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

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Abstract The purpose of this study is to understand how the abundance of the two dominant species, *Quercus rubra* (northern red oak) and *Quercus alba* (white oak), in a previous chestnut-oak forest in the Southern Appalachians has changed since the 1980s and may change in the future. Using spatially explicit data from the early 1980s and current data from 2007-08 of individually mapped trees on two plots on Salt Pond Mountain in southwest Virginia, this study looks at how the basal area and density of all tree species has 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 number of shade intolerant trees and intermediate shade tolerant trees including both *Q. rubra* and *Q. alba*. A correlation analysis of *A. pensylvanicum* abundance, *Quercus* seedlings, and light availability shows a negative relationship with abundance of *A. pensylvanicum* and light availability in the understory as well as *Quercus* seedling abundance. Both *Q. rubra* and *Q. alba* have experienced stand thinning, and the previous oak-chestnut forest has transformed to an oak-maple forest and will continue to become increasingly dominated by maples and other shade tolerant species.

Introduction

Oaks have dominated many of the forests of the eastern United States for over 10,000 years, and 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 suppression (Lorimer 2001), cattle grazing, hunting, logging, road building, and the introduction of new pathogens, insects, and flora (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 in range and increased in dominance (Abrams 2003). Oaks are an integral part of eastern U.S. deciduous forests; they provide nutrition for a wide range of wildlife such as deer, bears, songbirds, and small mammals (McShea and Healy 2002), and the abundance of oaks has a profound impact on the whole eastern deciduous biome (Wolff 1996). Understanding the factors that impact the abundance and distribution of oaks in the mixed deciduous forest of the eastern U.S., especially those factors introduced post Euroamerican settlement, will enable better prediction of how well oaks will survive in future climatic and disturbance regimes. This will provide a basis for creating new protocols for forest management that will not only enhance the survival of the oaks in the eastern forests, but will also result in an overall more robust forest ecology.

Forest succession is the directional change in forest composition and structure through time. Disturbances that can disrupt succession include events like fire, wind, disease, and herbivory that cause abrupt changes in forest structure and change resource availability, substrate availability, or the physical environment that can allow other tree species to become dominant (Pickett and White 1985). For example, fires increase soil nutrient availability and light availability in the understory allowing early successional species to increase in dominance. Overtime these early successional species are replaced by later successional species that are generally more shade tolerant (Bazazz 1979).

Both human-induced and natural disturbances influence the composition of the deciduous forests of eastern North America and affect oak dominance. Periodic fires were common before Euroamerican 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 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 species and maintaining light availability in the understory (Abrams 1992; Hibbs 1980; Lorimer 1984). Numerous studies have shown that fire suppression over the last century has promoted the replacement of oaks by less fire tolerant, but more shade tolerant species, such as species of *Acer* (maple), *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 the chestnut blight (*Chryphonectria parasitica*), a scomycete, 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, there was a large increase in abundance of several species of oak, especially *Quercus rubra* (northern red oak), as well as shade tolerant species such as *A. rubrum* and *Amelanchier arborea* (service berry) in the previous chestnut-oak forests of the eastern U.S. (Karban 1978; Keever 1953; McCormick and Platt 1980; Stephenson 1986; Woods and Shanks 1959).

In the eastern deciduous forests, other abiotic and biotic factors affect oak abundance as well, such as 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 years promote oak recruitment and dominance in the eastern deciduous forest by making oaks better competitors compared to other species (Bahari *et al*. 1985; Dickson and Tomlinson 1996). Relative to other eastern deciduous hardwood species, oaks have deep roots, xeromorphic leaves, and an ability to adjust osmotically, making them drought tolerant (Abrams 1990; Dickson and Tomlinson 1996). Heavy 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 strict hunting regulations and changes in land use, 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 impacts oak abundance by increasing oak mortality. Gypsy moths prefer oaks compared to other hardwood species, and allow oaks to be replaced by species such as *Acer* (Fajvan and Wood 1996). Since forests are dynamic and are affected by a suite of factors, it can be very useful to clearly document how these forests have changed through discrete time intervals in order to determine the causes of those changes.

In this study I use historical data from the 1980s of two mapped plots on a previous chestnut-oak forest on Salt Pond Mountain to look at how the abundance of the two dominant canopy species, *Q. alba* and *Q. rubra,* has changed since the 1980s. Stephenson (1986) compared data of a chestnut-oak stand on Salt Pond Mountain of the Southern Appalachians of Virginia 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 *C. dentata* may be a temporary mid successional transition. Studies done in Vermont and Wisconsin found *Q. rubra* to be a pioneer species that, after initial dominance, is replaced by shade tolerant species (Jokela and Sawtelle 1985, Marks 1942; Peet and Loucks 1977). Oak seedlings require high amounts of light to survive and grow and have poor survival under understory trees like *Acer* (Crow 1988; Lorimer 1984; Lorimer *et al.* 1994), and numerous studies have shown that these more shade tolerant trees have increased. *Acer pensylvanicum* (striped maple), the dominant understory tree in the forest understudy, is well adapted to live under heavy shade and has broad leaves which create a dense shade environment that can inhibit *Q. rubra* and *Q. alba* regeneration (Hibbs 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.

Q. rubra (part of red oak group, section *Lobatae* or *Erythrobalanus*) and *Q. alba* (part of white oak group, section *Leucobalanus or Lepidobalanus*) differ in many life history characteristics which affect their growth, recruitment, and mortality patterns and ultimately abundance (Nixon 1993; Manos *et al.* 1999). In general, *Q. alba* is the slower growing species of the two and longer lived (*Q. alba* can live to be over 200 years old where as *Q. rubra* usually lives to be less than 100). Additionally, *Q. alba* is considered slightly more shade tolerant than *Q. rubra* (Sanders 1965). *Q. alba* is more fire resistant (Abrams 1992; Hardin *et al*. 2001), more drought tolerant, and is found on more xeric sites than *Q. rubra* (Abrams, 1992; Bahari *et al.* 1985). *Q. alba* mast at longer intervals than *Q. rubra* and produce good acorn crops every 4 to 10 years, whereas acorn crops of *Q. rubra* occur every 2 to 5 years (Schopmeyer 1974). It takes two years for *Q. rubra* acorns to mature and germination occurs in the spring; with *Q. alba*, it takes only one year for its acorns to mature and germination occurs in the fall (Crow 1988; Fox 1982). *Q. rubra* acorns have 300% to 400% higher tannin levels than *Q. alba,* which gives them a bitter taste and makes them less palatable to wildlife (McShea and Healy 2002). The different life history characteristics of *Q. rubra* and *Q. alba* affect their ability to regenerate, grow, and survive through different disturbances in the eastern deciduous forests.

Understanding how the abundance of *Q. rubra* and *Q. alba* and other species have changed in discrete time intervals under known disturbance conditions and their growth, recruitment, and mortality patterns during those time intervals will allow for a better prediction of how oak dominance will shift in the future. The purpose of this study is to understand how the abundance of the two dominant species, *Q. rubra* and *Q. alba*, in a previous chestnut-oak forest in the Southern Appalachians has changed since the 1980s and to better predict how the forest composition will change in the future. However, 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 I specifically address are:

1.) How has the basal area and stem number of each tree species and overall forest diversity changed in the past 25 years?

2.) How much recruitment did each species experience since the 1980s?

3.) How do *Q. rubra* and *Q. alba* differ in their recruitment, growth and mortality patterns?

4.) What is the abundance of *Q. rubra* and *Q. alba* seedlings and is this correlated with the abundance of the dominant understory tree, *A. pensylvanicum* at the sampled sites?

I predict that in the past 25 years there has been an increase in shade tolerant trees, especially maples, and a decline in oaks and other shade intermediate tolerant and intolerant species due to the lack of disturbances that open up large canopy gaps. I predict that *Q. alba* has declined less than *Q. rubra* due to its different life history characteristics and slightly higher shade tolerance. Additionally, I predict that the abundance of both *Q. rubra* and *Q. alba* seedlings are higher where there is more light availability and fewer *A. pensylvanicum* trees.

