

The Pennsylvania State University
The Graduate School
Department of Ecosystem Science and Management

MID-ROTATION PATTERNS OF CHANGE IN DEVELOPING MIXED-OAK STANDS

A Thesis in
Forest Resources
by
Benjamin Silas Stein

© 2013 Benjamin Silas Stein

Submitted in Partial Fulfillment
of the Requirements
for the Degree of

Master of Science

May 2013

The thesis of Ben Stein was reviewed and approved* by the following:

Kim C. Steiner
Professor of Forest Biology
Thesis Advisor

James C. Finley
Professor of Forest Resources

Laura Leites
Research Associate of Forest Biometrics

Margot Kaye
Assistant Professor of Forest Ecology

Michael G. Messina
Director of the Department of Ecosystem Science and Management

*Signatures are on file in the Graduate School

ABSTRACT

Oak species (*Quercus* spp.) are becoming less prevalent in the Eastern forest landscape that they formerly dominated. One apparent reason for the decline in oaks is the increase in competition from more mesophytic species such as red maple (*Acer rubrum* L.). Characteristics of red maple's growth and development give it an advantage over oak species following harvest resulting in a transition from an oak-dominated composition to a mixed or red maple-dominated composition. However, there is uncertainty about whether red maple can sustain an initial advantage in density and abundance through the entire stand rotation.

In this study, we examine the composition of 46 formerly oak-dominated stands in central Pennsylvania, across three main physiographic regions. Prior to harvest, the stands had an average of 80% of their basal area in oak species, and oak made up over 45% of the basal area in every stand. We used data from these stands measured an average of 24.7 years (range 21-33) following clearcut harvest and, again, an average of 37.8 years (range 35-43) after harvest to study the changes in composition and structure. Of particular interest was the interaction occurring between the major oak species and their primary competitor, red maple.

Between the two measurements, oak's relative basal area increased by 6.8, 4.6 and 0.5 % in the Blue Ridge, Ridge and Valley and Appalachian Plateau regions, respectively. Red maple, on the other hand, decreased 5.2, 0.3, and 12.7 %, respectively. The relative density of the oak group increased 20.8, 9.3, and 1.6%, respectively, while red maple relative density decreased 2.1% in the Blue Ridge and increased 4.2 and 6.8% in the Ridge and Valley and Appalachian Plateau, respectively. The oak species averaged an 11.4, 5.6, and 2.0% increase in proportion of upper canopy occupied by its stems. Conversely, red maple experienced a 9.4, 2.4, and 18.9% decrease in the proportion of upper canopy occupied by its stems. Despite red maple's tendency to dominate stands following harvest there is evidence to support a shift in the growth of oak

species and a decline in red maple that occurs decades after harvest. The change in composition and structure of the stands is a movement towards pre-harvest conditions which were predominantly oak. The cause of these changes appears to be differences in inherent growth characteristics; however, it is unlikely that many of these stands will regain the dominance expressed prior to harvest.

TABLE OF CONTENTS

| | |
|--|-----|
| LIST OF FIGURES | vi |
| LIST OF TABLES..... | vii |
| ACKNOWLEDGEMENTS | ix |
| Mid-rotation patterns of change in developing mixed oak stands | 1 |
| Introduction..... | 1 |
| Methods..... | 9 |
| Location..... | 9 |
| Data Collection..... | 12 |
| Results..... | 17 |
| Changes from Pre- to Post-Harvest (Fourth Decade) Stand Conditions | 17 |
| Changes from Third to Fourth Decade Stand Conditions | 21 |
| Discussion | 30 |
| Conclusions | 40 |
| References..... | 44 |
| Appendix | 48 |

