

The Importance of Age, Competition and Succession in *Acer rubrum* Decline in a Northeastern
Mixed Deciduous Forest

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Abstract

Acer rubrum (red maple) and *Quercus rubra* (red oak) dominate many northeastern deciduous forests, including the Harvard Forest in Petersham, MA. These species have distinct ecological characteristics: red maples are an opportunistic, shade tolerant, relatively short-lived species, while red oaks are less shade tolerant, but live longer (Abrams and Kubiske, 1990; Lichtenthaler et al, 1981; Loach, 1970, Walters and Reich, 1996). The classical literature on succession suggests that over time red maples will therefore increase their dominance in mixed red oak-red maple stands (Abrams, 1998; Hibbs, 1983; Lorimer, 1984). However, data collected at the Harvard Forest has documented an apparent decline in the growth rate of red maples (Pederson, 2005). I hypothesized that this decline is due either to the species-specific life expectancy, or to competitive pressure exerted on the red maples, particularly by increasingly dominant red oaks. In order to investigate these hypotheses at both the individual and site level, I collected data on the size and distance between red maples and their competitors at three different sites at the Harvard Forest: a “control” site, an “open” site, and a “young” site. Additionally, I collected cores from these trees in order to determine age and long-term growth rates, and analyzed the available data on understory composition and tree mortality. I found that there was a weak positive correlation between red maple growth rate and age, suggesting that red maple growth is not limited by age. There was no significant correlation in red oaks. I also found that individual red maple growth rates are significantly limited by their level of competitive stress. Disturbance events release red maples from this competition, resulting in increased growth. In spite of the decline in the canopy, the understory is overwhelmingly dominated by red maple. This suggests that although individual red maples are declining or dying, it is unlikely that a large shift in species composition will occur at the site level. In fact, the interaction between red maple and red oak may result in a stable ecosystem.

1. Introduction

Between 2000 and 2006, the terrestrial biosphere sequestered 30% of anthropogenic carbon dioxide emissions (Canadell et al, 2007). Mature temperate forests are an essential part of that carbon sink (Bonan, 2008). Temperate deciduous forests in the Northeast have a variable carbon history. Historical deforestation for agriculture was a net source for atmospheric carbon (Albani et al, 2006), but more recent reforestation has made these forests a net sink, but there are large uncertainties about the future carbon budgets of these systems (Albani et al, 2006, Bonan, 2008, Canadell et al, 2007, Urbanski et al, 2007, others). Disturbance history plays an important role because of the impacts it has on species are present in forests and how quickly they are growing. Therefore understanding the drivers of change in species composition is important to predicting future carbon sequestration by temperate forests.

The purpose of this study was to examine how long-term interactions between two common deciduous tree species impact the future composition of their stands. This requires an understanding of how these two species fit into a successional framework, as well as their ecology. I will begin with an overview of the relevant literature on succession, followed by information about the two study species, focusing on studies carried out at the Harvard Forest, in central Massachusetts. I will continue by documenting previous studies describing the relationship between the species and their sometimes contradictory and inconclusive predictions about how red maple and red oak stands will develop in the future. This study focuses on filling in that knowledge gap, in order to predict more accurately the future composition of these forests in the Northeastern United States.

1.1 Succession

In 1856, Henry David Thoreau published “The Succession of Forest Trees”, in which he recounts being asked how a pine forest comes to be naturally replaced by an oak forest, and vice versa. In his response, he claims “It has long been known to observers that squirrels bury nuts in the ground, but I am not aware that any one has thus accounted for the regular succession of forests” (Thoreau, 1860). Since Thoreau’s somewhat unconventional explanation, many ecologists have worked hard to understand how and why forest communities undergo dramatic shifts over time. There have been many definitions of this process, known as succession, both complementary and competing. Clements and Gleason, two of the first ecologists to explore succession in detail, differed considerably in their opinion of how succession occurs. In his 1916 publication, Clements compares succession to the development of an organism, moving deterministically to a stable, mature state. Gleason (1917) argued for a more dynamic definition of the process, saying that random natural disturbances would make it unlikely for communities to reach an equilibrium state like the one described by Clements. This fundamental disagreement persisted for decades. Odum (1969) describes succession in terms of three defining attributes. Firstly, it is an orderly, directional, predictable process. Secondly, the community is the driving force of the change, rather than the physical environment. Thirdly, it eventually results in a stable, self-perpetuating system. Today, succession is defined as a predictable, sequential change over time in the relative abundance of dominant species (Huston and Smith, 1987). However the reason that forest stand composition cannot be perfectly predicted is that succession is initiated and driven by disturbance. The frequency, nature and severity of disturbance events are nearly impossible to forecast; therefore,

disturbance introduces an element of unpredictability into successional theory which accounts for the heterogeneity of successional systems.

1.1.1 Shade tolerance

There are a series of traits that are classically understood to define species that occur along different points on the timeline of succession (Huston and Smith, 1987, Goldberg, 1996). Early successional species tend to be smaller at maturity, grow rapidly, and are intolerant to low light conditions (Goldberg, 1996). Late successional species are larger at maturity, grow slowly and are tolerant to shaded conditions (Huston and Smith, 1987). In fact, shade tolerance is particularly important in determining the order of succession, because the shade tolerance of a sapling will determine the light environment in which it will thrive. Thus species level diversity in shade tolerance is a primary driver of succession in northern forest ecosystems (Loach, 1970, Walters and Reich, 1996). As the light environment of the understory changes, seedlings of different species will survive and thrive preferentially, which can eventually lead to shifts in species composition. Both growth rates and survival rates of seedlings are affected by their shade tolerance (Walters and Reich, 1996). However, shifts between relative growth rates and relative rates of survival of species of different levels of shade tolerance occur only at very low light levels (between 2% and 8% of full sunlight). In other words, shade intolerant species grow faster at all light levels except 2%, where those seedlings slow down dramatically or die (Walters and Reich 1996).

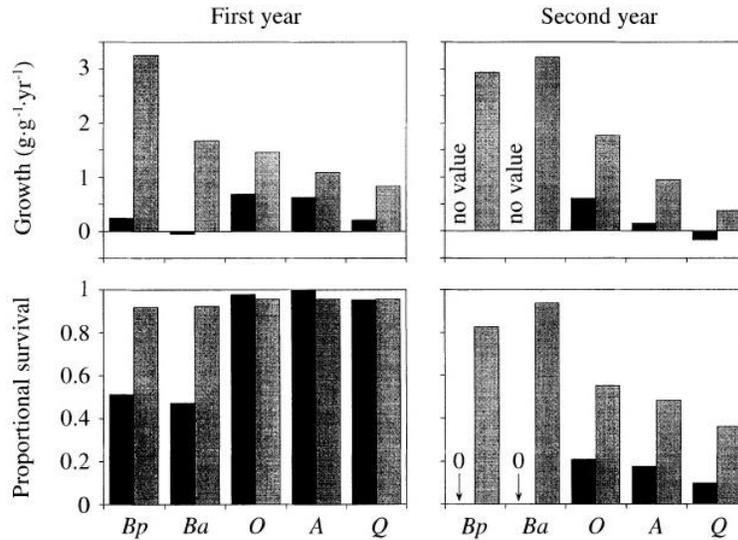


FIG. 1. Growth (proportional change in biomass) and proportional survival for the first and second growing seasons in 2% (black bars) and 8% (gray bars) light. Species are ordered (left to right) according to increasing initial seedling mass (Appendix) and seed mass (Walters et al. 1993a) and decreasing relative growth rate in high light (Walters et al. 1993a). Species acronyms are: *Bp* = *Betula papyrifera*, *Ba* = *Betula alleghaniensis*, *O* = *Ostrya virginiana*, *A* = *Acer saccharum*, and *Q* = *Quercus rubra*.

Figure 1: Taken from Walters and Reich (1996). Relative growth and survival of 5 species of differing high-light growth rates grown under low light conditions. Under low light conditions, the high light species (the species on the left) grow significantly less and have lower proportional survival than the species on the right, which have lower growth rates in high light conditions.

In fact, it seems that there may be an inherent trade-off between shade tolerance and growth rate in full sun: some species maximize their growth rates in open conditions, but also have a high light compensation point for growth (Figure 1). Others have lower growth in full sunlight but also have a lower light compensation point, allowing them to continue growing in shady conditions (Walters and Reich, 1996). Therefore shade tolerant species generally have high survivorship in low light, but low growth rates (Bazzaz, 1979). This has implications for the timing of successional shifts, as shade tolerant species should only have a distinct competitive advantage under a closed canopy, which generally occurs late in succession.

Species of different shade tolerances often have distinct physiology. For example, shade intolerant hardwood species tend to have greater leaf thickness and larger guard cells (Lichtenthaler et al, 1981). This helps categorize species as shade tolerant or intolerant. However, studies of shade tolerance draw heavily on greenhouse and manipulation experiments. Under these conditions, shade tolerance can be categorized based on an absolute list of characteristics. In natural forest stands, the absolute tolerance is less important than the *relative* tolerance of a species when compared to their neighbors (Barnes et al, 1997). Relative shade tolerance of seedlings provides us with a clue for the future composition of forests, because only species whose seedlings are best adapted to the light environment will survive to maturity.

In this study, I consider the interaction between red oak and red maple. These two species are both abundant in the northeast, and are commonly found growing together. Red maples are generally categorized as shade tolerant and red oaks are shade intolerant (based on Loach, 1970). According to successional theory, this knowledge can help predict what the interaction between these species might be on a successional timescale.

1.2 Red Maple Ecology

Red maple is one of the most abundant tree species in the Northeastern United States (Burns and Honkala, 1990). It is generally considered to be a mid-successional species (Burns and Honkala, 1990 and Hibbs, 1983). However, red maple is highly adaptable, as it has traits of both early and late successional tree species (Burns and Honkala, 1990). It is a shade tolerant species (Loach, 1970 and Abrams, 1998), but also grows rapidly in full light conditions (Abrams, 1998 and Hibbs, 1983). This seems to contradict the idea of the inherent tradeoff described

above by Walters and Reich (1996). Because of this adaptability, Abrams (1998) and Lorimer (1984) both predicted that their dominance in the Northeastern United States would increase over time. Red maple is a mesophytic species, thus surviving well on most soil types, but it is particularly well adapted for moist soil (Spurr, 1956). Like other wet-adapted species, red maples flower in early spring and release their seeds in the beginning to middle of the growing season (Barnes et al, 1997). Because they are released into a suitable growing environment, the seeds are not equipped with large food stores (Barnes et al, 1997). One documented adaptation of red maple seedlings to differing light conditions is that in high light, the leaf blades deflect downwards to hang vertically, but in low light they return to horizontal position (Grime, 1966 as cited by Barnes et al, 1997). This allows red maples seedlings to thrive in a wide variety of light levels.

1.3 Red Oak Ecology

Red oak is also a ubiquitous hardwood species in the northeast, but its range extends as far south as Alabama and Georgia, and as far west as Nebraska and Oklahoma (Burns and Honkala, 1990). It is found on upper and lower slopes and on a variety of soil types, (Burns and Honkala, 1990) but they prefer well drained soils (Spurr, 1956). Red oaks develop their seeds throughout the growing season, and release their acorns in early fall. The acorns must lie dormant for the winter and be able to sprout in spring, which means that they need substantial food storage in order to thrive (Barnes et al, 1997). The seedlings develop large root systems to combat dry, nutrient poor conditions (Barnes et al, 1997). In fact, red oaks in general have a very high root to shoot ratio, which means that they allocate a relatively high percentage of their resources to growth and storage in their roots (Barnes et al, 1997). Oak regeneration is

highly dependent on disturbance, particularly fire, to destroy competitors in the understory. Oak seedlings require a certain suite of conditions in order to successfully establish themselves, as they are neither the most shade tolerant nor the fastest growing in open conditions (Barnes et al, 1997). With widespread fire suppression in the northeast, many oak-dominated overstories have understories dominated by mesophytic species, commonly red maple (Barnes et al, 1997).

1.4 Red Maple and Red Oak: successional patterns

In spite of their distinct strategies, red oaks and red maples are commonly found together, and multiple studies have addressed their interaction already. There are a few competing hypothesis about where red maple ought to fit into successional patterns. Because it has characteristics of both early and late successional species, where it falls in practice is up for debate. Successional theory suggests that mixed stands of red maple and red oak will likely progress in one of the following ways:

1. The 'persistent understory hypothesis': that red maple will remain subordinate and has little potential to become a dominant canopy species (Lorimer, 1984). This could be due to higher mortality rate, slow growth, or negative effects of high sunlight conditions.