This is an observational field study combining historical data from the 1980s and current data from two mapped plots on Salt Pond Mountain in the Southern Appalachians of Virginia. I also conducted a census of current oak seedlings. The spatially explicit historical and current data enables me to see growth, recruitment, and mortality patterns for all species since the 1980s. The oak seedling census gives me insight into what the future recruitment for the two species looks like and if oak recruitment may be limited by the abundance of *A. pensylvanicum*.

Methods

Study area This study was conducted on two plots previously mapped (1982-1983) near Mountain Lake Biological Station in Giles County Virginia, USA, 37°22'N, 80°31'W. The first site, (MLBS plot), is a 0.5 ha plot at the Mountain Lake Biological Station. The second site (Twin Springs Plot) is a 3 ha plot about 1 km to the northwest on private land. The main canopy trees in both sites are *Quercus rubra* and *Q. alba*. The main understory trees in the plots are *Acer pensylvanicum* and *A. rubrum*. The history of the two sites is similar, but exact historical data are unknown. For about 140 years these two plots have been owned by the same family, and the land use has been similar. There has been some selective cutting, some grazing, and evidence of ground fires at both sites, but not since 1930.

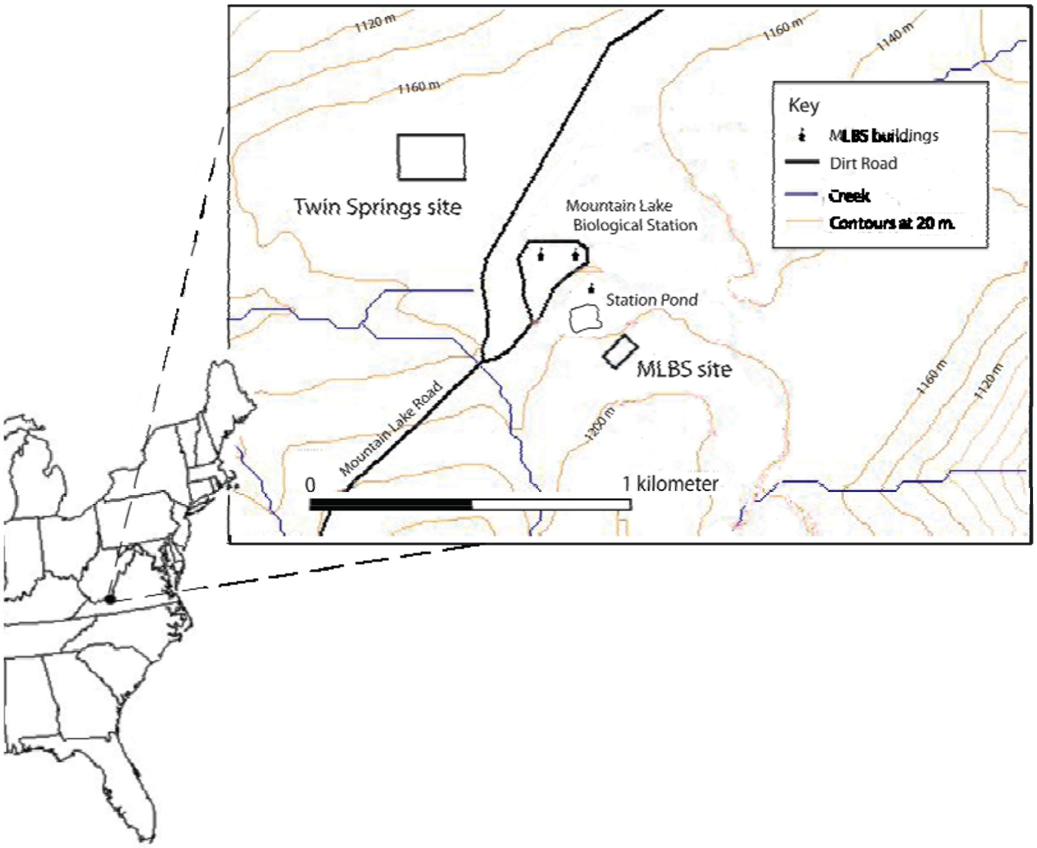

Figure 1. Locations of the MLBS and Twin Springs study sites.

Field methods I looked at spatial and temporal variation of abundance of *Q. rubra* and *Q. alba* in order to better understand how the distribution of the two species has changed in the past two decades and what biotic and abiotic factors may have contributed to that change. I used spatially explicit historical data from 1983-84 and data collected from 2007-08 from both sites. All trees in the MBLS plot and Twin Springs plot that were more than 1.4 meters tall were identified and mapped using quadrats and tape measures in 1983-84. The MLBS plot was mapped by a community ecology class taught by N. L. Christensen and H. M. Wilbur of Duke University in 1984 and the Twin Springs plot was first mapped by G. Parker of the Smithsonian Environmental Research Center in 1982 and 1983. The MLBS plot was remapped in 2007 by H. M. and R. B. Wilbur using redundant triangulation and INTERPOINT software (Boose *et al.* 1998), which maps trees to decimeter accuracy by using the distance of the tree to three known points (Boose *et al.* 1998).

In both the MLBS and Twin Springs plot, aspect, slope, soil pH, and soil moisture were estimated to see if there are any significant abiotic differences between the plots. Three different soil samples were taken at each of five different locations evenly spaced in the Twin Springs plot and three different locations evenly spaced in the MLBS plot. This gave a total of 15 soil samples in the Twin Springs plot and 9 soil samples in the MLBS plot. In both plots the soil samples were taken at mid day in June 2008 two days after heavy rain with the goal of comparing water retention between the sites. Soil moisture and pH were measured in accordance to Carter (1992).

In order to answer my first three questions of how the forest composition has changed since the 1980s and how mortality and growth among size classes of *Q. rubra* and *Q. alba* vary, I needed to re-census the Twin Springs plot. Due to time constraints, I sampled half of the 3 ha plot by dividing it into 12 sections. Each section was divided into four 25 m by 25 m subplots and two diagonally opposing subplots in each section were randomly sampled. All *A. pensylvanicum* trees were excluded due to their high density in the understory making it difficult to distinguish *A. pensylvanicum* trees on the 1983 map and new *A. pensylvanicum* recruits. All other trees on the 1983 map were located and their DBH (diameter at breast height, 1.4m) and condition (alive, alive but dying, snag (standing dead tree), log) were recorded. All new recruits (trees not present in 1983 and at least 1.4 m. tall in 2008) excluding *A. pensylvanicum* were identified and their DBH, condition, and location were recorded. These newly mapped trees were accurate to within one meter and the location was obtained using distance and heading to the nearest mapped tree on the 1983 map. One subplot in each section of the Twin Springs plot was divided into 25 5m x 5m quadrats for a total of 300 quadrats. Similarly, the MLBS plot was divided into 250 square 5m X 5m quadrats. Abundance of *A. pensylvanicum* was recorded in each quadrat on both plots and the DBH of each stem was recorded to the nearest centimeter.

I conducted a seedling census to understand the differences in abundance of *Q. alba* and *Q. rubra* seedlings and their relationship with light availability, and with the abundance of *A. pensylvanicum* trees. On June 2008 in each of the same 550 5 m x 5 m quadrats in both plots the number of *Q. rubra, Q. alba, Q. prinus,* and *Q. velutina* seedlings were recorded as well as percent canopy cover using a convex spherical densitometer (Forestry Suppliers, Jackson, MS). I divided seedlings into three categories: true seedlings - trees that germinated in 2008; herb layer seedlings - trees less than 25 cm in height; and shrub layer seedlings - trees between 25 cm and 1.4 m in height. True seedlings were distinguished from herb layer seedlings because they still obtained nutrients from the acorn and lacked a woody stem.

Data analysis To determine differences in soil moisture, soil pH, and canopy cover among the plots, mean and standard error were calculated. Soil moisture was calculated as:

$$\text{Species moisture (g/g)} = {(M_1 - M_2)}/{M_2}$$

where M_1 is the soil mass at the time the soil samples were taken and M_2 is the soil mass after drying.