LIST OF FIGURES

| | |
|--|----|
| Figure 1: Physiographic provinces and the locations of stands used in this study..... | 9 |
| Figure 2: Comparison of 3 rd and 4 th decade oak relative basal area..... | 24 |
| Figure 3: Comparison of 3 rd and 4 th decade red maple relative basal area..... | 25 |
| Figure 4: Comparison of 3 rd and 4 th decade oak stocking..... | 26 |
| Figure 5: Comparison of 3 rd and 4 th decade red maple stocking..... | 27 |
| Figure 6: Average percentage of stems in upper canopy (dominants and codominants) for various species and species groups in three physiographic provinces. Values were calculated by averaging individual stand percentages, and the bars were scaled to 100% to facilitate comparisons between stand ages and provinces | 32 |
| Figure 7: Basal area by measurement period and province | 53 |

LIST OF TABLES

| | |
|--|----|
| Table 1: Basal area for each species group by physiographic province and measurement period. Different letters within columns indicate significant differences at the .05 confidence level. | 18 |
| Table 2: Percentage of total basal area accounted for by each species group by physiographic province and measurement period. Different letters within columns indicate significant differences at the .05 confidence level. | 19 |
| Table 3: Stocking percentages for each species group by physiographic province and measurement period. Different letters within columns indicate significant differences at the .05 confidence level..... | 21 |
| Table 4: Stocking percentages for each species group by physiographic province and measurement period. Different letters within columns indicate significant differences at the .05 confidence level..... | 23 |
| Table 5: Net change in relative basal area between 3 rd and 4 th decades by physiographic province and species group. Different letters within rows indicate significant differences at the .05 confidence level. Asterisk indicates significant change from 3 rd to 4 th decade. | 24 |
| Table 6: Change in stocking between 3 rd and 4 th decades by physiographic province and species group. Different letters within rows indicate significant differences at the .05 confidence level. Asterisk indicates significant change from 3 rd to 4 th decade..... | 26 |
| Table 7: Quadratic mean diameter by physiographic province and decade of measurement. Different letters within columns indicate significant differences at the .05 confidence level | 26 |
| Table 8: Change in quadratic mean diameter between 3 rd and 4 th decades by physiographic province and species group. Different letters within rows indicate significant differences at the .05 confidence level. Asterisk indicates significant change from 3 rd to 4 th decade | 29 |
| Table 9: Percent of stems in the upper canopy (dominant/co-dominant) represented by each species by physiographic province and decade of measurement. Different letters within columns indicate significant differences at the .05 confidence level | 30 |
| Table 10: Absolute change in percentage of stems in the upper canopy occupied by each species group within physiographic province. Different letters within rows indicate significant differences at the .05 confidence level. Asterisk indicates significant change from 3 rd to 4 th decade... .. | 31 |

| | |
|--|----|
| Table 11 : Percent change in trees per acre relative to 3 rd decade, by province and species. Different letters within rows indicate significant differences at the .05 confidence level..... | 33 |
| Table 12 : Average changes between 3 rd and 4 th decade in basal area by physiographic province and canopy strata; upper (dominant and codominant) and lower (intermediate and suppressed). The designation a,b is for differences between upper and lower canopy class within a species. The designation x,y is for differences between oak and red maple within a canopy class..... | 39 |
| Table 13 : Average number of trees per acre for each species by physiographic province and decade of measurement. Different letters within columns indicate significant differences at the .05 confidence level..... | 54 |
| Table 14 : Analysis of variance output for 3 rd to 4 th decade comparisons of basal area | 55 |
| Table 15 : Analysis of variance output for pre harvest to 4 th decade comparisons of basal area..... | 56 |
| Table 16 : Analysis of variance output for 3 rd to 4 th decade comparisons of relative basal area..... | 57 |
| Table 17 : Analysis of variance output for pre harvest to 4 th decade comparisons of relative basal area..... | 58 |
| Table 18 : Analysis of variance output for 3 rd to 4 th decade comparisons of stocking | 59 |
| Table 19 : Analysis of variance output for pre harvest to 4 th decade comparisons of stocking..... | 60 |
| Table 20 : Analysis of variance output for 3 rd to 4 th decade comparisons of quadratic mean diameter..... | 61 |
| Table 21 : Analysis of variance output for 3 rd to 4 th decade comparisons of canopy classifications | 62 |

ACKNOWLEDGEMENTS

First and foremost I would like to thank my family and friends for their support. Without their assistance and reassurance, I would not have made it. From my family I received no shortage of encouragement and support; emotional and sometimes financial. My fellow graduate students and friends were always nearby when it was time to celebrate or commiserate.