2. The 'transitory red maple hypothesis': that red maples opportunistically grow quickly following a disturbance event, but are unable to persist at later stages of succession (Lorimer, 1984).

3. The 'red maple dominance hypothesis', suggesting that red maple will achieve dominance over other red oak over time, due primarily to its highly shade tolerance seedlings (Lorimer, 1984).

In one study looking at long-term vegetative data in a mixed central Appalachian forest, McEwan and Muller (2006) found that red maple had increased in dominance over time. This gain was primarily at the expense of some of the less shade tolerant species, such as red oak. In fact there is substantial research suggesting successional shifts from oak species to maple species (Lorimer, 1984 and Abrams, 1998). The primary evidence is based on seedlings; in the understory of most Northeastern mixed wood, deciduous forest, red maple is the dominant seedling (Abrams and Downs, 1990). Red oak is not as shade tolerant, and therefore oak seedlings are often out competed in the understory (Lorimer, 1984). This has led many studies to predict that the red maple dominance hypothesis is most likely (ego: Lorimer, 1984; Abrams, 1998; Abrams and Downs, 1990; McEwan and Muller, 2006; Spurr, 1956).

1.6 Alternative theory: The storage effect

Other studies suggest that classical successional theory may not adequately explain the interaction occurring in mixed deciduous forests. Hibbs (1983) found that succession at the Harvard Forest after the 1938 hurricane did not seem to follow the dominance hypothesis described by Lorimer (1984). Ten years after the hurricane, red maple was a dominant species, but within forty years red oak had become co-dominant with red maple. Oliver (1975) also studied the forest structure and reconstructed its regeneration after the 1938 hurricane at the Harvard Forest. Like Hibbs (1983), he concluded that red maples gave way to red oak after an initial phase of dominance, finding that red oaks overtopped red maples and therefore gained a competitive advantage. He also concluded that just because red maple dominated the understory, does not necessarily imply that they will eventually dominate the canopy, as red oaks will continue to grow robustly in the canopy. Tackett (2012) found no significant increase

of red maples greater than 10 cm DBH between 1978 and 2011, in spite of an increase in understory stem density from 138 stems/ha to 2187 stems. In fact, red maples had not increased since the 1930s. This evidence suggests that the classical concepts supporting red maple dominance over red oak may be flawed, and that red oak may be able to maintain canopy dominance in spite of a red maple understory. The concept behind this new hypothesis is known as storage theory. Storage theory suggests that in long-lived organisms with many reproductive events can co-exist in a persisting, stable system (Warner and Chesson, 1985). This is because the ability of an organism to reproduce offspring that survive to maturity is “stored” in the long-lived individual. Therefore the composition of the young cohort of organisms cannot comprehensively predict the future composition of mature organisms. The idea of storage theory is clearly distinct from the successional concept of a climax community, which suggests a system of highly shade tolerant trees under which nothing is able grow except its own progeny. Storage theory suggests a stable, heterogeneous system that has the potential to change in the future. In this study I will use both successional theory and storage theory to predict the future composition of red maple and red oak stands.

1.7 Study focus and hypotheses

Currently, red maples at the Harvard Forest are in decline. Dendrometer data for the last 19 years, as well as cores taken on many of these same trees, show a significant decline in growth among the red maple trees since 1992 (Pederson, 2005). Red oaks have significantly higher average growth rates, and have not exhibited a similar decline (Urbanski et al, 2007 and Pederson, 2005). This species- specific decline is not due to any pest or disturbance affecting red maples disproportionately; in fact the most recent pest that impacted this site was an

infestation of gypsy moth in 1981, which preferentially defoliate red oak trees (Pederson, 2005). The shifting climate is also not driving this decline, according to a climate sensitivity analysis performed on the red oaks and red maples at this site (Pederson, 2005). He found that neither species were strongly limited by climatic conditions of the region, and that growth rates of both species were more closely related to temperature than to precipitation. This suggests that the differences in growth trends cannot be explained by climatic factors.

The primary purpose of this study was to analyze the past and present stand dynamics at Harvard Forest in order to predict the likely future stand composition of red maple/red oak mixed forests across New England. The apparent decline in red maple growth that has been described in the data collected at the Harvard Forest suggests that these stands are unlikely to be dominated by red maple in the near future. This runs contrary to the predictions of successional theory, and in order to examine this contradiction I investigate why red maple is declining. The two hypotheses tested in this study are:

1. Red maple growth is limited after a certain age.
2. Competition between red maples and red oak is limiting red maple growth rates.

As a shorter lived species, the relative fitness of red maples may decrease as the forest has matured. Because the red maples of the Harvard Forest are still relatively young (the Harvard Forest itself is only around 150 years old), I predict that age will not be a key determinant of growth rate in red maples. Rather I predict that red maples will be limited by competition with their neighbors, and that high levels of competitive stress will strongly inhibit red maple growth. This competition hypothesis suggests that at a certain point during the successional pattern, red oaks gain an advantage over red maples and out-compete their neighboring trees.

This could be due to a competitive edge in light, by gaining a height advantage; or a competitive edge in nutrients, by extending their root systems. Regardless of the mechanism, competition would have a similar effect in limiting red maple growth.

By understanding the predictors of red maple growth rates, we can more accurately predict what changes will occur in the composition of mature trees. However the older cohort is an illustration of past dynamics, whereas saplings suggest what the future may hold.

Successional theory suggests that a forest understory dominated by red maple would imply that red maple will eventually dominate the ecosystem. Storage theory suggests that even if the understory is dominated by red maple, the composition of the mature trees is also significant as these trees will continue to reproduce, potentially changing the composition of the understory in time. Using both of these theories will be critical for predicting future compositions and dynamics of this type of forest across the Northeastern United States.

2. Methods

2.1 Harvard Forest: Area Description and Land Use History

The Prospect Hill tract of the Harvard Forest is a 375 hectare area located at 42.5N 72.1W in central Massachusetts. The elevation ranges from 220 to 410 m above sea level, and the soil is mainly sandy loam glacial till, with some alluvial and colluvial deposits. The forest as a whole is a transition hardwood community, and the plots included in this study are of mixed deciduous forest, dominated by red maple and red oak. This site is typical of Northeastern mixed deciduous forests (Pederson, 2005).

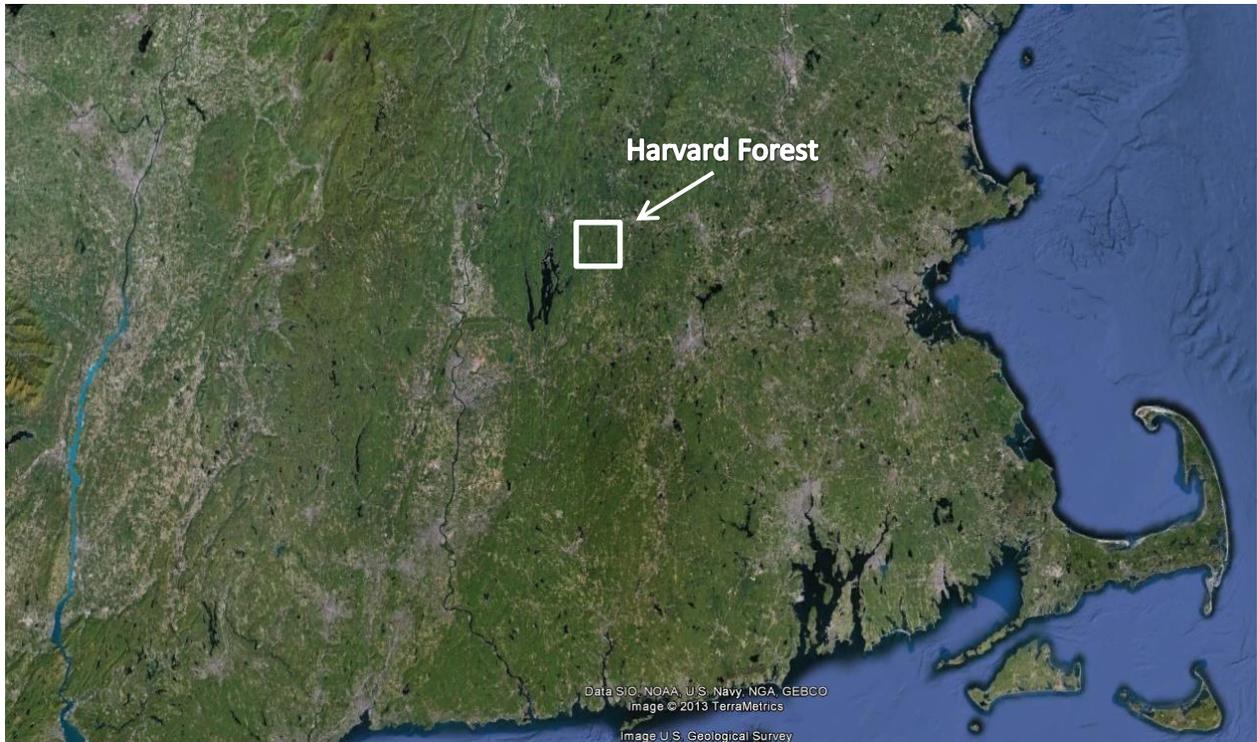


Figure 2: Satellite image of Massachusetts, with the Harvard Forest indicated. Courtesy of Google Earth.

Understanding the land use history at the Harvard Forest is crucial to putting this study into the larger context of forest stand dynamics over time. Disturbance, the catalyst of succession, is often caused by humans. Therefore understanding the human land use of a forest helps us understand the present dynamics. The Prospect Hill tract of the Harvard Forest has the benefit of being a well-studied research area; with long-term records available (Foster, 1992). From 1820-1880 the site was approximately 80% deforested, and used for woodlots, pasture and tilled farmland (Foster, 1992). Reforestation began at some sites as early as 1850, and progressed as a statewide trend of agricultural abandonment ensued (Foster, 1992). Since the reforestation of the Prospect Hill tract, there have also been some significant natural disturbances that had an impact stand dynamics. The hurricane in 1938, for example, negatively affected about 75% of standing trees (Foster and Boose, 1992). In 1981 there was a

gypsy moth invasion that defoliated red oak across the Prospect Hill tract (Pederson, 2005). These, among other disturbance events, play an important role in shaping the forest as it exists today, in part because of the impact that disturbance has on succession.

2.2 Site Descriptions

For this study, I took a variety of measurements at three distinct sites: the environmental monitoring station eddy flux tower site (“tower”), the cut site (“cut”), and the Little Prospect Hill site (“LPH”) (Figure 3).



Figure 3: Relative location of cut, tower and LPH sites at the Prospect Hill tract of the Harvard Forest.

These three sites are all part of the same contiguous tract of forest, and have similar species composition and abiotic attributes. The primary difference between these sites is in their disturbance histories. For the purposes of this study, I treat the tower site as a control

site, as it has been relatively undisturbed since its regrowth following agricultural and logging management. The cut site (as the name implies) was selectively harvested in the winter of 2000-2001, therefore I designated this as the “open” site. The LPH site was severely burned in 1957, killing nearly all of the overstory trees. The LPH site is thus a “young” site.

2.3 Field measurements:

For each red maple tree, I took a measurement of the diameter at breast height (DBH) using a specially marked measuring tape. I also took four measurements of crown radii (at approximately 90 degree angles), estimated the relative canopy position (either dominant, co-dominant, intermediate, or suppressed) and noted down the trees that had overlapping crowns. These trees were designated as competitors. For each competitor, I noted the species, took the DBH and four crown radii, estimated the relative canopy position and measured the linear distance between that tree and the “focus” red maple tree it is competing with. Crown radii were measured using a “periscope level”; a simple device with bubble levels in three orientations and mirrors. When level, the image in the device is the image of what is directly above (at 90 degrees). This allowed me to position myself directly under the edge of the canopy of the tree, and measure the radius of the tree crown using a tape measure (which could be hooked to a tree’s tag). These measurements were made on 40 red maples at the tower site, 40 at the cut site and 20 at the LPH site.

