, mortality of seedlings, inability of herb layer juveniles to enter the shrub layer, or inability of shrub layer juveniles to enter the understory (Johnson *et al.*, 2002). Both *Quercus rubra* and *Q. alba* produce good acorn crops every few years (Schopmeyer, 1974; Sork *et al.*, 1993), and so the densities of the true seedlings are likely dependent on whether or not there was a favorable mast year (Sork *et al.*, 1993). Our results showed that lack of recruitment was most likely not due to lack of oak true seedlings or herb layer juveniles but due to an inability of herb layer juveniles to enter the shrub layer or high mortality of shrub layer juveniles. The lack of oak recruitment despite the high number of white oak herb layer juveniles in the TS plot, unlike the MLBS plot, indicate that the lack of recruitment is due to an inability of herb layer juveniles to enter the shrub layer. Interestingly, *Q. alba* was moderately common in the shrub layer on the MLBS plot but not on the TS plot, and *Q. rubra* was very rare in the shrub layer of both plots. The lack of *Q. rubra* and *Q. alba* in the shrub layer on the TS plot and the presence of only *Q. alba* in the shrub layer on the MLBS plot support the hypotheses that *Q. alba* is more shade tolerant and that the TS plot is successional more advanced than the MLBS plot.

The correlation analysis of oak juveniles and light availability indicated that light limited their survival in the herb and shrub layers. Other studies that have also found oak juveniles to be strongly correlated with environmental gradients, especially light (Collins and Carson, 2004). The significant negative relationship between *Acer pensylvanicum* abundance and light availability in the understory suggested that the broad leaves of *A. pensylvanicum* create dense shade in the understory and may inhibit oak regeneration. Lorimer *et al.* (1994) also reported that oak seedlings have a very low survival rate under understory trees such as *Acer*.

Deer were regularly seen foraging on both our plots (Redmond, pers. obs.). Studies have shown that deer negatively affect the survival of herb layer and shrub layer oak juveniles (Tilghman, 1989; Kittredge and Ashton, 1995; Stange and Shea, 1998; Russel, 2001; Rooney, 2003), because of selective browsing on oak seedlings compared to other trees, such as *Acer pensylvanicum* and *A. rubrum* (Tilghman, 1989; Kittredge and Ashton, 1995). Mortality by

deer browsing is likely be a contributing factor affecting the transition from the herb to the shrub layer.

#### FUTURE FOREST COMPOSITION CHANGES

Understory trees can influence composition of the canopy by affecting the regeneration of potential canopy species (Phillips and Murdy, 1985; Clinton *et al.*, 1994). *Castanea dentata* was one of the dominant understory tree species on both plots in 1983–1984 (Tables 1 and 2) but was replaced by *A. pensylvanicum* (Tables 1 and 2). *Acer pensylvanicum* has broader leaves than *C. dentata* and creates a more shaded forest floor (King, 2003). *Acer pensylvanicum* is a gap-phase species that performs best in small gaps (Sipe and Bazazz, 1995) and depends on canopy trees for shading. As large canopy gaps open up due to disturbances, trees that have been able to live under dense shade environments but can also tolerate the high levels of lights will increase in dominance (Sipe and Bazzaz, 1995). The canopy species *A. rubrum*, along with *Tsuga canadensis* and possibly *Quercus alba* will likely increase in abundance because they can survive in a shaded understory (Minckler, 1965). *Quercus rubra* was able to dominate after more intense disturbances, such as fire or the chestnut blight, but in the past century the disturbance regime has shifted to localized gap-dynamics enabling *A. pensylvanicum*, *A. rubrum* and *T. canadensis* to increase in abundance (Orwig *et al.*, 2001; Abrahamson and Gohn, 2004).

#### CONCLUSION

The majority of species on our two plots declined in numbers, and the previous oak forest now includes more mesic and shade tolerant species in the understory. Over the past 25 y, there has been a decline in all intermediate shade tolerant and shade intolerant trees including both *Quercus rubra* and *Q. alba* and a large increase in the number of *Acer pensylvanicum* trees since the 1980s. The decrease in oak abundance is due to a lack of recruitment and high mortality of small trees. Increased abundance of *A. pensylvanicum* appears to have a negative effect on oak seedling and herb layer juvenile survival by decreasing light availability in the understory, and it also likely contributed to the high mortality of small oak trees. These trends are likely to continue for both oak species, while we expect that more shade tolerant trees like *Tsuga canadensis* and intermediate shade tolerant species like *A. rubrum* and possibly *Q. alba* will continue to increase in abundance.

This observational study of one forest in the Southern Appalachians supported trends seen in other eastern deciduous forests (McDonald *et al.*, 2002; Abrams, 2003; Nowacki and Abrams, 2008). Our study focused on light availability as a driving factor for changes in species composition, but to further understand recruitment, growth, and mortality of *Quercus rubra* and *Q. alba* research is needed on the effects of nutrient availability, deer abundance, gypsy moth abundance, fire frequency, and annual weather trends and variation.

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