Quercus velutina (black oak) can be difficult to distinguish from *Q. rubra*, particularly without acorns or young leaves, so the historical data for *Q. rubra* may be mixed with some information for *Q. velutina*. The two species are part of the same red oak subgenus and have been known to hybridize (Nixon 2008). The data from these two species, *Q. rubra* and *Q. velutina*, were combined when looking at the change in forest composition and oak mortality patterns. The spatially explicit historical data and current data enabled me to document exactly how the forest composition has changed from 1983-1984 to the present by looking at the change in basal area (m^2 per hectare) and density (number of stems per hectare) of all tree species. In both plots, I used the measure of abundance and DBH of *A. pensylvanicum* from the quadrats to estimate the current total density and basal area of *A. pensylvanicum*. Species diversity was evaluated for both plots in 1983-84 and 2007-08 using Shannon-Weavers index of diversity (H') which incorporates both species evenness and species richness (Hulbert 1971). A separate measurement of species evenness (J') was calculated since H' alone doesn't show the degree to which species richness and species evenness contribute to species diversity. 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. Species diversity was calculated as:

$$\text{Species diversity (H')} = -\sum p_i \ln p_i$$

where p_i is the proportion of total basal area (or stem density) per hectare of species i. Species evenness was calculated as:

$$\text{Species evenness (J')} = {}^{H'}\!/_{H'_{max}}$$

where H'_{max} is the maximum amount of diversity possible within a given population and equals ln(number of species) (Elliot *et al.* 2002).

The spatially explicit historical data and current data enabled me to analyze how growth and mortality patterns of *Q. rubra* and *Q. alba* vary among the two species, among size classes, and plots. In analyzing the data I divided the oak trees mapped into 3 different size classes: small tree (DBH 0-5cm), subcanopy (5-20cm) and canopy (>20cm). These size classes were based on previous gathered data of *Q. alba* and *Q. rubra* on the MLBS plot that showed the relationship between DBH and canopy strata level and agree with other *Quercus* studies that relate DBH and canopy strata level in the eastern deciduous forests (McDonald *et al.* 2003). I calculated the mortality rate based on size class of both *Q. rubra* and *Q. alba,* and I used a Pearson chi squared test to see if there were significant differences in mortality rate between species, plot and size class. Due to the non-normality of the growth rate data, I performed a nonparametric Wilcoxon test to see differences in growth rate of *Q. rubra* and *Q. alba*.

In analyzing the oak true seedling and herb layer seedling data, I pooled data gathered for *Q. prinus* and *Q. alba*, both part of the same white oak subgenus, as well as for *Q. velutina* and *Q. rubra*, both part of the same red oak subgenus, due to the difficulty in distinguishing seedlings of the same subgenus. Using the data gathered from the 5 x 5 meter quadrats I performed a nonparametric Wilcoxon test to determine if the abundance of white oak and red oak seedlings were significantly different between the plots, between the two subgenera, and between each other. The Wilcoxon test was used due to the nonnormal distribution of the seedling data. I did a correlation analysis to see if there was a correlation between white oak and red oak seedlings, the abundance of *A. pensylvanicum*, and light availability. Additionally, I did a correlation analysis of *A. pensylvanicum* abundance and light availability. All statistical analysis were done using JMP (version 8, SAS institute, Cary, North Carolina, USA) and a *P* values less than 0.05 were considered significant.

Results

Plot differences The MLBS plot and Twin Spring plot are similar in abiotic factors based on soil moisture, soil pH, canopy cover and slope. There are no significant differences between soil moisture or soil pH (Table 1), the slope on both plots never exceeds four degrees, and both plots have a dense canopy cover (Table 1).

Table 1. Mean, standard error (SE) and sample size (n) of soil moisture and soil pH measurements taken in both the Twin Springs plot and the MLBS plot at mid day two days following heavy rain following.

Plot	Measurement	Mean	SE	n
Twin Springs	Soil Moisture (g/g)	0.347	0.016	15
	Soil pH	4.22	0.067	15
	Canopy Cover	96.8%	0.137	300
MLBS	Soil Moisture (g/g)	0.359	0.029	9
	Soil pH	4.42	0.060	9
	Canopy Cover	95.1%	0.150	250

There were substantial differences in forest composition between the MLBS plot and the Twin Springs plot in 1983-84. In 1983-84, species diversity was twice as high and species evenness was 64% higher in the Twin Springs plot than in the MLBS plot in terms of basal area (Tables 2 and 3). Additionally, the average basal area of an individual tree was higher in the Twin Springs plot (100 cm^2) than in the MLBS plot (88 cm^2). *Q. rubra* was the dominant species in terms of basal area in both plots, but *Q, rubra* was over twice as dominant in the MLBS plot than in the Twin Springs plot (Tables 2 and 3). In terms of stem number, *A. pensylvanicum* and *C. dentata* were the dominant species in the Twin Springs plot (27 and 23% respectively), and in the MLBS plot *C. dentata* was the dominant species (44%), and *A. pensylvanicum* was not very abundant (less than 5%) (Tables 2 and 3).

Table 2. Percent basal area (BA)**,** relative stem density**,** and +/- one standard error of each species in 1983 and 2008 on the Twin Springs plot. Species with a total basal area less than 1% in both 1983 and 2008 constitute the "other" row and include *Betula lenta, Crataegus sp., Prunus serotina, Hammamalus virginiana, Ilex montana, Nyssa salvatica, Kalmia latifolia, Rhododendron calendulaceum, Sassafras albidium* 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.

Twin Springs	**1983**		**2008**	
Species	**BA (%)**	**Stem (%)**	**BA (%)**	**Stem (%)**
*Quercus rubra**	34.0 +/- 2.8	5.9 +/- 0.5	37.2 +/- 1.0	6.8 +/- 0.6
Acer rubra	18.2 +/- 2.0	12.1 +/- 1.5	21.9 +/- 2.4	12.5 +/- 1.3
Quercus alba	22.8 +/- 2.3	5.2 +/- 0.6	17.7 +/- 2.0	3.9 +/- 0.6
Quercus prinus	10.3 +/- 1.6	2.0 +/- 0.4	10.1 +/- 1.8	1.9 +/- 0.5
Amelanchier arborea	4.1 +/- 0.6	7.0 +/- 0.7	3.7 +/- 0.6	6.2 +/- 1.2
Acer pensylvanicum	1.1+/- 0.2	27.4 +/- 3.5	5.1 +/- 0.4	63.1 +/- 2.8
Magnolia acuminata	0.6 +/- 0.4	0.5 +/- 0.2	1.3 +/- 0.7	0.7 +/- 0.3
Tsuga canadensis	0.4 +/- 0.2	0.4 +/- 0.1	1.2 +/- 0.4	0.8 +/- 0.5
Carya sp.	1.3 +/- 0.3	0.8 +/- 0.1	1.0 +/- 0.4	0.7 +/- 0.2
Castanea dentata	2.6 +/- 0.4	24.2 +/- 2.8	0.4 +/- 0.2	1.7 +/- 0.4
Robinia pseudo-acacia	3.1 +/- 0.5	2.4 +/- 0.4	0.0 +/- 0.0	0.0 +/- 0.0
Other	1.4 +/- 0.4	12.1 +/- 2.5	0.4 +/- 0.2	1.6 +/- 0.8
Total per hectare	35.8 m^2 +/- 0.3	3591 +/- 5.53	35.1 m^2 +/- 0.45	1985 +/- 3.08
Species Diversity (H')	1.832 +/- 0.037	2.180 +/- 0.053	1.719 +/- 0.040	1.380 +/- 0.063
Species evenness (J')	0.602 +/- 0.012	0.716 +/- 0.019	0.565 +/- 0.015	0.453 +/- 0.026

Table 3. Percent basal area (BA) and relative stem density of each species in 1983 and 2008 on the MLBS plot. Species with a total basal area less than 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	**1984**		**2007**	
Species	**BA (%)**	**Stem (%)**	**BA (%)**	**Stem (%)**
*Quercus rubra**	76.8	20.1	76.9	18.4
Acer pensylvanicum	0.1	4.9	7.0	39.5
Quercus alba	10.3	10.5	6.4	11.0
Acer rubrum	3.2	4.5	6.0	24.2
Robinia pseudo-acacia	3.6	1.0	1.4	0.6
Carya sp.	1.8	1.8	1.1	1.4
Castanea dentata	3.0	43.2	0.0	2.3
Amelanchier arborea	0.8	2.2	0.9	1.6
Other	0.4	11.8	0.3	1.0
Total per hectare	26.1 m^2	2952	30.1 m^2	2016
Species Diversity (H')	0.913	1.695	0.907	1.562
Species evenness (J')	0.367	0.682	0.365	0.629

Changes in forest composition Species diversity and species evenness have decreased substantially in the Twin Springs plot (37 and 37 % respectively) and decreased slightly in the MLBS plot (8 and 8% respectively) based on stem density from 1983-84 to 2007-08 (Tables 2 and 3). A similar trend was found for both species diversity and species evenness in terms of basal area (Tables 2 and 3). Stand thinning occurred on both plots; the total number of stems decreased by 32% on the MLBS plot and by 44% on the Twin Springs plot. The overall basal area decreased slightly by 3% on the Twin Springs plot and increased slightly by 15% on the MLBS plot (Tables 2 and 3). The average basal area of an individual tree increased by 69% in the Twin Springs plot (100 cm^2 to 177 cm^2) and by 77% in the MLBS plot (88 cm^2 to 149 cm^2) from 1983-84 to 2007-08.