2.4 Tree Cores:

Additionally, I took cores from a subset of these trees for two of the sites: the cut site and the eddy flux tower site. The trees at the LPH site had cores taken in 2007 by Julian Hadley, so I did not core these trees. First, I eliminated trees that were not tagged, and therefore had

no previous data on growth. Next, I sorted the remaining focus trees by competition index and divided them into “low competition”, “medium competition”, and “strong competition”.

Within these groups, I used a random number generator to choose 10 trees from each of these groups to core (along with their oak competitors). Because the vast majority of the competitors were oak (and the majority of these sites are dominated by red maple and red oak) I did not core any trees that were not either of these species. For each tree, I took 2 cores at breast height (1.37 m). I collected the cores with either a 17 inch or a 20 inch increment borer (Ben Meadows) and stored them in plastic straws until they were processed.

2.4.1 Core processing and measurement

First, I mounted the cores onto wooden blocks, ensuring that the vascular strands were oriented perpendicular to the block (in other words, the cores were mounted in the same orientation that they were in the tree) and dried them for at least 48 hours. Next I sanded the cores to a flat surface using an orbital sander and paper of intermediate roughness. Then I sanded them with increasingly fine sandpaper (up to at least 600 grit) until the annual rings were clearly visible.



Figure 4: Completed cores marked for aging. The difference in wood type is clearly visible between the red maple and red oak.

Once the cores were processed, I used dissecting microscope to count the number of rings on all of the cores. Additionally I measured the distance between the annual rings on each core to the nearest 0.01mm using a Velmex tree ring measuring system. For each tree, the older age derived from the two cores was used in the analysis. This is because not all cores reached the pith at the center of the tree, so using the age from the core that includes the pith is more accurate. The annual growth rates were averaged between the two cores from each tree.

2.5 Data analysis:

2.5.1 Quantifying competition

Historically, quantifying competition was studied in order to inform forestry practices and plantation management. However the methods that were developed are also useful for understanding forest ecology. Alternative methods for best quantifying competition on individual trees have been reviewed many times. Competitive stress for an individual tree can be measured many different ways. Spatial analysis and stem mapping has been used to gain accurate reconstructions of relative sizes and locations of competitors (Bella, 1971). However simple indices including size and distance have been shown to work with equal accuracy (Lorimer, 1983, and Tome and Burkhart, 1989). The most straightforward of these indices is the sum the diameters of all competitors divided by the diameter of the focus tree (Lorimer, 1983). The most commonly used index was developed by Heygi (1974). His method also includes the distance between each competitor tree and the focus tree by dividing each size ratio by the linear distance between the stems before summing the terms (Heygi, 1974). Other studies have suggested including additional factors to characterize the nature of the competitive interaction more fully. Holmes and Reed (1991) suggest including factors to account for relative crown size or root competition, but saw little increase in significance when tested against growth rates. Ward (1964) created a competition index based on crown size, rather than DBH or basal area, and reported a significant relationship between this index and growth rate.

Accurately identifying competitors is another key to quantifying competition. Some indices use a constant “search radius”, and include every tree within a certain distance as a

competitor (examples in Lorimer, 1983 and Tome and Burkhart, 1989). Bella (1971) defines a competitor as a tree with an overlapping crown, as light competition causes the highest levels of competitive stress on forest trees (Walters and Reich, 1996). Lorimer (1983) found that the significance of the index increased when only trees with an equal or higher crown class to the focus tree were considered competitors.

2.5.2 Competition Indices:

Based on this review of the classical literature surrounding forest competition indices, I created 3 simple distance- dependent indices with which to quantify competitive stress. The first index is based on Heygi, (1974):

$$CI = \Sigma(BA_c/BA_f)/distance_{f-c}$$

where BA_c is the basal area of a competitor tree, BA_f is the basal area of the focus red maple tree, and $distance_{f-c}$ is the distance between the two. A tree was considered a competitor if any part of its crown was directly above any part of the focal tree's crown (based on Bella, 1971). Only trees in an equal or higher crown class as the focal tree were considered competitors (Lorimer, 1984).

A second index I calculated was based on the idea that the interaction between neighbors shouldn't be weighted linearly with distance. Therefore the second index is

$$CI = \Sigma(BA_c/BA_f)/\text{sqrt}(distance_{f-c})$$

in which BA_c is the basal area of a competitor tree, BA_f is the basal area of the focus red maple tree, and $\text{sqrt}(distance_{f-c})$ is the square root of the distance between the two.

The third competition index I calculated was a modified version of Heygi (1974), but rather than using the ratio of the basal area I used the ratio of the crown areas:

$$CI = \Sigma(CA_c/CA_f)/distance_{f-c}$$

where CA_c is the crown area of a competitor tree, CA_f is the basal area of the focus red maple tree, and $distance_{f-c}$ is the distance between the two. The crown area was calculated based on the average of the four crown radii measured above. This index was inspired by the relationship between average crown area and growth rates (Ward, 1964).

Calculating multiple indices, based on different size and distance parameters, additionally helps to reaffirm any trends seen in the data. If similar trends are reported by all three indices, then the relationship between competition and growth rate can generally be assumed to be robust. Although size-distance ratios are not perfectly descriptive models, analyzing all three indices helps to minimize bias introduced by using one index as opposed to another.

2.5.3 Analyzing the core annual measurements: Discussion of Cross-Dating

In order to determine the age of the trees that I cored, I simply counted the number of annual rings present on the core. Similarly, I calculated an average basal area increment (BAI) by subtracting the width of the annual ring from the basal radius, and used that to determine the previous year's basal radius. I then calculated the difference between the basal area in one year and the next, and averaged the BAI from each year across the two cores taken from each tree.

Many dendrochronology studies include a statistical cross-dating of cores before using the ring width measurements. In short, cross-dating involves using statistical analysis to match up narrow and wide rings from different cores in order to identify specific years' growth. I did not cross-date these cores, which is possibly a source of bias in this data. However, for the

scope of this project, cross dating did not seem necessary. First, this project is not tracking climate fluxes of specific annual factors impacting growth rate, rather it looks broadly at stand level trends over time. Because I am not interested in comparing a particular year's growth response to a particular year of climate, the biased introduced should be minimal. The impact of not cross-dating has already been assessed on trees at the tower site (Figure 5). While cross-dating is critical for assessing climatic responses and cumulative carbon storage, average long term growth patterns follow the same trajectory.

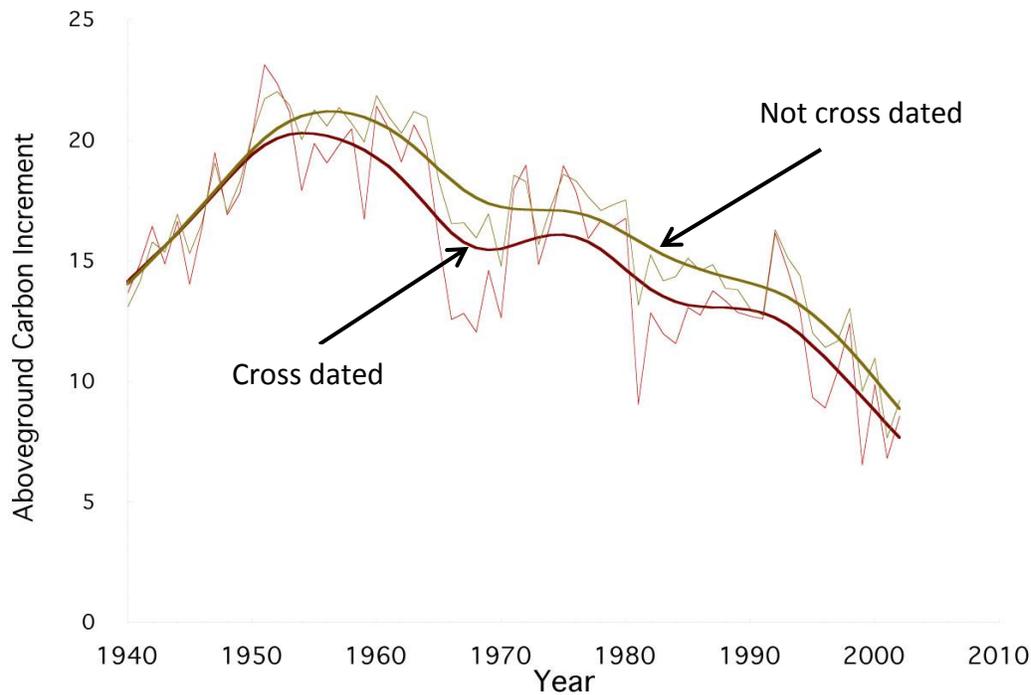


Figure 5: Comparison of aboveground carbon increment of tree cores taken from the tower plots of the Harvard Forest in 2003. Show with the permission of Neil Pederson, from a talk given on March 5th, 2013.

Secondly, the bias introduced is one directional. As noted in Pederson (2005), many of the red maples are missing some of their annual rings, particularly from the past few decades.

Pederson (2005) did an analysis of the impact of not cross-dating these cores, and found that the average growth rates were slightly inflated, but the trends remains the same. Therefore by not cross-dating, it is likely that I am slightly overestimating the growth rate of the maples. Because the difference between the maples and the oaks seems to be significant even without cross-dating, we can safely assume that cross-dating the cores would not have altered the conclusions of this study.

Finally, this site experienced a severe gypsy moth defoliation in 1981 (Pederson, 2005), Gypsy moth has a strong preference for red oak, and the impact on the growth rates of this event is clearly visible in the red oak cores (Figure 6).

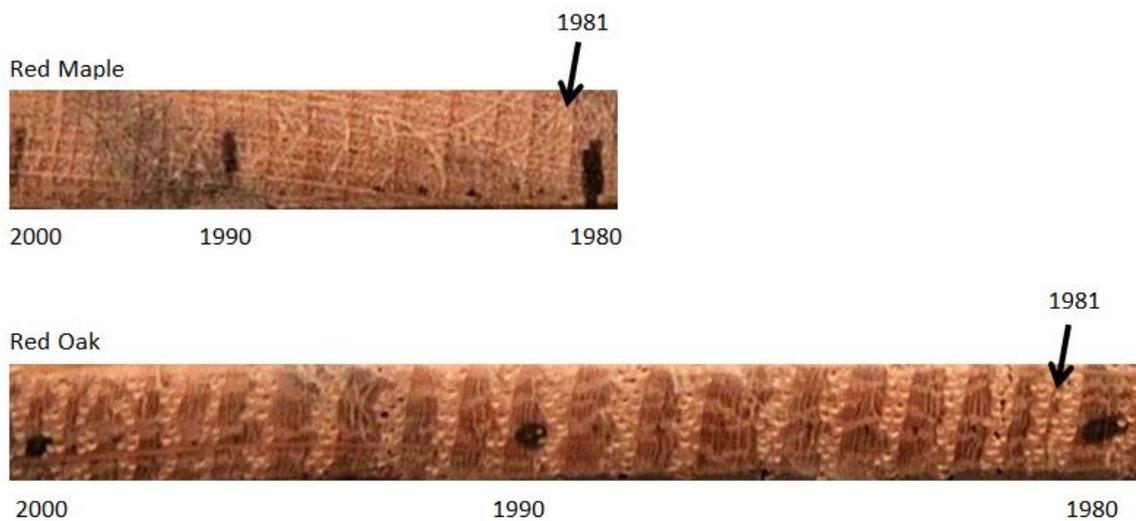


Figure 6: Comparison of red maple and red oak cores from 1980-2000. Gypsy moth defoliation is very evident in red oaks, and visible in red maple (slightly whiter). Shown at same scale- red oak increases much more over the same two-decade time period.

Using this identifying year, these cores can be easily cross-dated for the last 31 years with a simple visual test. Some red maples were also defoliated by the gypsy moth, and their 1981 ring shows up very narrow and in some cases white (Pederson, 2005). For these cores, seeing

the 1981 ring also is an effective way to cross-date these cores. However, fewer of the maples has an obvious response to the gypsy moth (as few red maples were in fact defoliated), which makes these data less certain. However as discussed above, the cross-dating should not change the conclusions that can be drawn from this study.