A great deal of gratitude goes to my adviser for providing me with this opportunity and guiding me through the process. I have gained so much knowledge and experience in forestry and elsewhere, and for this I will always be thankful to Dr. Steiner. I would also like to thank my committee members and others who have provided me with technical help while working on my thesis; Dr. Finley, Dr. Leites, Dr. Kaye, and Dr. Zenner.

Lastly, I would thank the Pennsylvania Department of Conservation and Natural Resources, Bureau of Forestry for their support and labor in gathering data used for this project.

Mid-rotation patterns of change in developing mixed oak stands

Introduction

The importance of oaks (*Quercus* spp.) to the ecosystems they inhabit, and to the human economy cannot be overstated. Over thousands of years, humans have developed numerous uses for oak such as for heating with charcoal and firewood, transportation in shipbuilding and railroad ties, and in homes as furniture and flooring (Thirgood 1971, Hardin et al. 1996). In nature, oaks serve as a source of both food and shelter for countless species of mammals, birds, insects, and fungi (Johnson et al. 2007). Any reduction in the abundance of oak will inevitably lead to a reduction in the uses and services it provides. The literature on oak has documented and acknowledged the decrease in oak's former dominance in our Eastern forest landscape (Fei et al 2011, Abrams 2003, Lorimer 1993, Lorimer 1984). There is most likely not one reason for the decrease in oak dominance, but a combination of several causes; including but not limited to, fire suppression (Abrams 1992), red maple development (*Acer rubrum* L.) in the understory (Lorimer 1984), deer browsing (George et al. 1999), and climate changes (Lorimer 1993). The purpose of this paper is to describe the development of formerly oak dominated stands as they regenerate in the presence of abundant red maple competition.

Fei et al. (2011) determined that oaks have been declining in abundance in areas where they once were prevalent, and all but two oaks have experienced a decrease in

density as well. Although oak volume has increased in all ecoregions of the eastern United States, other species have increased to a greater degree resulting in a decrease in the importance value $((\text{relative density} + \text{relative volume})/2)$ of oak volume. Since at least 1980, oak in the central hardwood region, which contains our study area, has experienced widespread decreases in importance value, density, relative density and volume. Furthermore, Abrams (2003) has done comprehensive research on the broad ranging white oak (*Quercus alba* L.) and found that it experienced little recruitment in the past century and white oak forests have been in decline from European pre-settlement to present day.

Fei and Steiner (2007), using US Forest Service Forest Inventory and Assessment (FIA) data concluded that with few exceptions, red maple is increasing in abundance in states where it naturally occurs and this increase is strongest in the sapling size class. If the understory density remains high as these stands continue to develop, these trees could reach a dominant overstory position and possibly replace oaks (Lorimer 1984). Across central Pennsylvania, the abundance of red maple in pre-harvest stands results in a clear regeneration advantage over oak seedlings and sprout origin seedlings through age seven in recently harvested oak stands (Fei and Steiner 2009). In their study, Fei and Steiner (2009) found the advantage was maintained for three decades following harvests. The cause of this advantage is not only derived from plentiful, small seedlings but also red maple's ability to sprout from dormant buds. Abundant, suppressed overstory and mid-story red maples that are present prior to harvest make large contributions to sprout origin regeneration following harvest. By age seven, sprout origin regeneration alone can recapture the canopy space occupied by red maple prior to harvest.