Q. rubra has remained the dominant species in terms of basal area on both plots (37 and 77% at Twin Springs and MBLS respectively). In 1983-84, *C. dentata* was the dominant species in terms of stem number on the MLBS plot (43%) and *A. pensylvanicum* and *C. dentata* were the dominant species in terms of stem number on the Twin Springs plot (27 and 23% respectively) (Tables 2 and 3). On both plots today, *A. pensylvanicum* is the dominant species in terms of stem number (63.1 and 39.5% Twin Springs and MLBS respectively) and *C. dentata* is no longer very abundant (less than 3 %) (Tables 2 and 3).

On both plots the majority of species experienced more mortality than recruitment, and many species declined in numbers and basal area by over 50% (Fig. 2 and Fig. 3). Additionally, all *Vaccinium corymbosum* stems died on the Twin Springs plot (n=248) and on the MLBS plot (n=16) by 2008. On the Twin Springs plot, all stems of *Crataegus sp.* (n=2), *Sassafras albidium* (n=23) and *Robinia pseudo-acacia* (n=129) also died by 2008. *Rhododendron calendulaceum* declined in numbers by 94% in the MLBS plot (n=326) and by 99% in the Twin Springs plot (n=202).

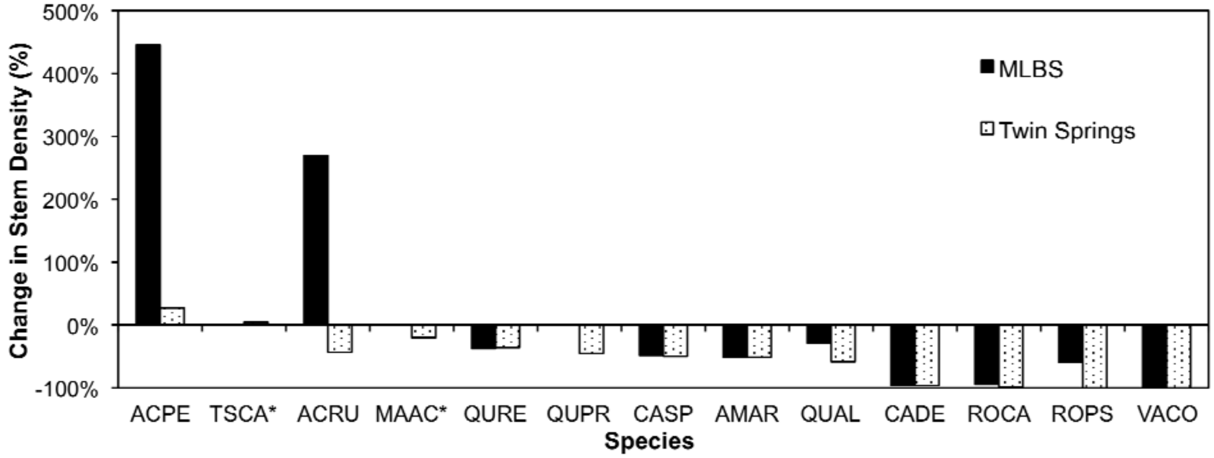

Figure 2. Percent change in stem density from 1983-84 to 2007-08 of each species on the MLBS plot and Twin Springs plot. Species with a total basal area or stem density that were less than 1% in 1983-84 and 2007-08 in both plots are not listed and include *Betula lenta* and *Prunus serotina* on both plots, and *Crataegus sp., Hammamalus virginiana, Ilex montana, Nyssa salvatica, Kalmia latifolia, and Sassafras albidium* on the Twin Springs plot. Species codes are the first two letter 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 Table 4).*Note that species with an asterisk are present on the Twin Springs plot, but not on the MLBS plot.

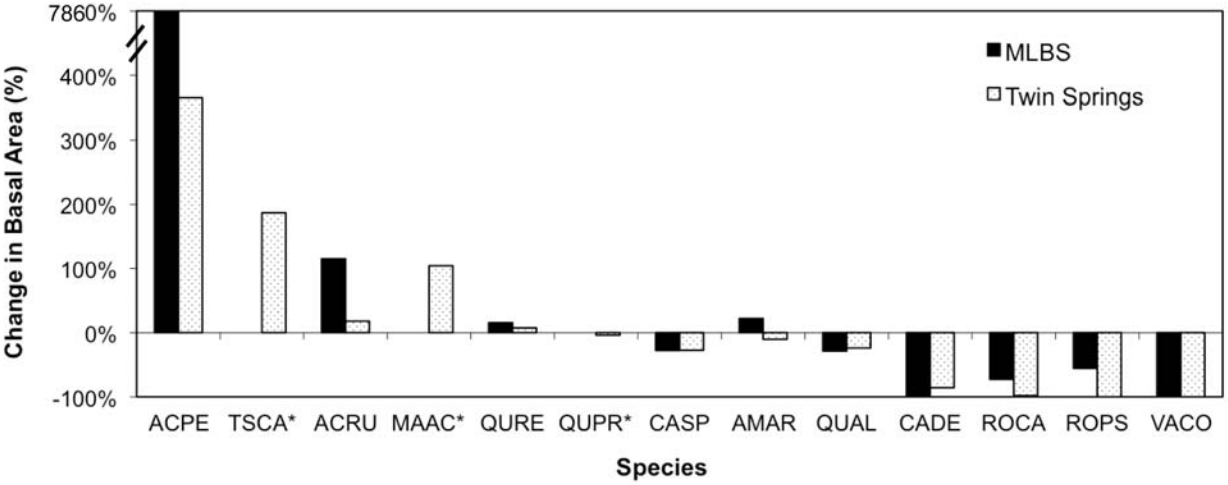

Figure 3. Percent change in basal area from 1983-84 to 2007-08 of each species on the MLBS plot and Twin Springs plot. Species with a total basal area or stem density that were less than 1% in 1983-84 and 2007-08 in both plots are not listed and include *Betula lenta* and *Prunus serotina* on both plots, and *Crataegus sp., Hammamalus virginiana, Ilex montana, Nyssa salvatica, Kalmia latifolia, and Sassafras albidium* on the Twin Springs plot. *Note that species with an asterisk are present on the Twin Springs plot, but not on the MLBS plot. **Note that the y-axis jumps from 400% to 7860%. Species codes are the first two letter 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 Table 4).

On the Twin Springs plot, only *A. pensylvanicum* and *Tsuga canadensis* increased in numbers since the 1980s and were also the only species besides *Amelanchier arborea* to have recruitment of stems greater than 1.4 m in height (Fig. 2 and Table 4). In the MLBS plot, *A. pensylvanicum* and *A. rubrum* experienced the most recruitment and were the only two species to increase in numbers since the 1980s (Table 4). In both plots, *A. pensylvanicum* experienced the most recruitment in the past two decades, and there was no oak recruitment in the Twin Springs plot and little oak recruitment in the MLBS plot (Table 4). In the MLBS plot, *Q. alba* had over eight times more recruitment than *Q. rubra* (Table 4).