2.6 Additional data:

I have additionally included data collected by the Wofsy-Munger research group, which provides detailed information about the trees at the tower and cut sites. Data for the tower site is available since 1993, including detailed DBH measurements on all tree stems larger than 10 cm DBH, understory surveys collected in 2004, 2006 and 2010, and information about mortality when it occurs. Similar data for the cut site is available from 1999-2007. I used the available raw data and analyzed it within the framework of this project.

3. Results and Discussion

3.1 Analysis of long-term dynamics at the Harvard Forest:

In order to assess the drivers of changing dominance occurring at the Harvard Forest, I first put the present dynamics into context by determining the long term changes that have already occurred at these sites. One indicator of past growth rates and disturbance regimes is to consider the current age distribution at the three sites (Figure 7 and Figure 8).

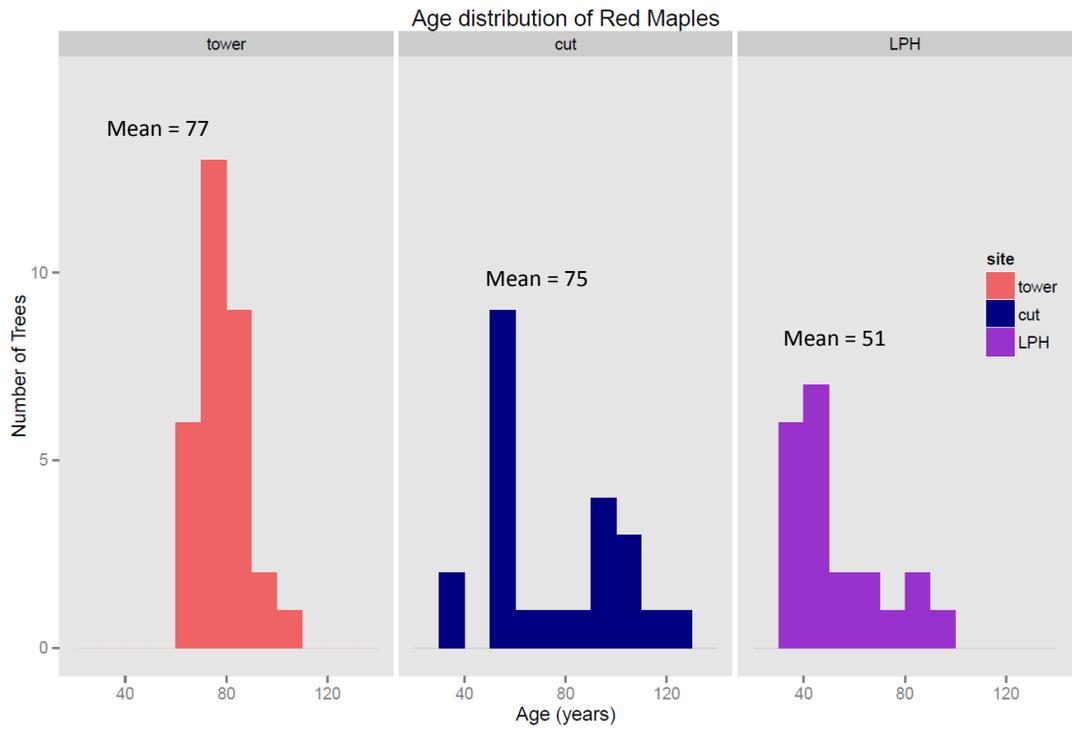


Figure 7: Age distribution of red maples at all three sites at the Harvard Forest.

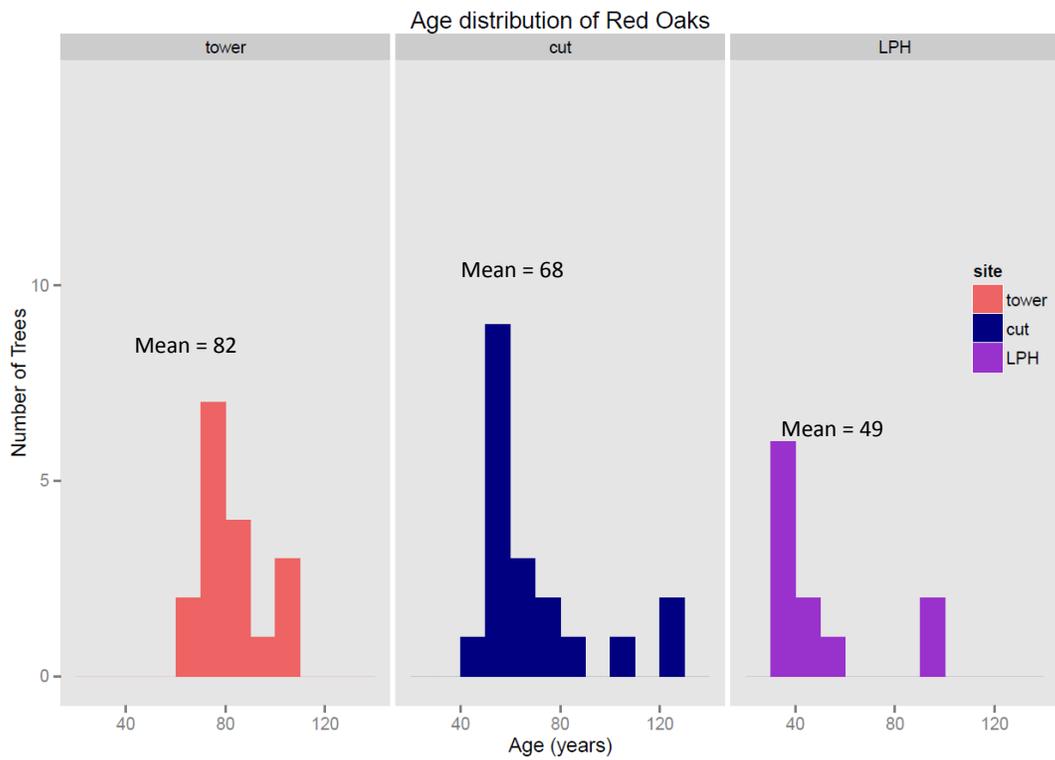


Figure 8: Age distribution of red oaks at all three sites at the Harvard Forest.

Red maples and red oaks at each of the sites are not significantly different in age ($p > 0.1$). Age of red maples and red oaks at the tower site are not significantly different from red maples and red oaks at the cut site ($p > 0.1$). Red maples at LPH are significantly younger than red maples at the other sites ($p < 0.001$). Red oaks at LPH are also significantly younger than red oaks at the other two sites ($p < 0.001$). The effect of the severe burn at the LPH site in 1957 ago is clearly visible in the age distribution at that site- there are very few trees older than 55 years. The age distributions show that all three of these sites are relatively even aged. The distribution of ages at the cut site could have been impacted by the selective harvest, which may explain its oddly shaped distribution. The fact that red oaks and red maples are not significantly different at these sites is also important- it shows that the differences in growth rates or size are not due to a difference in the time of colonization.

Determining the relative growth trends of the two species is also critical to understanding the history of interaction between them. At the tower site, red maple basal area increment increased significantly between 1930 and 1955 (slope = 0.18, $p < .001$, $r^2 = .8359$) but decreased since 1955 (slope = -0.0529, $p < 0.001$, $r^2 = 0.6832$) (Figure 9). Red oaks at the tower site did not have a significant trend over either period (1930 to 1955: slope = 0.135, $p = .127$, $r^2 = 0.0564$, 1955-2012: slope = 0, $p = .658$, $r^2 = 0$). These trends show that red maples are gradually decreasing in the mid and upper canopy relative to red oaks at the tower site. The red oak growth rates are more variable over time than the red maple, but they remain significantly higher over the entire time period. The only point in the time series when red maple and red oak growth rates are comparable is in 1981. As noted previously, there was severe gypsy moth defoliation in 1981, which is clearly visible in the growth rates of red oaks.

Gypsy moths preferentially eat red oak, which explains why the decrease is not apparent in the red maple growth trends.

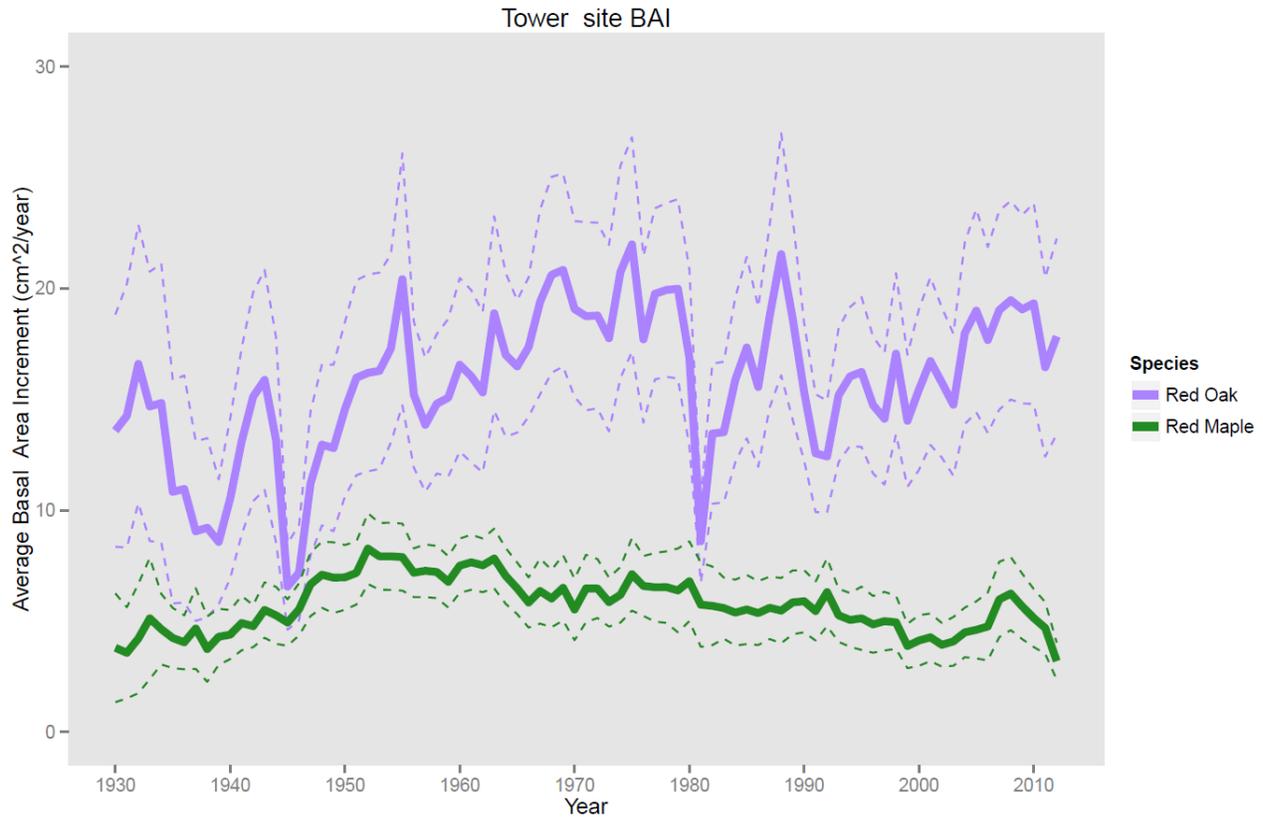


Figure 9: Average BAI over time at the tower site. Time series for each species is only shown for years where there are available data from four or more tree. Dashed lines represent 95% confidence interval.

At the LPH site, red maples decreased since 1955, however the decrease has been minimal and at a slower rate than at the tower plot (slope= -0.02, $p = 0.046$, $r^2 = 0.061$) (Figure 10). Red oaks at LPH, like those at the tower site, had no significant trend (slope = -.02, $p = .432$, $r^2 = 0$). The gypsy moth defoliation of 1981 had a significant impact on red oak growth rates. It is not surprising that the decrease at this site is less severe than at the tower site. Due to the 1957 burn, this site is primarily in an earlier stage in stand development. Based on the growth

trends at the tower site, which showed increasing growth rates early on in stand development, the slight decline occurring now at the LPH site is likely to become more apparent over time.