By the 3rd decade after harvest, many stands in the data set used for this study had transitioned to red maple stands and is thought to have occurred due to abundant red maple advance regeneration (Gould 2005). Oak stands that converted to red maple after harvest had significantly more overstory red maple and advance red maple regeneration stocking prior to harvest compared to stands that reverted to oak. Higher overstory stocking likely contributed both large amounts of seed prior to harvest and prolific stump sprouts following harvest, presenting competition to oak. If increasingly more red maple reaches the overstory with each subsequent rotation, further increasing competition through seedlings and sprouts, then oak could be easily phased out on these sites. This feedback loop is discussed by Nowacki and Abrams (2008). They described how shade-tolerant, mesophytic species promote a cool, moist environment, which lacks dry fuels preferred by fire-adapted species like oak. The red maple understory and subsequent overstory is a significant impediment to the establishment and initial growth of young oak trees.

Red maple as a competitor is threatening to other species due to its broad distribution and ecophysiological characteristics. It exhibits characteristics of both early and late successional species and its physiological traits (e.g., strong stomatal control, low foliar nutrient requirements, and shade tolerance) allow it to survive across a broad range of conditions (Abrams 1998). Additional traits of red maple, such as high rates of seed production, and high shade tolerance, also appear to contribute to red maple's competitive status vis-à-vis oak.

Lorimer (1984) documented dense understory red maple development in Northeast region upland oak stands. It therefore follows that, where oak regeneration is

poor, there is evidence to support transition toward red maple dominance, particularly on moist sites. Similarly, Hix and Lorimer (1991) found that on good to average sites in southwestern Wisconsin, northern red and white oaks are predicted to be replaced by sugar maple (*Acer saccharum* Marsh.) as the dominant species. It is important to note that in both studies authors acknowledge the paucity of competitive, advance oak regeneration probably contributed to maple's regeneration advantage.

When it occurs, the initial dominance of red maple may be short lived. Red maple has a short to medium lifespan and generally does not exceed 150 years of age (Walters and Yawny, *Silvics of NA*). This species grows rapidly early, but growth slows when the trees reach pole size. Oak, as a genus, are generally a longer-lived with white oak (*Quercus alba* L.), northern red oak (*Quercus rubra* L.) and chestnut oak (*Quercus prinus* L.) living up to 450, 300 and 450 years of age, respectively. Oaks are characterized as not being particularly fast-growing nor highly competitive in the early life stages, but capable of establishing a deep root system (Hardin et al. 1996). However, following heavy partial cutting established oaks have shown the ability to compete with sugar maples even though they were smaller and younger at the time of harvest (Lorimer 1983). These contrasting juvenile growth traits help to explain early dominance by red maples following harvest, but they may favor oak in the long term.

On a study site in New England, following the 3rd decade of growth, northern red oak occupied the upper crown classes with red maple and black birch (*Betula lenta* L.) in subordinate crown classes. Prior to the 3rd decade, northern red oak had been equal or smaller in size compared to other species even though all species were of the same cohort (Oliver 1978). Another study in two southern red oak (*Quercus falcata*

Michx.) / sweetgum (*Liquidambar styraciflua* L.) stands found southern red oak was sparse and slow growing during the first several decades following clearcutting; based on development seen in the data it, the researchers predicted that by age 30-35 years, southern red oak height would exceed sweetgum (Johnson and Krinard 1988). These two studies described similar growth patterns for red oaks; significant diameter increases for subordinate oaks followed by increases in height, ultimately leading to oak domination. In West Virginia, dendroecological analysis was performed in second growth stands and determined they likely regenerated with seedlings of mixed composition (e.g. northern red oak, sugar maple, black cherry, hickory, white ash). The resulting mature stand was dominated by northern red oak (Schuler and Fajvan 1999). Together these studies suggest that regenerating mixed species composition stands dominated by non-oak species, seem to experience species shifts midway through of a stand's rotation, provided advance oak regeneration present.

Hibbs (1983) studied 40 years of forest succession after a clearcut in New England and found that by year 40 oak constituted a mere 7.5% of the stems but these accounted for 37.5% of all dominant stems and 15.5% of the basal area (BA). Meanwhile, red maple constituted 30.5% of the stems but only 16.7% of the dominant stems and 9.6% of the basal area. This demonstrates oaks capacity to achieve structural dominance despite lacking numerical dominance.