Table 4. Recruitment of all species in both the MLBS and Twin Springs plot based on number of stems per hectare. Species with a total basal area or stem density that were less than 1% in 1983-84 and 2007-08 in both plots constitute the other row and include *Betula lenta* and *Prunus serotina* on both plots, and *Crataegus sp., Hammamalus virginiana, Ilex montana, Nyssa salvatica, Kalmia latifolia, and Sassafras albidium* on the Twin Springs plot. *Note that *A. pensylvanicum* recruitment number is the minimum number possible recruited. Individual *A. pensylvanicum* were not relocated on the Twin Springs or MLBS map. The number of *A. pensylvanicum* recruits listed is the number alive in 2007/8 minus the number alive in 1983. Therefore, the annual rate of recruitment would be higher than suggested by these net 23 or 25 year differences.

		Recruitment (stems per HA)	
Species	**Species Code**	**MLBS**	**TS**
*Acer pensylvanicum**	ACPE	650*	268*
Tsuga canadensis	TSCA	0	6
Acer rubra	ACRU	428	0
Magnolia acuminata	MAAC	0	0
Quercus rubra + Quercus velutina	QURE	16	0
Quercus prinus	QUPR	0	0
Carya sp.	CASP	0	0
Amelanchier arborea	AMAR	18	0.67
Quercus alba	QUAL	134	0
Castanea dentata	CADE	0	0
Rhododendron calendulaceum	ROCA	0	0
Robinia pseudo-acacia	ROPS	16	0
Vaccinium corymbosum	VACO	0	0
Other		0	0

Recruitment, growth, and mortality patterns of *Q. rubra* and *Q. alba* There has been more mortality than recruitment of both *Q. rubra* and *Q. alba* in both plots as evidenced by their decline in stem density (Table 3 and 4). There has been no oak recruitment in the Twin Springs plot, some *Q alba* recruitment in the MLBS plot and very little *Q. rubra* recruitment in the MLBS plot (Table 4). Size class significantly affects mortality of *Q. rubra* and *Q. alba* in both plots (Fig. 4). Small trees of both *Q. rubra* and *Q. alba* experienced higher mortality than subcanopy trees, which experienced higher mortality than canopy trees (χ^2 tests all $p < 0.0006$; Fig. 4). *Q. alba* mortality was significantly higher than *Q. rubra* for subcanopy trees in both plots (MLBS $\chi^2_1 = 4.57$; $p = 0.03$; Twin Springs $\chi^2_1 = 7.39$; $p = 0.006$; Fig 4), and also significantly higher for canopy trees in the Twin Springs plot ($\chi^2_1 = 9.82$; $p = 0.002$; Fig. 4). There was significantly more mortality in the Twin Springs plot than in the MLBS plot for small and subcanopy *Q. alba* trees and subcanopy *Q. rubra* trees (χ^2_1 tests all $p < 0.02$; Fig. 4).

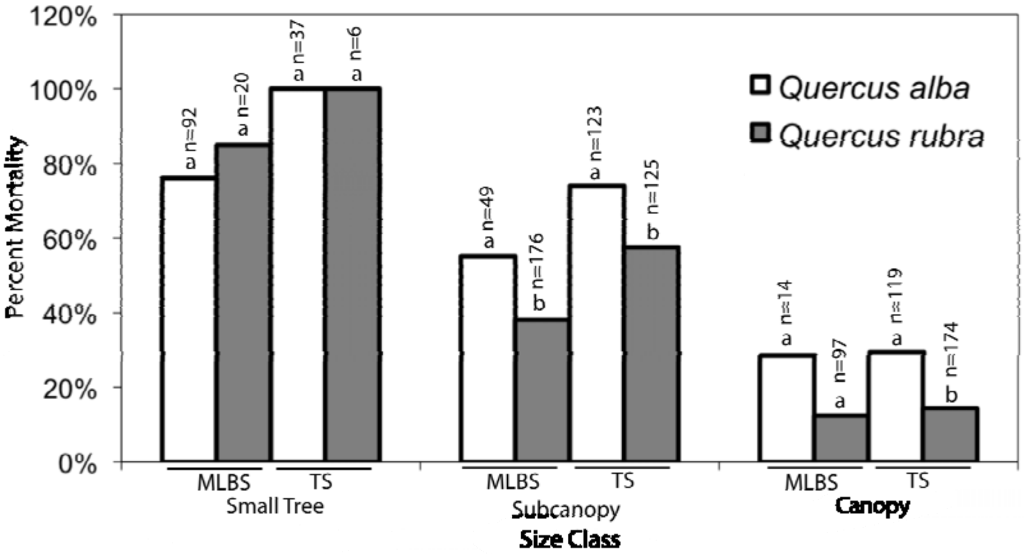

Figure 4. Percent mortality of Q. rubra and Q. *alba* in the Twin Springs (TS) plot and the MLBS plot from 1983-84 and 2007-08. N shows the number of trees in the size class that were alive in 1983-84. There were significant differences among size class within both plots and species ($p < 0.05$, χ^2_1 tests), and there were significant differences in mortality among plots of Q. *alba* in the small tree size class ($p=0.001$, χ^2_1 tests) and of both Q. *alba* and Q. *rubra* in the subcanopy size class ($p<0.02$, χ^2_1 tests). Different letters indicate significant differences ($p < 0.05$, χ^2_1 tests) in mortality among species within the same size class and plot.

In both the MLBS and Twin Springs plot, *Q. rubra* has a significantly higher relative growth rate (RGR) than *Q. alba* in the canopy size class (all $p<0.005$, Wilcoxon test; Fig. 5). Small trees of *Q. alba* have a statistically significantly higher RGR than subcanopy trees, which have a higher RGR than canopy trees ($p<0.001$, Wilcoxon test; Fig. 5), and a similar but statistically insignificant trend was seen for *Q. rubra* ($p>0.2$, Wilcoxon test; Fig. 5).

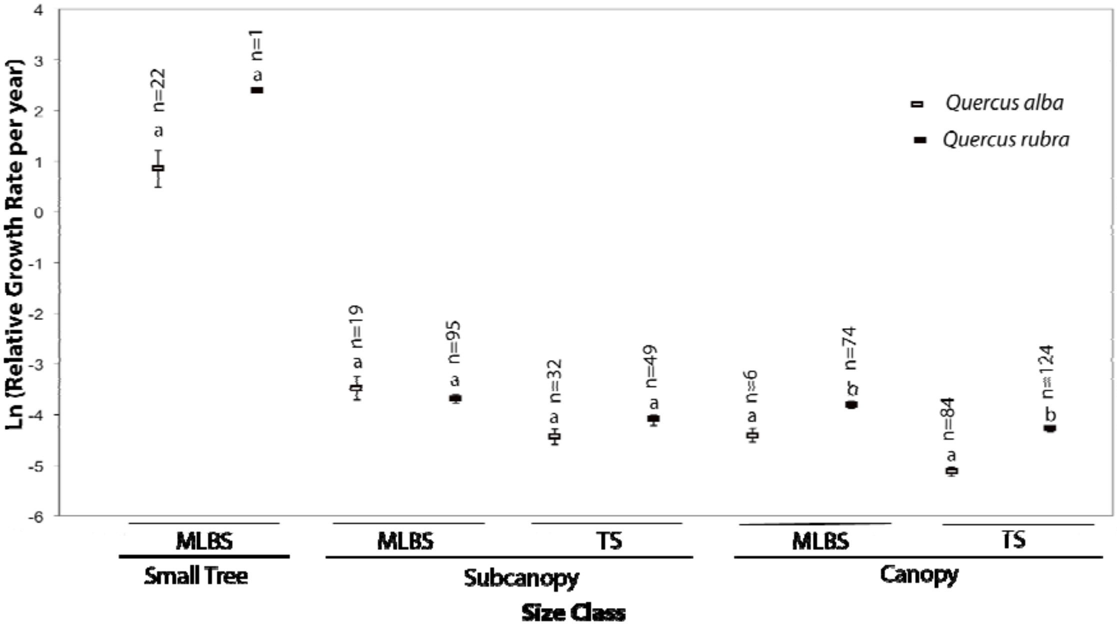

Figure 5. Relative growth rate of *Q.* rubra and *Q. alba* in the Twin Springs (TS) plot and the MLBS plot from 1983-84 and 2007-08. N shows the number of trees in the size class that survived from 1983-84 to 2007-08. There were significant differences among size class within both plots of *Q. alba* (all p <0.05, Wilcoxon test), but not of *Q. rubra* (all p>0.2, Wilcoxon test). There were significant differences in growth among plots of *Q. alba* and *Q. rubra* in the subcanopy size class and of *Q. rubra* in the canopy size class (all p<0.008, Wilcoxon test). Different letters indicate significant differences (p <0.05, Wilcoxon test) in growth among species within the same size class and plot.