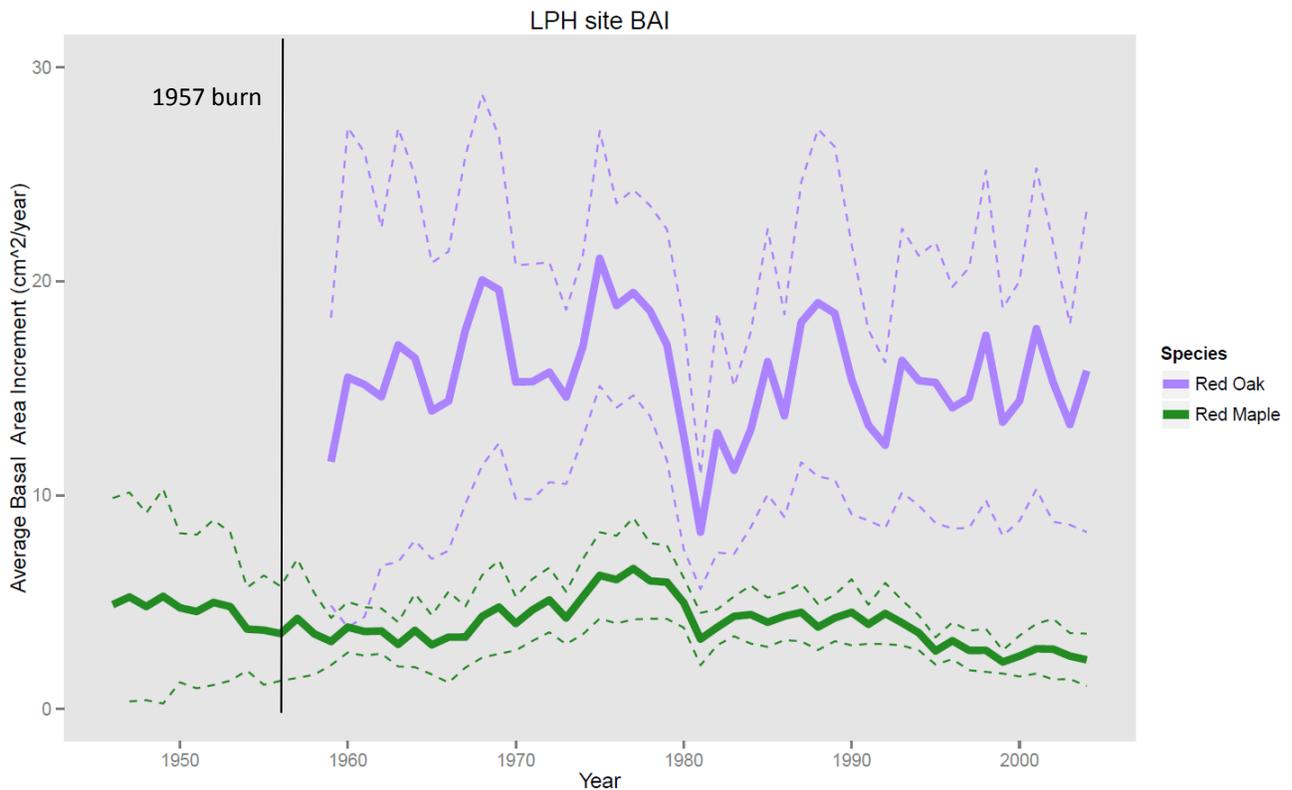


Figure 10: Average BAI over time at the LPH site. Time series for each species is only shown for years where there are available data from four or more tree. The vertical line represents the severe burn that occurred in 1957, killing the majority of canopy trees. Dashed lines represent 95% confidence interval.

Evaluating the cut site over this same time periods would be misleading, because of the strong effect of the cut in the winter of 2000-2001. Therefore I evaluated it over the period before 1955 and from 1955-2000. Until 1955, red maple increased marginally (slope = 0.014, $p = 0.0313$, $r^2 = 0.081$) and red oak decreased slightly (slope = -0.061, $p = 0.0185$, $r^2 = 0.149$) (Figure 11). Between 1955 and 2000, red maples continued to increase slightly (slope = 0.025, $p = 0.0011$, $r^2 = 0.2$) and red oaks followed no significant trend (slope = -0.014, $p = 0.36$, $r^2 = 0$).

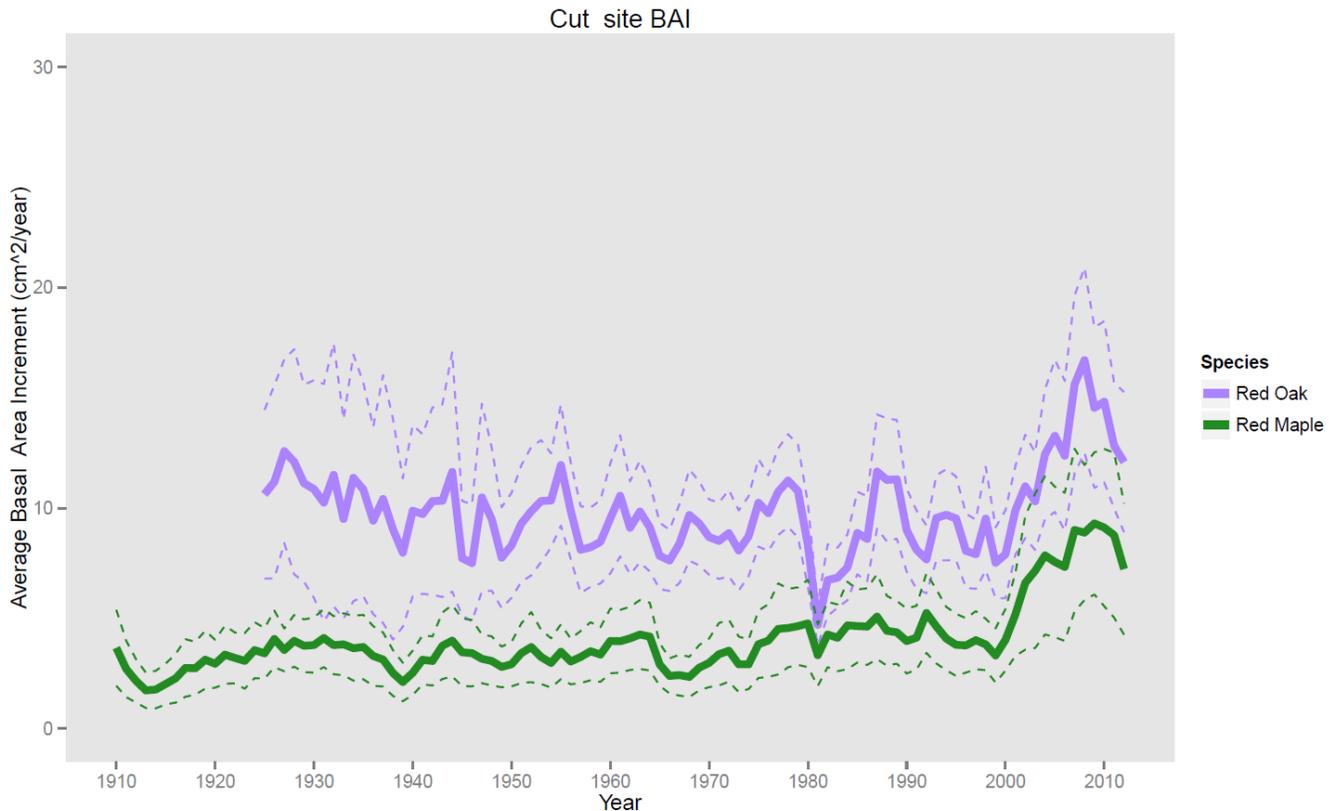


Figure 11: Average BAI over time at the cut site. Time series for each species is only shown for years where there are available data from four or more tree. Dashed lines represent 95% confidence interval.

Based on these three reconstructions of growth rate over time, it seems that red maples in the mid and upper canopy grow much more slowly than red oaks, regardless if the trees are significantly younger (at the LPH site) or recently disturbed (at the cut site). The rate of red maple decline is very slow, and red maples remain more abundant than red oaks overall.

While long term growth rates impart valuable information of the relative success of the two species, it only shows the dynamics between the trees that have survived to today.

Another attribute of forest stands that additionally illustrates the effects of growth, mortality and regeneration over time is size distribution. For the last 20 years, the Wofsy-Munger group has been measuring the diameter of trees at the tower site. The size distribution exhibited

there (and the changes in distribution over time) reflects how red maples and red oaks at this site have fared over the last 20 years (Figure 12 and 13).

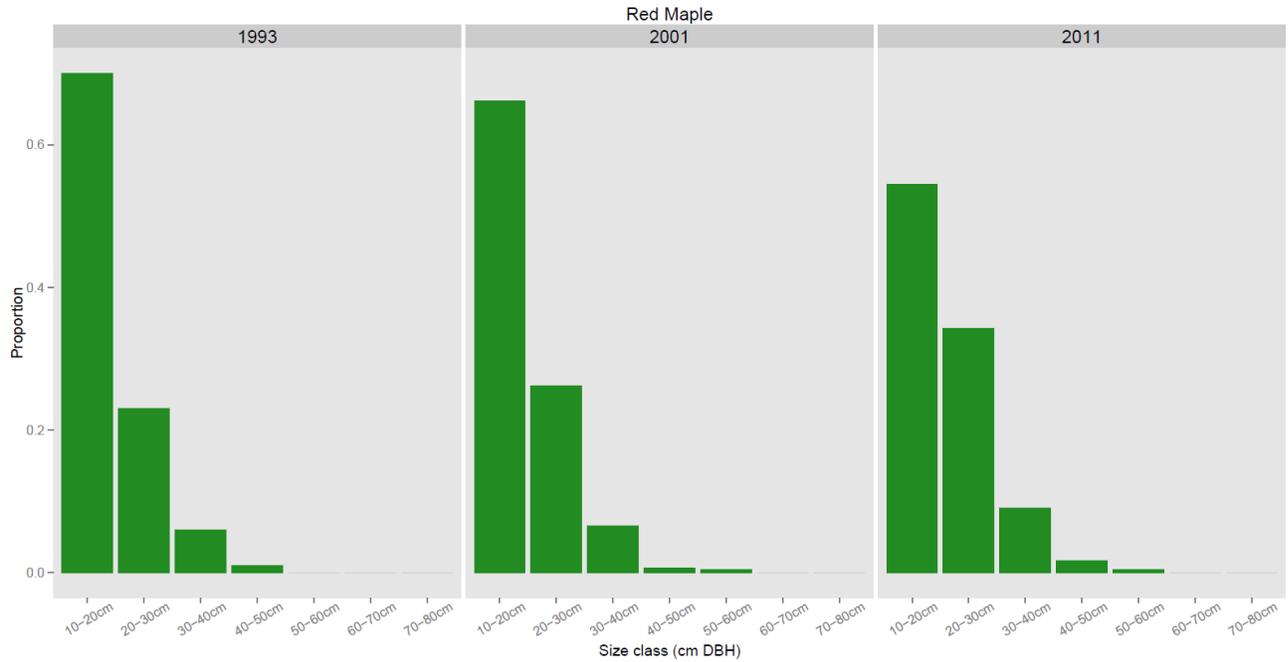


Figure 12 : Change in size distribution from 1993-2011 in red maples at the tower site.