The combination of recruitment, growth, and mortality patterns of *Q. rubra* and *Q. alba* has caused the DBH distribution of both *Q. rubra* and *Q. alba* to shift to the right and down in the past two decades in both plots, showing that not only there has been more mortality than recruitment, but also that the trees that survived have grown (Fig. 6). In both plots there has been a decline in numbers of *Q. rubra* and *Q. alba* in the smaller size classes (Fig. 6). In the MLBS plot *Q. alba* has more of an inverse J shaped DBH distribution whereas *Q. rubra* has a more bell shaped DBH distribution in both 1984 and 2007 (Fig. 6). Similarly, in 1983 in the Twin Springs plot *Q. rubra* shows a more bell shaped DBH size class distribution where as *Q. alba* has more trees in the smaller size class (Fig. 6). However, by 2008 in the Twin Springs plot both *Q. rubra* and *Q. alba* show a more bell shaped DBH size class distribution.

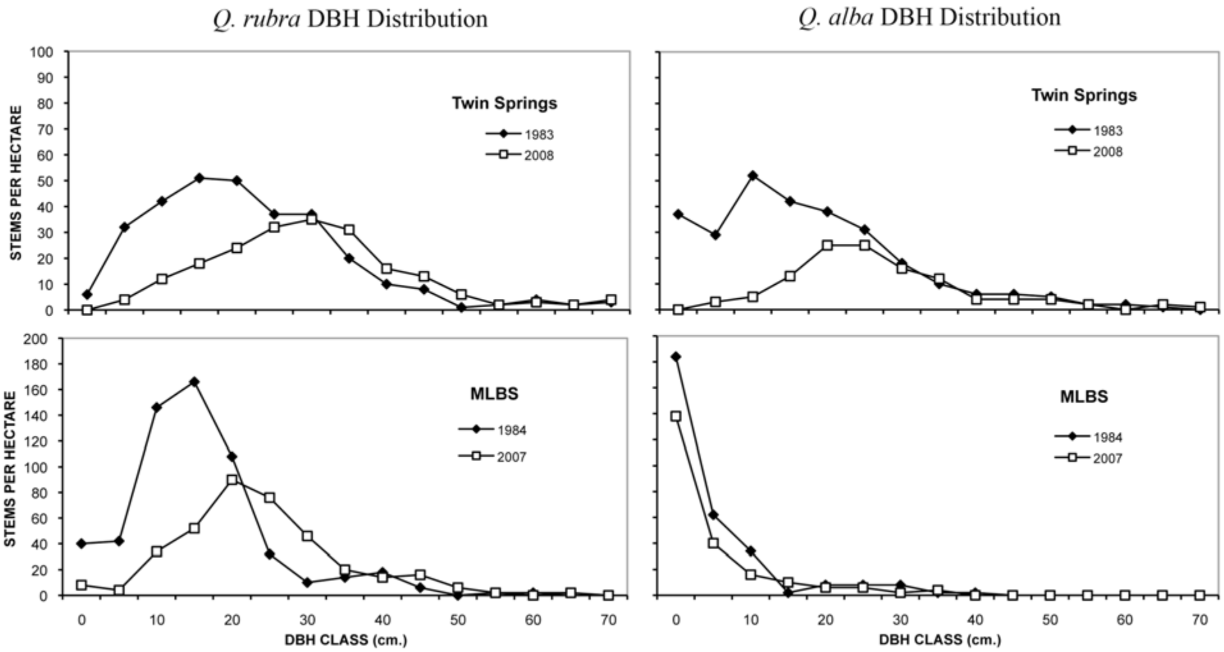

Figure 6. Size class distribution based on DBH (cm.) of *Q. rubra* and *Q. alba* in 1983-84 and in 2007-08 in the MLBS and Twin Springs plot. Upper left and upper right show the size class distribution of *Q. rubra* (left) and *Q. alba* (right) in the Twin Springs plot in 1983 and in 2008. Lower left and lower right show the size class distribution of *Q. rubra* (left) and *Q. alba* (right) in the Twin Springs plot in 1984 and in 2007.

***Quercus* seedling abundance, *Acer pensylvanicum* abundance, and light availability** In both plots there are significantly less shrub layer seedlings than herb layer seedlings of both *Q. rubra* and *Q. alba* (all $p < 0.0001$, Wilcoxon test) (Fig. 7). The Twin Springs plot has significantly more *Q. alba* true seedlings and *Q. alba* herb layer seedlings than the MLBS plot (all $p<0.0001$, Wilcoxon test) (Fig. 7). The MLBS plot has significantly more *Q. rubra* true seedlings, *Q. rubra* herb layer seedlings, and *Q. alba* shrub layer seedlings than the Twin Springs plot (all $p<0.0001$, Wilcoxon test) (Fig. 7). In the Twin Springs plot, there are significantly more *Q. alba* than *Q. rubra* true seedlings and herb layer seedlings (all $p<0.0001$, Wilcoxon test) (Fig. 7). In the MLBS plot, there are significantly more shrub layer seedlings of *Q. alba* than *Q. rubra* ($p<0.0001$, Wilcoxon test), but significantly less true seedlings and herb layer seedlings of *Q. alba* than *Q. rubra* ($p<0.0002$, Wilcoxon test) (Fig. 7).

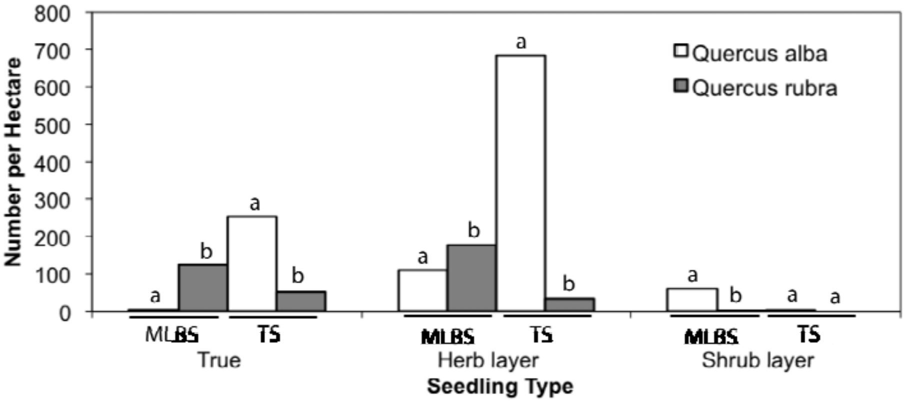

Figure 7. Abundance of *Q. alba* and *Q. rubra* true, herb layer, and shrub layer seedlings per hectare in both the MLBS and Twin Spring (TS) plot. There were significant differences in seedling abundance among seedling types within both plots and species (all p <0.0001, Wilcoxon test). There were significant differences in seedling abundance among plots (all p<0.001, Wilcoxon test), except for *Q. rubra* shrub layer seedlings (p=0.27, Wilcoxon test). Different letters indicate significant differences (p <0.05, Wilcoxon test) in seedling abundance among species within the same seedling type and plot.

There is a significant negative relationship between the number of *A. pensylvanicum* trees present and the number of white and red oak herb layer seedlings in the Twin Springs plot and red oak herb layer seedlings in the MLBS plot (Table 5). There is no significant relationship with *A. pensylvanicum* number and oak true seedling number in both of the plots (Table 5). Similarly, there is a significant positive relationship with canopy openness and the number of both red and white oak herb layer seedlings in both plots, except with white oak herb layer seedlings in the MLBS plot (Table 5). Additionally, there is no significant relationship with canopy openness and true oak seedling number except with red oak in the Twin Springs plot (Table 5). There were not sufficient shrub layer oak seedlings in the Twin Springs plot and red oak shrub layer seedlings in the MLBS plot for a correlation analysis (Fig. 7). In the MLBS plot, there was a significant negative correlation with the abundance of white oak shrub layer seedlings and the abundance of *A. pensylvanicum* (Spearmans $\rho = -0.19$, $p = 0.0028$). There is a significant negative relationship between the abundance of *A. pensylvanicum* in terms of basal area and canopy openness in both the MLBS plot (Spearmans $\rho = -0.23$, $p = 0.0002$) and the Twin Springs plot (Spearmans $\rho = -0.39$, $p < 0.0001$).