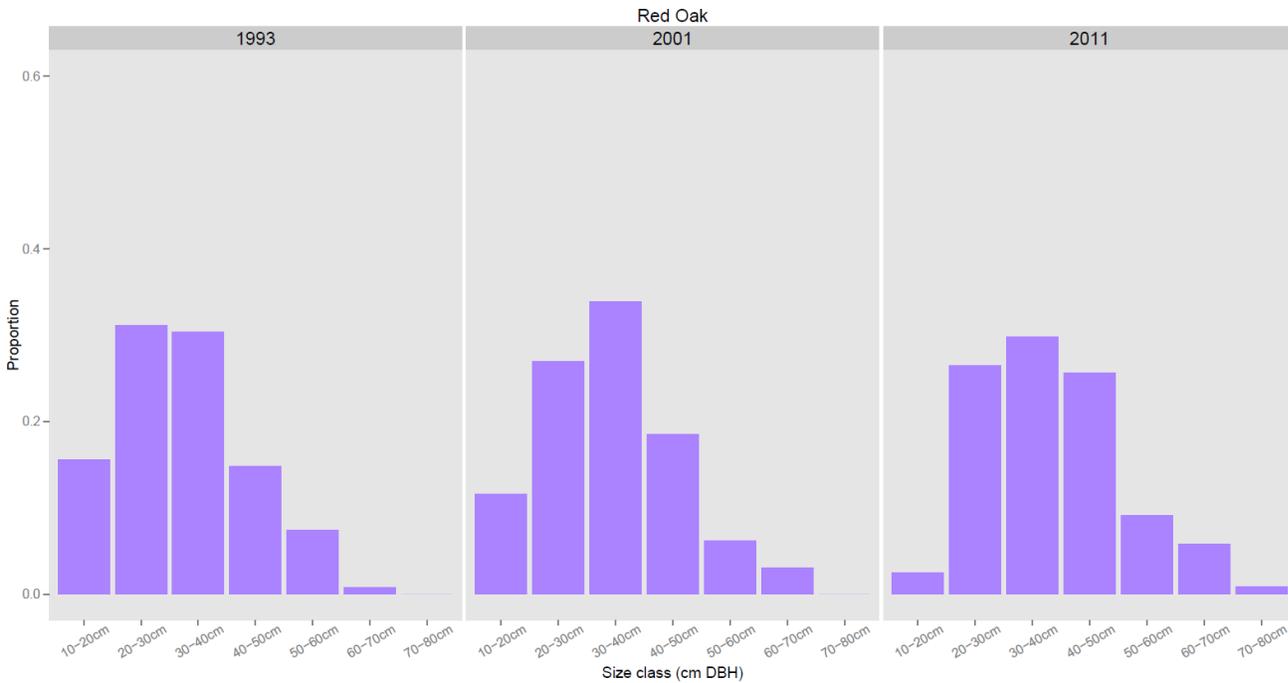


Figure 13: The change in size distribution of red oaks since 1993 at the tower site.

Red maples exist primarily in the smallest size category, although they are becoming more evenly distributed over time (Figure 12). Red oaks have almost completely lost all trees in the smallest size class, and are evenly distributed in the size classes between 20 and 50cm DBH (Figure 13). Red oaks have declined in both size classes below 30cm DBH, and have only increased in size classes above 40 cm DBH.

The change in size distribution has not only been due to trees growing out of size classes- there has also been significant mortality over this period for both species. Red maples decreased their number of stems from 300 stems in 1993 to 233 stems in 2001 (a 22.3% decrease). Red oaks decreased from 135 stems in 1993 to 121 stems in 2001 (an 11.57% decrease). As trees become larger with age, it is common for there to be a higher mortality than recruitment rate. However red maples had a relatively high rate of mortality, both in stem number and in biomass. The higher mortality exhibited in red maples is consistent with the decline in growth rates.

Taken together, this data on historical red maple and red oak dynamics suggests that red maples greater than 10 cm DBH are in gradual decline. Their average growth rate is decreasing, their mortality rate is higher than that of red oak, and while they are the same age they are primarily smaller trees than the oaks that they compete with.

3.2 Analysis of age and competition as drivers of red maple growth rates

Having established the nature of red maple decline in the canopy, I tried to determine what is driving this change. In order to investigate this, I tested what factors were good indicators of growth rates in red maple. Age is a significant factor for predicting basal area

increment in red maples, suggesting that red maples generally grow faster when they are older (Figure 14). However, the slope of the relationship is very small, and there is considerable scatter, suggesting that age is not the most important factor. In red oaks, age is not a significant factor in predicting growth rate (Figure 15).

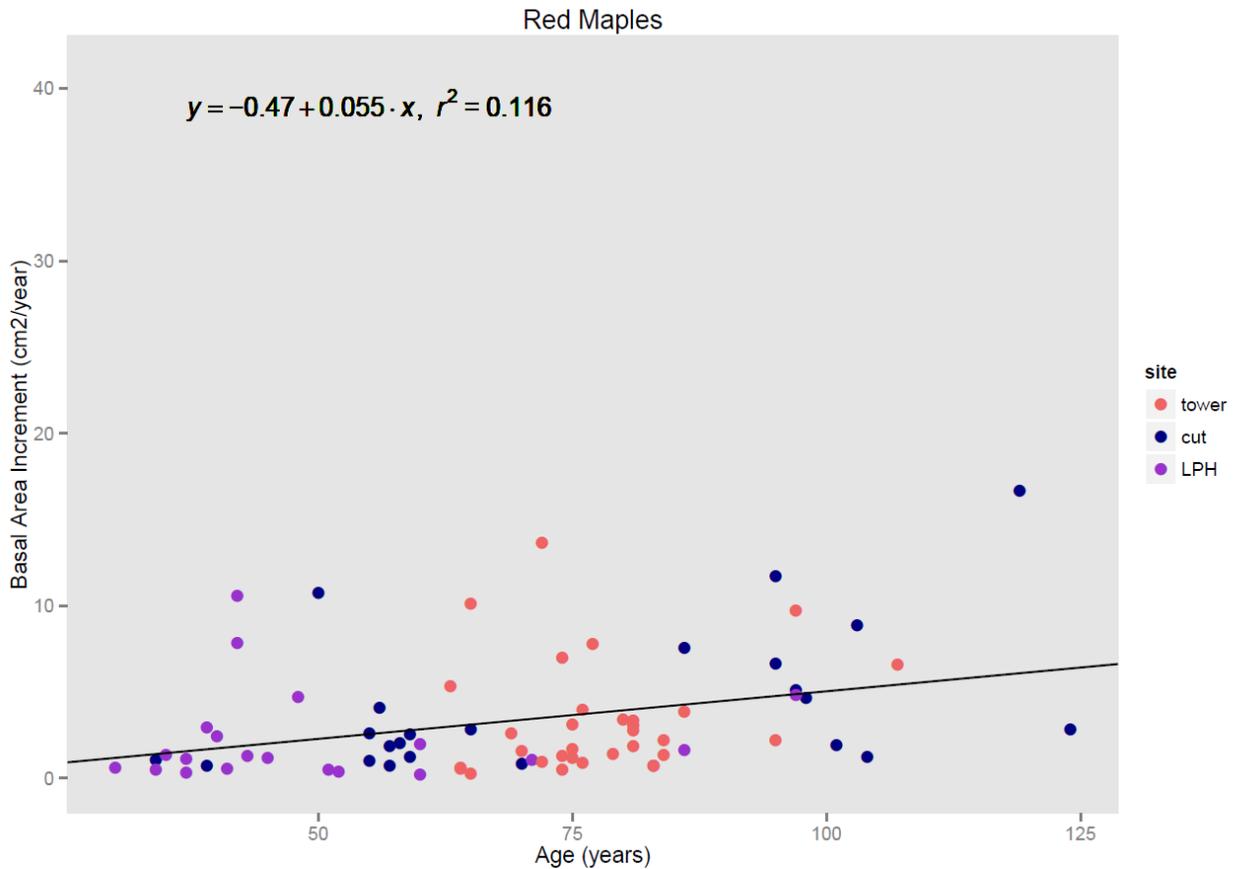


Figure 14: Age vs. Basal Area Increment (cm²/year) for red maple trees at all three sites at the Harvard Forest. Trend is significant at $p < 0.001$. Note: the data on trees at the cut site is based on a calculation of BAI in 2000, and their corresponding age in that year in order to avoid confounding this relationship with the response exhibited by trees at that site to disturbance. BAI measurements are calculated based on the dendrometer data collected at the sites.

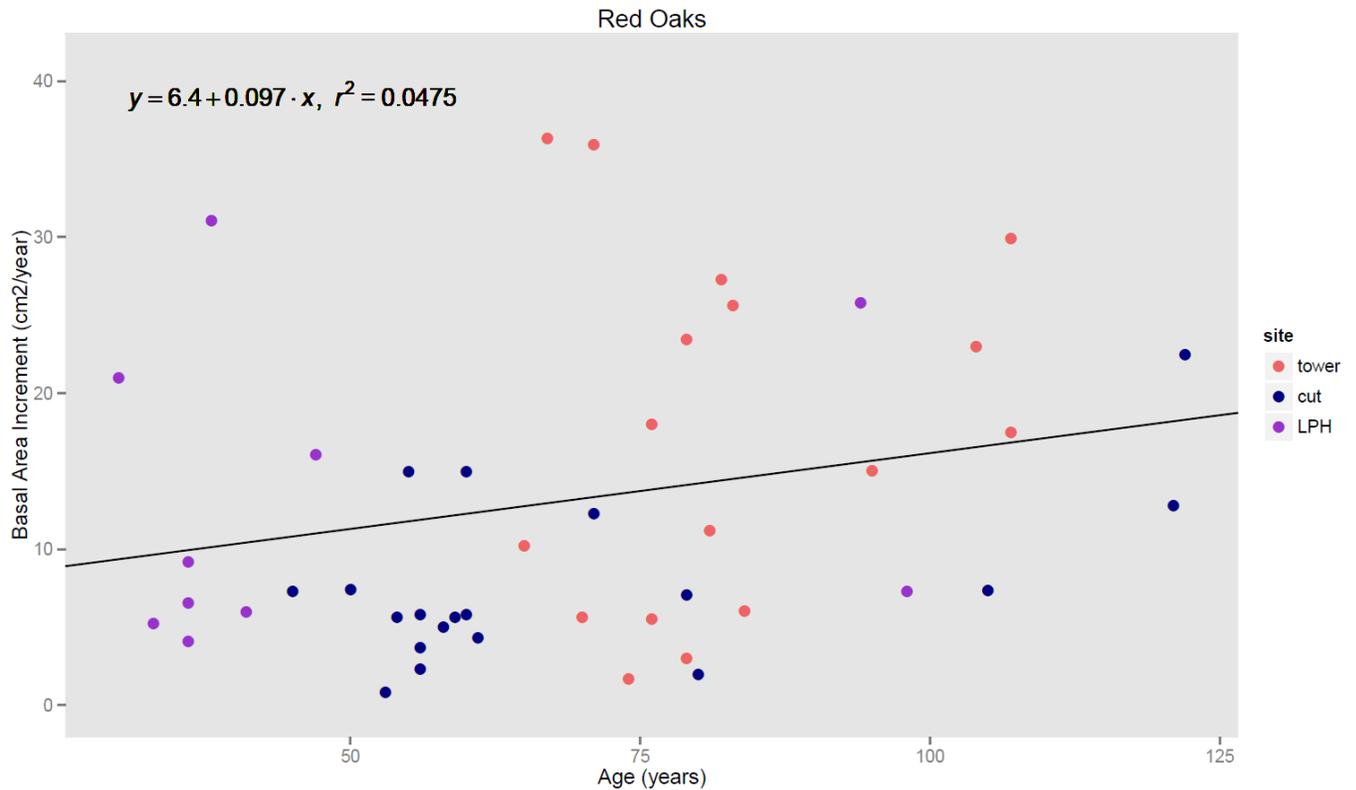


Figure 15: Age vs. Basal Area Increment (cm²/year) for red oak trees at all three sites at the Harvard Forest. Trend is not significant ($p > 0.1$). Note: the data on trees at the cut site is based on a calculation of BAI in 2000, and their corresponding age in that year in order to avoid confounding this relationship with the response exhibited by trees at that site to disturbance. BAI measurements are calculated based on the dendrometer data collected at the sites.

These relationships suggest that red maples are not limited by age. Although red maple is classically considered a short-lived tree species, decline in red maple fitness does not seem to occur within the age range of trees included in this study. It is likely that the positive relationship exhibited by red maples is in fact symptomatic of other factors of success. The successful red maples survive and flourish, possibly because they were under less competitive pressure in the past. Looking instantaneously at the age/growth rate relationship now, the successful red maples seem to be the older trees, while the younger ones are suppressed and therefore growing more slowly. The high mortality rate among red maples suggests that many

of the young, suppressed maples will die, and the red maples growing in more advantageous environments will survive. The fact that a similar relationship does not exist in red oaks suggests that red oaks may not be experiencing the same pressures, and the fact that red oak mortality is lower than that of red maple reinforces this assumption.

While age does not seem to be a good predictor of red maple growth rate, competition has a stronger relationship with growth. Using any of the three competition indices I calculated, competition was a significant indicator of red maple growth rate (Figures 8-10).