Table 5. White and Red Oak true seedling and herb layer seedling abundance correlation analysis with canopy openness and the abundance of *A. pensylvanicum* in both the MLBS plot (n=300 5m X 5m quatrats) and the Twin Springs plot (n=500 5m X 5m quatrats). Bold *P values* indicate significance ($P < 0.05$; Spearmans Test).

R = Red Oak W= White Oak		**True Seedlings**				**Herb Layer Seedlings**			
		Twin Springs		MLBS		Twin Springs		MLBS	
		R	W	R	W	R	W	R	W
Acer pensylvanicum	Spearman's ρ	0.14	0.04	0.02	0.01	-0.13	-0.30	-0.18	-0.12
	P	**0.014**	0.480	0.740	0.860	**0.037**	**<0.001**	**0.004**	0.057
Canopy Openness	Spearman's ρ	-0.09	0.011	0.00	0.03	0.12	0.30	0.21	0.06
	P	0.117	0.850	0.950	0.590	**0.037**	**<0.001**	**<0.001**	0.350

Discussion

The forest understudy of the Southern Appalachians in the past 25 years has changed to being less oak dominated and more maple dominated (Fig. 2 and Fig. 3). *A. pensylvanicum* has increased the most in abundance, and the majority of other species have declined. There has been a lack of oak recruitment, and *A. pensylvanicum* seems to negatively affect regeneration of both *Q. rubra* and *Q. alba.*

Plot differences The MLBS plot and Twin Springs plot are similar in soil moisture, soil pH, slope, canopy cover (Table 1), but the two plots differed substantially in forest composition in 1983-84, which likely affected how the forest composition of the two plots changed over time. In 1983-84, the Twin Springs plot had a higher species diversity and species evenness than the MLBS plot (Tables 2 and 3). Additionally, on average each individual tree in the Twin Springs plot had a larger basal area. *Q. rubra* was the dominant tree species in both plots in terms of basal area, but it was over twice as dominant in the MLBS plot (Tables 2 and 3). In terms of stem number, *A. pensylvanicum* was one of the dominant species in terms of stem number in 1983-83 in the Twin Springs plot (Table 2), unlike in the MLBS plot (Table 3).

Forest composition changes In both plots, there has been more mortality than recruitment for the majority of species and stand thinning has occurred leading to a less diverse forest: there are fewer species overall and the species are less evenly distributed in terms of both stem number and basal area (Tables 2 and 3). *Q. rubra* is still the dominant species in terms of basal area in both plots (Tables 2 and 3), yet it has decreased in numbers (Fig. 2). On the other hand, *A. pensylvanicum* has increased the most both in numbers and in basal area (Fig. 2 and Fig. 3), has experienced the most recruitment (Table 4), and has the greatest density on both plots (Tables 2 and 3). These results support both Jokela and Sawtelle (1985) and Peet and Loucks (1977), who found *Q. rubra* to be a pioneer species that, after initial dominance, is replaced by *Acer* species.

The canopy cover is very dense in both plots (Table 1), and only shade tolerant species experienced a positive increase in stem density since the 1980s. Other than *A. pensylvanicum*, *T. canadensis* on the Twin Springs plot and *A. rubrum* on the MLBS plot were the only species to have a positive increase in stem density (Table 4). *T. canadensis* is one of the most shade tolerant species in the eastern deciduous forest and can establish and persist under a closed canopy where it receives as little as 5% of full sunlight (Baker 1949; Goerlich and Nyland 2000; Graham 1941; Hough 1960). *A. rubrum* is also shade tolerant, but only moderately shade tolerant compared to *T. canadensis* and *A. pensylvanicum* (Baker 1949; Graham 1941). This supports my prediction that in the past 25 years there has been an increase in shade tolerant species and a decline in intermediate tolerant and shade intolerant species.

The lack of recruitment and high mortality of shade intolerant species and intermediate shade tolerant species suggests that light availability in the understory is a limiting factor towards species regeneration and survival, especially in the Twin Springs plot. In the Twin Springs plot, very shade intolerant tree species such as *Sassafras albidium* and *Robinia pseudo-acacia* are no longer present, and on the MLBS plot, *R. pseudo-acacia* declined by over 60% in stem density. *Q. rubra, Q. alba, Amelanchier arborea,* and *Carya* spp. all declined in both plots and have intermediate shade tolerance (Baker 1949; Minckler 1965; Sander 1965; Smalley 1965). Both plots have light levels less than 5% (Table 1), and these findings agree with Kobe *et al.* (1995) who found that at these light levels there are large survivorship differences among northern hardwood species depending on their shade tolerance. *Vaccinium corymbosum* and *Crataegus* spp. are shade intolerant understory shrubs (Rogers 1974; Sharps 1974) and experienced complete mortality. *Rhododendron calendulaceum* is an intermediate shade tolerant shrub that declines as forests mature and canopies close (Carey 1994) and experienced high rates of mortality and no recruitment in both plots. Abrahmanson and Gohn (2004) found dense ground cover of *Vaccinium sp.* and *R. calendulaceum* under a mixed-oak over-story, but sparse ground cover beneath dense canopy of either *T. canadensis* or *A. pensylvanicum.* The high mortality of these species is likely linked to the increased abundance of *A. pensylvanicum* and *T. canadensis.*

In both plots since the 1980s, *A. pensylvanicum* experienced very high recruitment (Table 4). The only other recruits on the Twin Springs plot were *T. canadensis,* and one *A. arborea* tree, which is highly variable in its shade tolerance (Humbert *et al.* 2007). In the MLBS plot, there was moderate recruitment of more intermediate shade tolerant species such as *A. rubrum* and *Q. alba,* and very minor recruitment of *Q. rubra, A. arborea,* and *R. pseudo-acacia* (Table 4). The lack of recruitment of intermediate shade tolerant and shade intolerant species suggest that light is a limiting factor to species regeneration and that seedlings have not been able to survive and grow in the understory to become a small tree.

Recruitment, growth, and mortality patterns of *Q. rubra* and *Q. alba* In both plots, *Q. rubra* has increased in basal area unlike *Q. alba* (Fig. 3), but both species have declined in stem density (Fig. 2). The increase in basal area of *Q. rubra* is likely due to its faster growth rate and lower percent mortality of subcanopy and canopy trees than *Q. alba* (Fig. 4 and Fig. 5). However, the lack of small *Q. rubra* trees (Fig. 6), the higher mortality of small *Q. rubra* trees in the MLBS plot (Fig. 5), and lower recruitment of *Q. rubra* (Table 4), indicate that *Q. rubra* is less able to regenerate compared to *Q. alba* as predicted. The more bell shaped DBH distribution of *Q. rubra* compared to the more inverse J-shaped DBH distribution of *Q. alba* in 1983-84 shows that *Q. rubra* is less able to regenerate and have trees in the smaller size classes to replace the canopy trees than *Q. alba* (Fig. 6). The higher abundance of *Q. alba* small trees may be due its higher shade tolerance allowing *Q. alba* to last longer in the understory with limited light availability.

While *Q. alba* may be better able to regenerate than *Q. rubra,* both species experienced very high mortality rates of small trees in the MLBS plot and complete mortality of small trees in the Twin Springs plot. Additionally, there has been low oak recruitment in both plots. There has been no oak recruitment in the Twin Springs plot, some recruitment of *Q. alba* in the MLBS plot, and very little recruitment of *Q. rubra* on the MLBS plot (Table 4). The high mortality of *Q. alba* small trees accompanied with no recruitment caused the shift to a more bell shaped DBH distribution of *Q. alba* in the Twin Springs plot and indicates that it isn't able to regenerate similar to *Q. rubra* (Fig. 6). This shift in size class distribution of *Q. alba* and *Q. rubra* was seen by Christensen (1977) in a mixed-oak forest in North Carolina from 1950 to 1975, and oaks are showing the same bell shaped DBH distribution in mixed-oak forests in the northeastern U.S. today (Abrahamson and Gohn 2004; Orwig 2001). These studies indicate that there is a regional decline in both *Q. rubra* and *Q. alba* throughout the eastern United States.

***Quercus* seedling abundance, *Acer pensylvanicum* abundance, and light availability** The oak seedlings densities varied considerably among species, among plots, and among types (true, herb layer, and shrub layer). *Q. alba* and *Q. rubra* produce good acorn crops every few years (Schopmeyer 1974), and so the densities of the true seedlings are likely dependent on whether there was a favorable masting year (Sork *et al.* 1993). For both *Q. rubra* and *Q. alba* in both plots, there are significantly less shrub layer seedlings than herb layer seedlings (Fig. 7). In particular, in the Twin Springs plot there are over 100 times more *Q. alba* herb layer seedlings than shrub layer seedlings (Fig. 7). Besides *Q. alba* in the MLBS plot, there were very minimal amounts of shrub layer seedlings in either plot.

There are several possible explanations for the lack of oak recruitment: a lack of acorns, an inability of the acorns to germinate, mortality of true seedlings, an inability of herb layer seedlings to enter the shrub layer due to lack of growth or mortality, or an inability of shrub layer seedlings to become small trees. My results show that lack of recruitment is most likely not due to lack of oak true seedlings and herb layer seedlings but due to a lack of shrub layer seedlings. The Twin Springs plot had no oak recruitment unlike the MLBS plot (Table 4), but there are over five times more white oak herb layer seedlings of in the Twin Springs plot than in the MLBS plot (Fig. 7). On the other hand, there were significantly more white oak shrub layer trees in the MLBS plot than in the Twin Springs plot. This indicates that the lack of recruitment is due to high mortality of seedlings in the transition from the herb layer to the shrub layer. In the Monongehala National Forest of West Virginia, Collins and Carson (2004) found that small trees and shrub layer seedlings of *Q. rubra* and *Q. alba* were the determining life stages of the future distribution patterns of the two species and had the strongest correlations with the environmental gradients measured (aspect, slope index, site index, elevation and stand age). Furthermore, they found that the sites where *Q. alba* and *Q. rubra* small trees and shrub layer seedlings were most abundant had high light availability (Collins and Carson 2004). The high mortality rates of small trees and lack of shrub layer seedlings may be due to the low light availability in the understory.

The correlation analysis of oak seedlings and light availability indicates that light is a limiting factor in oak herb layer seedling and shrub layer seedling survival (Table 5). The significant negative relationship between *A. pensylvanicum* abundance and light availability in the understory shows that the broad leaves of *A. pensylvanicum* create a dense shade environment in the understory, inhibiting oak regeneration. The abundance of red and white oak herb layer seedlings and shrub layer seedlings increased when there were fewer *A. pensylvanicum* trees (Table 5). This agrees with Lorimer's (1994) findings that oak seedlings have a very low survival rate under tall understory trees such as *Acer,* and supports my hypothesis that *Q. rubra* and *Q. alba* seedlings are more abundant when there is more light availability and fewer *A. pensylvanicum* trees.

Predation by deer is another factor that affects oak seedling survival. Deer are seen foraging in the MLBS plot and Twin Springs plot regularly (Redmond, pers. obs.), but their exact abundance is not known. Studies have shown that deer negatively affect the survival of oak seedlings, primarily herb layer and shrub layer seedlings, due to predation (Kittredge and Ashton 1995; Stange and Shea 1998, Rooney 2003, Russel 2001; Tilghman 1989). Deer have been known to selectively browse oak seedlings compared to other tree species such as *A. pensylcanicum* and *A. rubrum* (Kittredge and Ashton 1995; Tilghman 1989). Deer are likely one of the limiting factors to oak regeneration and have likely promoted the shift seen from a more oak dominated forest to a more maple dominated forest.

Future forest composition changes Understory trees have been known to influence composition by affecting the regeneration success of potential canopy trees (Beckage *et al.* 2008; Clinton *et al* 1994; Phillips and Murdy 1985). *Castanea dentata* was one of the dominant understory tree species in both plots in 1983-84 (Tables 2 and 3), but today *A. pensylvanicum* is the dominant understory tree and *C. dentata* is no longer very abundant (Tables 2 and 3). *A. pensylvanicum* has broader leaves than *C. dentata* and creates a more densely shaded environment in the understory (King 2003). It appears that the high abundance of *A. pensylvanicum* trees has limited light availability in the understory. The low light availability in the understory has likely inhibited the ability of shade intolerant and intermediate tolerant species to survive and regenerate and has enabled shade tolerant species such as *A. pensylvanicum* and *T. canadensis* to increase. The increase in *A. pensylvanicum* can also affect other species through competition for water and nutrients, allelopathy, and litter quality.

The difference in recruitment and mortality patterns of each tree species between the two plots is likely linked to the high density of *A. pensylvanicum* trees that the Twin Springs plot had in 1983 compared to the MLBS plot in 1984. *A. pensylvanicum* was the dominant understory tree in the Twin Springs plot in 1983 with over 960 stems per hectare compared to the MLBS plot in 1984 which had only 144 stems per hectare (Tables 2 and 3). The Twin Springs plot had more stand thinning than the MLBS plot and one hundred percent mortality of small oak trees (Fig. 4), recruitment of only very shade tolerant species (Table 4), a high loss in species diversity (Table 2), and no shrub layer oak seedling unlike the MLBS plot (Fig. 7). Today, the MLBS plot has a high density of *A. pensylvanicum* trees like the Twin Springs plot did in the past and will likely experience changes similar to the changes that the Twin Springs plot experienced since 1983. *A. pensylvanicum* is the dominant understory tree, appears to negatively effect oak seedling survival, and creates a shade dense environment that likely negatively affects the survival and recruitment of other tree species.

A. pensylvanicum is adapted well to live under heavy shade which it helps create, but it can not tolerate high levels of light, depends on canopy trees for shading, and will always remain a subcanopy or understory tree in the eastern deciduous forests. *A. pensylvanicum* is a gap-phase species and performs best in small gaps (Sipe and Bazazz 1995). 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 light in the canopy will increase in dominance (Sipe and Bazzaz 1995). *T. canadensis* is one of these species and has already begun to increase in dominance. *A. rubra* and possibly *Q. alba* are two other species that will likely increase in abundance due to their ability to survive in a shaded understory for longer periods of time compared to other hardwood species (Minckler 1965). *Q. rubra* was able to dominate after more intense disturbance events like fire or the chestnut blight fungus, but in the past century the disturbance regime has shifted to more localized gap-phase events enabling *A. pensylvanicum, A. rubrum* and *T. canadensis* to increase in dominance (Abrahamson and Gohn 2004; Orwig *et al.* 2001).

Conclusion The majority of species in the two plots have experienced stand thinning, and the previous oak-chestnut forest has transformed to an oak-maple forest and will likely continue to become more and more maple dominated. There has been a decline in all intermediate shade tolerant and shade intolerant trees including both red and white oak on Salt Pond Mountain and a huge increase in the number of *A. pensylvanicum* trees since the 1980s. The decrease in oak abundance is likely due to a lack of recruitment and high mortality of small oak trees. Increased abundance of *A. pensylvanicum* appears to have a negative affect on oak seedling and herb layer tree survival by decreasing light availability in the understory and likely contributed to the high mortality of small oak trees. Both *Q. rubra* and *Q. alba* have been experiencing high mortality and low recruitment. This trend is likely to continue for both species until the abundance of *A. pensylvanicum* declines. I predict that more shade tolerant trees like *T. canadensis* will continue to become more dominant. Intermediate shade tolerant species like *A. rubrum* and *Q. alba* that are better able to survive in the understory with limited light compared to other hardwood species will also gain more dominance once *A. pensylvanicum* is no longer able to regenerate.

This was one observational study done in one forest in the Southern Appalachians, and further research is needed to see how the forest has changed elsewhere. This study focused on light availability as a driving factor for changes in species composition, but further research is also needed on the effect of nutrient availability, deer abundance, gypsy moth abundance, and annual weather changes on recruitment, growth, and mortality rates of *Q. rubra* and *Q, alba*. Additionally, more research is needed on how *A. pensylvanicum* became so dominant, and what may limit its ability to regenerate in the future.

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