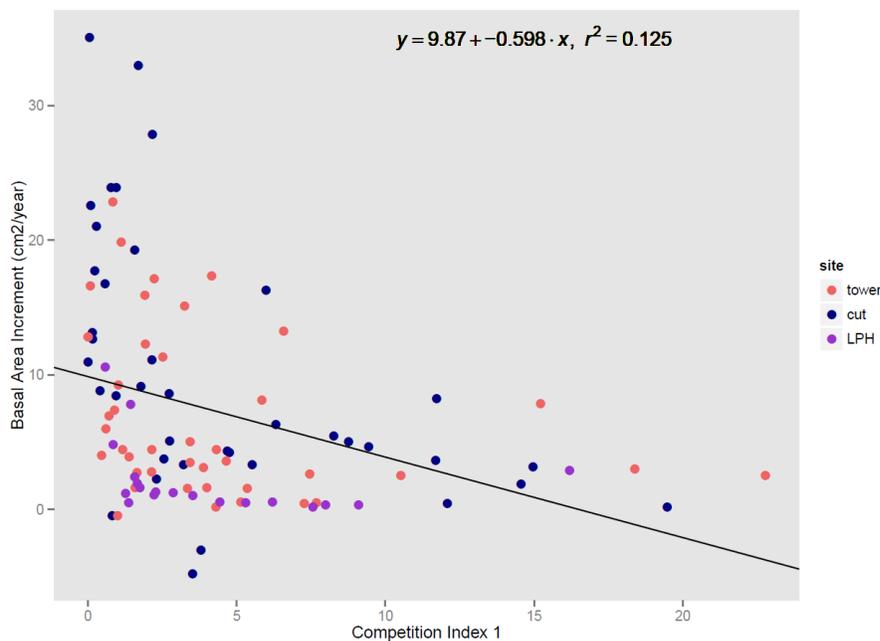


Figure 16: Competition Index 1, calculated as $\Sigma(BA_c/BA_f)/\text{distance}_{f-c}$ vs. BAI at all three sites at the Harvard Forest. Trend is significant at $p < 0.001$. BAI measurements are calculated based on the dendrometer data collected at the sites.

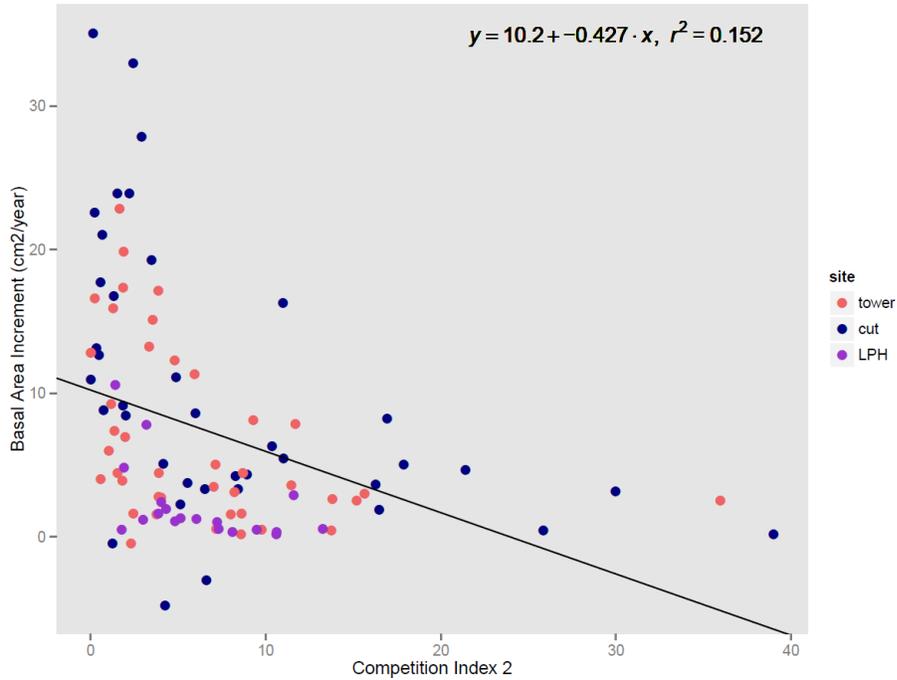


Figure 17: Competition Index 2 calculated $\Sigma(BA_c/BA_f)/\text{sqrt}(\text{distance}_{f-c})$ vs. BAI at all three sites at the Harvard Forest. Trend is significant at $p < 0.001$. BAI measurements are calculated based on the dendrometer data collected at the sites.

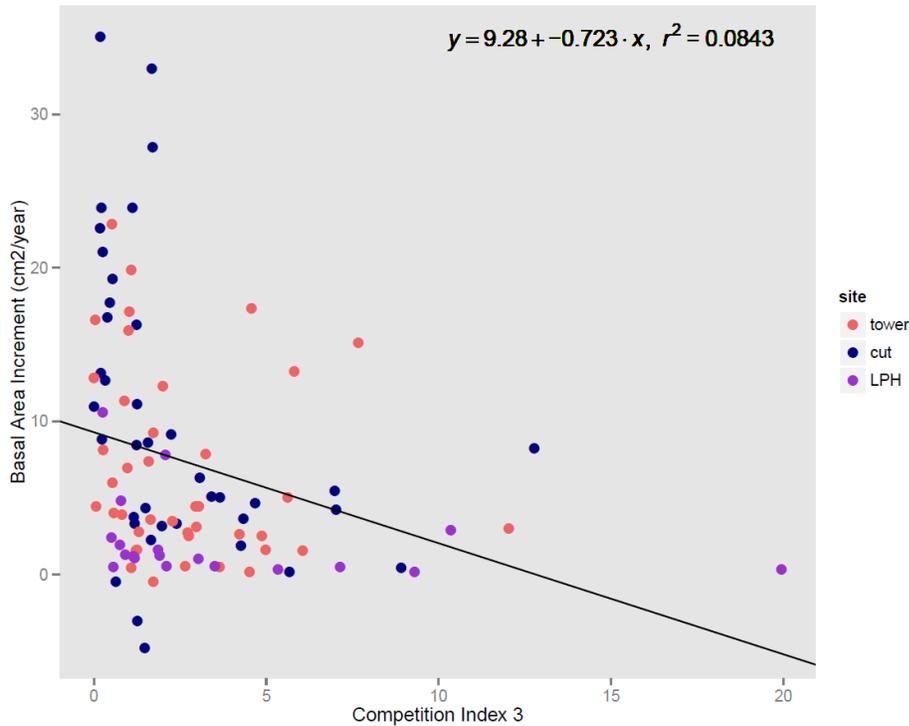


Figure 18: Competition Index 3 calculated $CI = \Sigma(CA_c/CA_f)/\text{distance}_{f-c}$ vs. BAI at all three sites at the Harvard Forest. Trend is significant at $p < 0.01$. BAI measurements are calculated based on the dendrometer data collected at the sites.

Of the three indices, competition index two has the highest r^2 , suggesting that it is the most adept at quantifying competitive stress. This suggests that the other two indices are overweighting distance, as competition index 2 uses the square root of the distance between competitors, rather than the absolute distance. The index with the worst fit is competition index 3, which uses canopy area rather than basal area as the size term. This suggests that basal area is a better measure of relative size of competitors than canopy area. All three indices are significant at $p < 0.01$, suggesting that measuring competition at the individual level justifies trends seen at larger scales that point to competition as a significant factor affecting red maple growth rates.

There is also site-level evidence that competition is driving red maple decline, based on growth rates following a disturbance event. The cut site was selectively harvested in the winter of 2000-2001. This was not a severe disturbance or clear cut, and today the site looks almost identical to the tower site. This provides us with an opportunity to see how these species respond to a small disturbance event, which may to release some of these trees from competitive pressures by removing their neighbors.

Based on the growth rates calculated from the cores taken at the cut and tower sites, red maples were growing at similar rates and with similar inter-annual trends in the decade preceding the harvest (Figure 19). After the cut, some of the red maples at the cut site were released from competition, and the average growth rate of maples at the cut site is significantly higher in the decade since the harvest than the one preceding the harvest (Table 1).

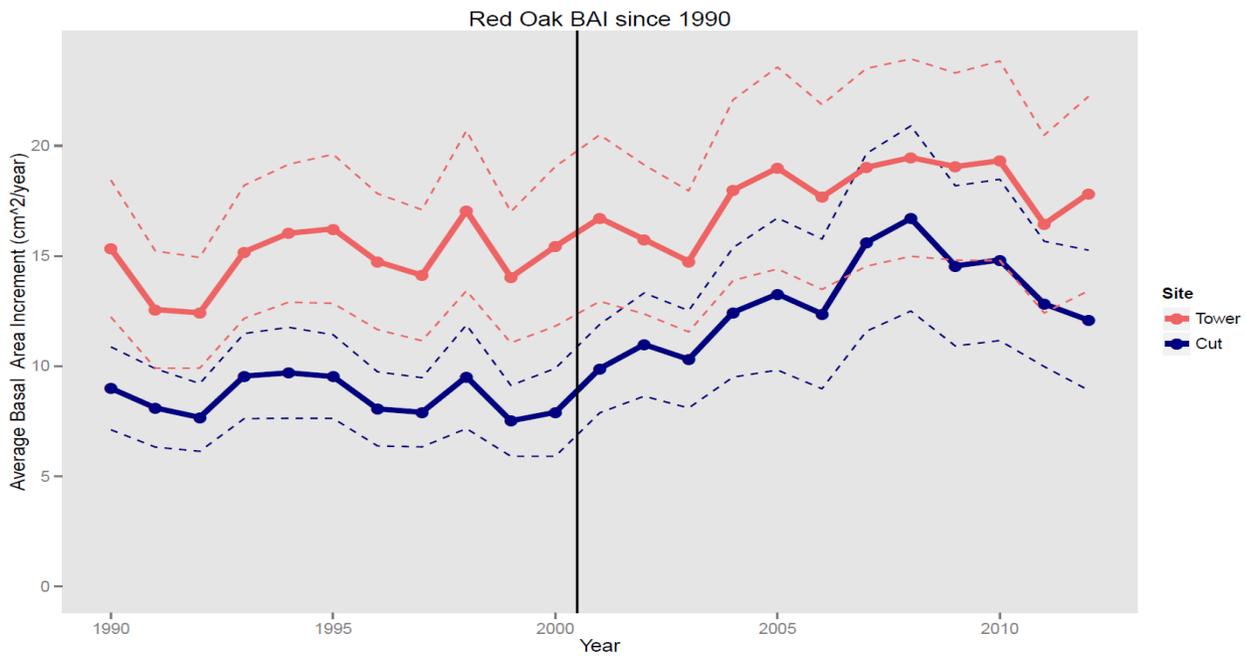
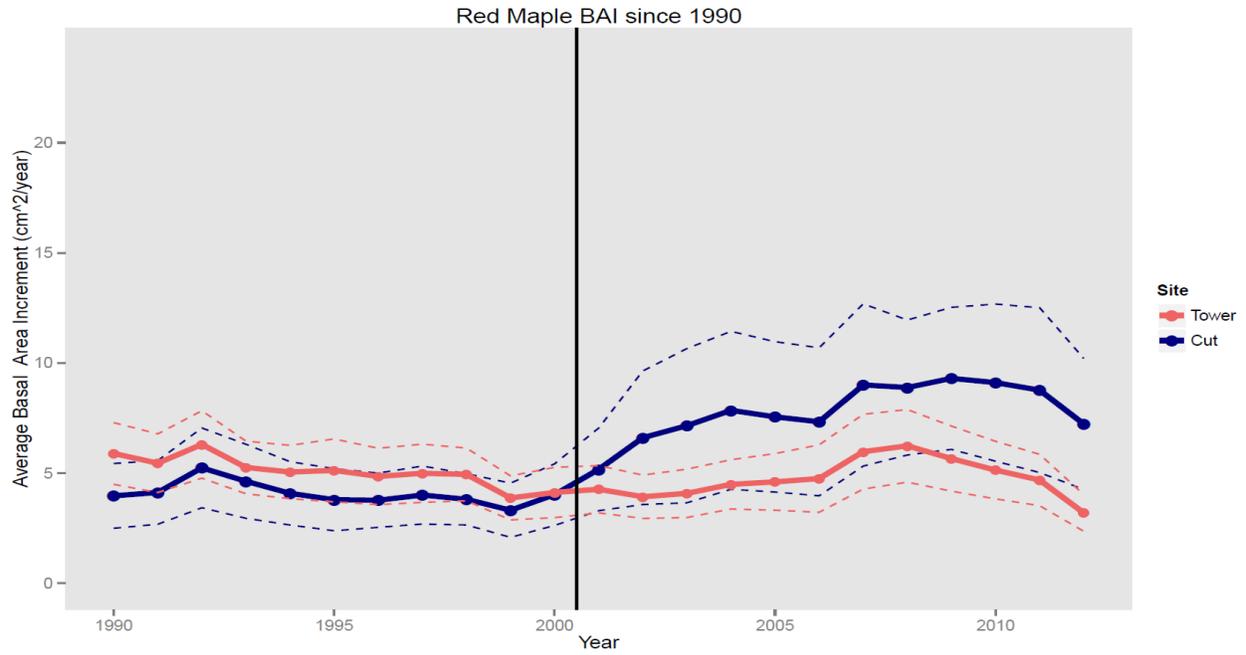


Figure 19: Upper panel shows red maple growth rates at the cut and tower sites from 1990-2012. Lower panel shows red oak growth rates at the cut and tower sites from 1990-2012. Vertical line represents the timing of the cut (winter of 2000-2001).

Table 1: Results of paired t-test

Site	Species	Mean of differences (between average growth rate during 1990-2000 and 2001-2012)	p value
Cut	Red Maple	3.93	0.00945
Cut	Red Oak	4.5	0.000693
Tower	Red Maple	-0.3	0.2774
Tower	Red Oak	2.969	0.00867

Red oaks at the two sites also show similar inter-annual trends, but the response to the release is less dramatic. Although the absolute increase in growth rate is larger than the increase in red maple growth rate, as a percent increase it is much smaller: red maple growth rate increased by 92%, whereas the red oak increased by only 51%. It is also interesting to compare the cut oaks to the tower oaks. The tower oaks did not experience a disturbance event, but their growth rates did increase significantly over the last decade (Table 1). Because the cut and tower oaks seem to follow similar trends in growth rates, we can assume that the cut oaks would have experienced a similar increase over the last decade even if there had been no harvest. Therefore the response to a release in competition is much lower in red oak than in red maple.

The tower oaks seem to be growing at a consistently faster rate than the cut site oaks. This may be partially explained by the fact that on average, the oaks at the tower site are larger than the oaks at the cut site (Table 2). Red oaks at the cut site decreased in average size following the harvest. Red maples at the cut site are also smaller on average than red maples at the tower site, but the result of the harvest was an increase in the average size of red maples. This helps to explain the difference in relative response to the harvest and the resultant release from competition.

Table 2: Comparison of average size of trees in 2000 and 2001 (harvest occurred at the cut site in the winter of 2000-2001)

Site	Year	Species	Average basal area	standard deviation
Cut	2000	Red Maple	136.6	166.3
Cut	2000	Red Oak	675.4	530.6
Cut	2001	Red Maple	161.2	203.2
Cut	2001	Red Oak	553.3	399.7
Tower	2000	Red Maple	310.7	261.1
Tower	2000	Red Oak	998.7	689.9
Tower	2001	Red Maple	309.6	264.2
Tower	2001	Red Oak	997.6	693.8

3.3 Analysis of the understory: predicting future dynamics

While studying trees with DBH > 10 cm demonstrates the past interactions and dynamics, it is not necessarily the best predictor of the future. In order to forecast how these species will progress, we must also consider their relative regeneration patterns. As suggested by the literature, red maple saplings are far more abundant, both in stems and biomass, due to their relatively high shade tolerance (Figure 20). This dominance is more pronounced at the cut site than at the tower site- the understory of the cut site has 25x more red maple biomass per unit area than red oak biomass, and the understory of the tower site has about 6x more. Based on the available data from the tower site, this trend is relatively consistent over time (Figure 21).

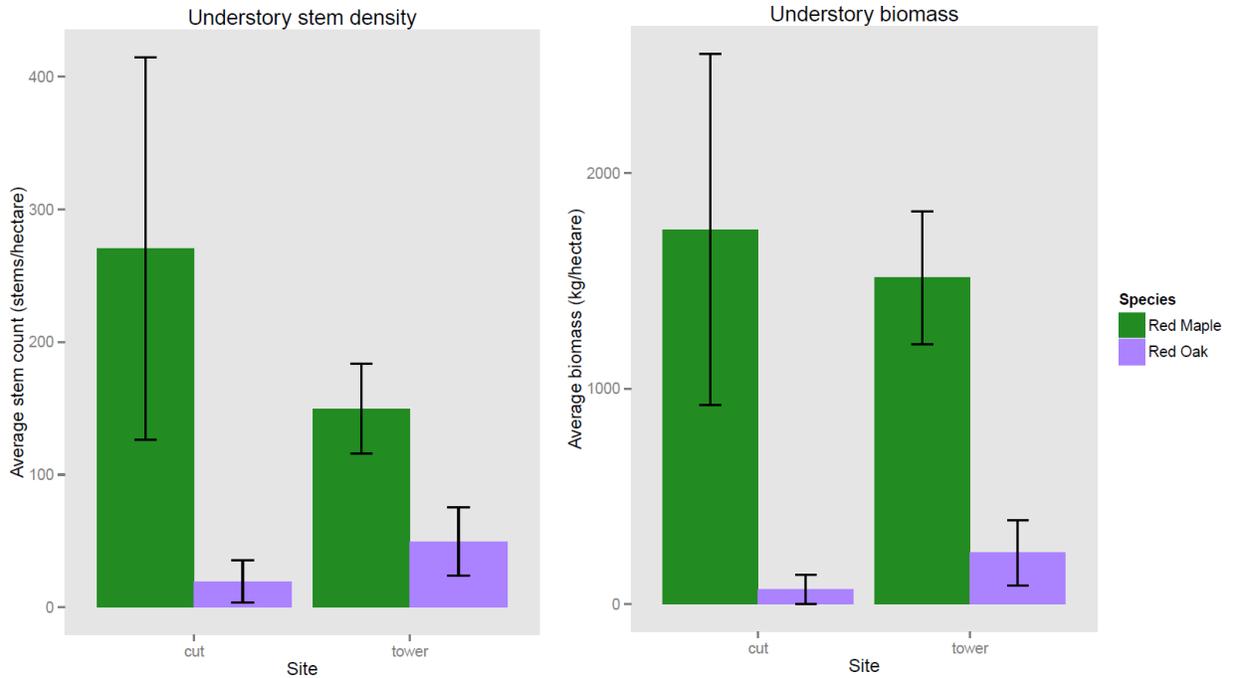


Figure 20: Understory stem density and biomass per area at the cut and tower sites for red maple and red oak in 2006.

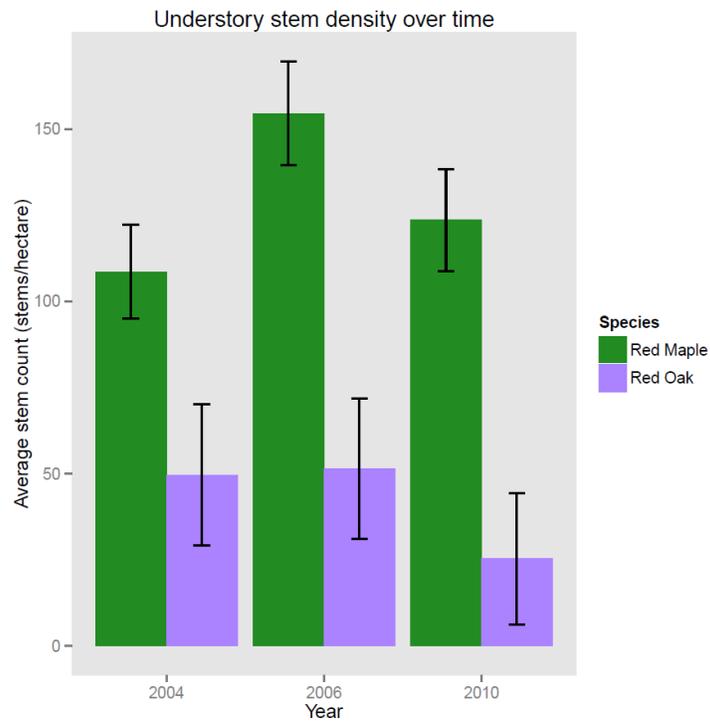


Figure 21: Tower site understory composition over time in average number of stems per hectare.

Historically, red oak forests were impacted by a variety of natural disturbances, including fire. Due to the reduction of these disturbances in recent decades, more mesophytic competitors (in this case, red maple) have outcompeted red oak saplings in the understory. This is significant when considering the future composition of the forest. Currently, red maple dominance in the understory is well established and consistent. If the system continues along this path, red oak saplings will continue to be outcompeted and will not reach maturity.

4. Conclusions

There are three significant conclusions to draw from this study.

1. Red maples are gradually declining, driven primarily by competition with red oaks.
2. Red oaks have historically grown and continue to grow more quickly than red maples.
3. The understory is dominated by red maple, and this dominance seems to be stable over time.

Based on these three pieces of evidence, I propose that storage theory more accurately portrays and predicts the dynamics red oak/red maple systems. Studies which cite succession predict that red maple will ultimately gain dominance over red oaks because red maple saplings are more shade tolerant. Succession does not fully describe the dynamics occurring at the Harvard Forest, as it does not predict or account for the effects of the decline in red maples. Storage theory incorporates the condition of overstory trees into the prediction of future trends. This accounts for the gradual decline of red maple, as well as the robust growth of red

oak. In light of storage theory, I predict that mixed red oak/red maple stands will remain relatively stable in species composition over time. As larger red maples decline in growth rate, they are replaced by saplings, which grow abundantly in the understory. Red oaks are growing vigorously, and based on historical growth rates are likely to continue to do so. Currently they are not successfully producing saplings that reach 10 cm DBH, but they continue to produce acorns annually. Given a disturbance event (such as a fire) or change in environmental conditions, red oak saplings could be given the right conditions to grow into mature trees. A large disturbance event could also have a positive impact on the suppressed red maples, which have been shown in this study to exhibit a significant increase in growth following disturbance.

Succession is a useful theoretical tool for illustrating forest processes over time. It highlights how a certain trait, such as shade tolerance, can play a critical role in the survival and fitness of a given species in a specific system. The shade tolerance of red maple is important to consider when making predictions about the future of the forest, but predictions of dominance should not be exclusively based on the relative shade tolerance of saplings. Red maple dominance would require a significant change in fitness of red oaks in the canopy, and historically even significant disturbance events haven't decimated red oak populations. Neither the selective harvest in 2000-2001 nor the 1981 gypsy moth defoliation had a lasting negative impact on red oaks. In fact, the selective harvest had a slight positive impact on red oak growth rates. The gypsy moth defoliation only significantly impacted red oak growth rates for a few years, after which they recovered entirely. Significantly changing the dominance of red oaks in the canopy would require an extreme disturbance, and maybe one that would fundamentally alter the nature of the system.

Future Research

Understanding how species fit into long term patterns, as well as how they interact on both an individual and site level is crucial for predicting future forest composition. This is critical to making assumptions about how these systems will sequester CO₂. Therefore, future research should focus on connecting long-term stand dynamics to modeling ecosystem change, particularly in forecasting forest carbon sequestration (Albani et al, 2006). Response to disturbance has already been identified as a significant factor influencing carbon sequestration, but including the long-term processes of forests would help better describe the likely future sequestration.

The location of this study makes it ideal for investigating the connection between stand dynamics and carbon modeling. The Harvard Forest EMS eddy flux tower has been tracking CO₂ sequestration since the 1992, and has measured an increasing rate of sequestration over that period (Urbanski et al, 2007). The increasing rate of sequestration has been attributed primarily to the increase in red oak growth rates (Urbanski et al, 2007). Following the current trajectory, sequestration may continue to increase. The long term volatility of red oak growth rates illustrated in this study adds perspective to this increase. This study additionally shows historical growth responses to disturbance events. This information can inform forecasts on the responses of this system to future disturbances. Finally, the implication from this study that the relationship between red oak and red maple seems to be relatively stable informs carbon models on the likely future vegetative composition of the forest. Thus pairing historical studies of long-term forest dynamics with real time data on carbon sequestration can help to better inform carbon models.

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