Arthur (1997) described stand development following overstory harvest of a central Kentucky stand dominated by oak, hickory (*Carya spp.*) and tulip-poplar (*Liriodendron tulipifera* L.). From ages 5 to 11 the importance of red maple decreased and the importance of oak and tulip-poplar increased. These shifts marked a movement

towards pre-harvest conditions and appeared to relate to different life history traits and competitiveness methods of oak.

Typically, studies of contemporary second-growth forests show oak invariably achieves dominance (Oliver 1978, Schuler and Fajvan 1999, Tift and Fajvan 1999). However, many of the stands in these supporting studies, as well as the stands harvested to initiate the current study, likely originated under management regimes that are different than at present, specifically in regards to wild land fire management. Many of Pennsylvania's forests were heavily logged and repeatedly burned in the mid-1800s to early 1900s (Powell and Considine 1982). Logging and frequent fire could have favored the oak-dominated stands that were harvested to initiate the present study. Frequent fire is useful in removing thin-barked understory species while favoring oak (Brose et al. 2001, Abrams 1992), but many factors (e.g., size, resprouting capacity, and light requirements of potential resprouters) must be considered before using fire as a tool to promote seedling development and recruitment into the canopy (Arthur et al. 2012). Frequent, low-intensity fires alone may not create the canopy disturbance necessary to produce the light intensity required by oak to recruit into the canopy. In the absence of fire, shade-tolerant species accumulate in oak forest understories. After overstory removal, understory trees are released and succession to a more shade-tolerant species composition is accelerated (Abrams and Downs 1990). Due to the difference in practices and policies involved in harvesting around the turn of the 20th century from today's harvesting practices, the future dominance of oak in younger stands may be less certain. Furthermore, subsequent rotations may experience increasingly less dominance by oak as

more shade tolerant species achieve permanent positions in the overstory and contribute to the development of shade tolerant understories.

Useful research on competitive development of species within oak stands has been done using retrospective stem analysis to draw conclusions about the growth of individual trees in competition with specific neighbors (Oliver 1978, Schuler and Fajvan 1999, Zenner et al. in-press), but such studies have a critical limitation; they cannot account for trees lost to mortality. A more powerful approach would be to use permanent plots to monitor stand development for many decades, but opportunities for such studies are exceedingly rare. In the present study, non-fixed study plots were sampled at each measurement period and the data are necessarily aggregated to a stand-level basis. Therefore, we are limited in describing individual tree-to-tree competitive interactions. However, the data set provides an opportunity to study changes in stand-level composition and structure at mid-rotation in formerly oak-dominated stands.

Although several studies have indicated a mid-rotation shift in favor of oak dominance, very little has been done on this topic specific to Pennsylvania's oak forests. The scope of this thesis is to detect and characterize mid-rotation shifts in favor of oak that may occur in stands across central Pennsylvania. Most of the previous studies on regenerating oak stands either monitor development of a young stand as it regenerates, or perform retrospective analysis on a terminal stand. Our study is unique as it examines stands at an intermediate point in stand development and uses fixed locations to more accurately track gains and losses. Furthermore, our study observes many stands across a diverse landscape which gives us greater inference about oaks innate ability to latently achieve dominance, as opposed to looking at once instance of an oak dominated stand.

By re-visiting stands previously inventoried, we were able to observe stand-level changes in composition and structure. These changes formed patterns, which provide a deeper understanding of oak and red maple development and interaction during this period of stand development. We also sought to determine stand development trajectory of these two groups. We expected to see patterns indicating increased oak dominance in each of the three physiographic provinces, and that this increase would occur at the expense of red maple.

Methods

Location

This study was conducted in naturally occurring stands in central Pennsylvania spanning three physiographic provinces, the Appalachian Plateau, the Ridge and Valley, and the Blue Ridge (Figure 1).

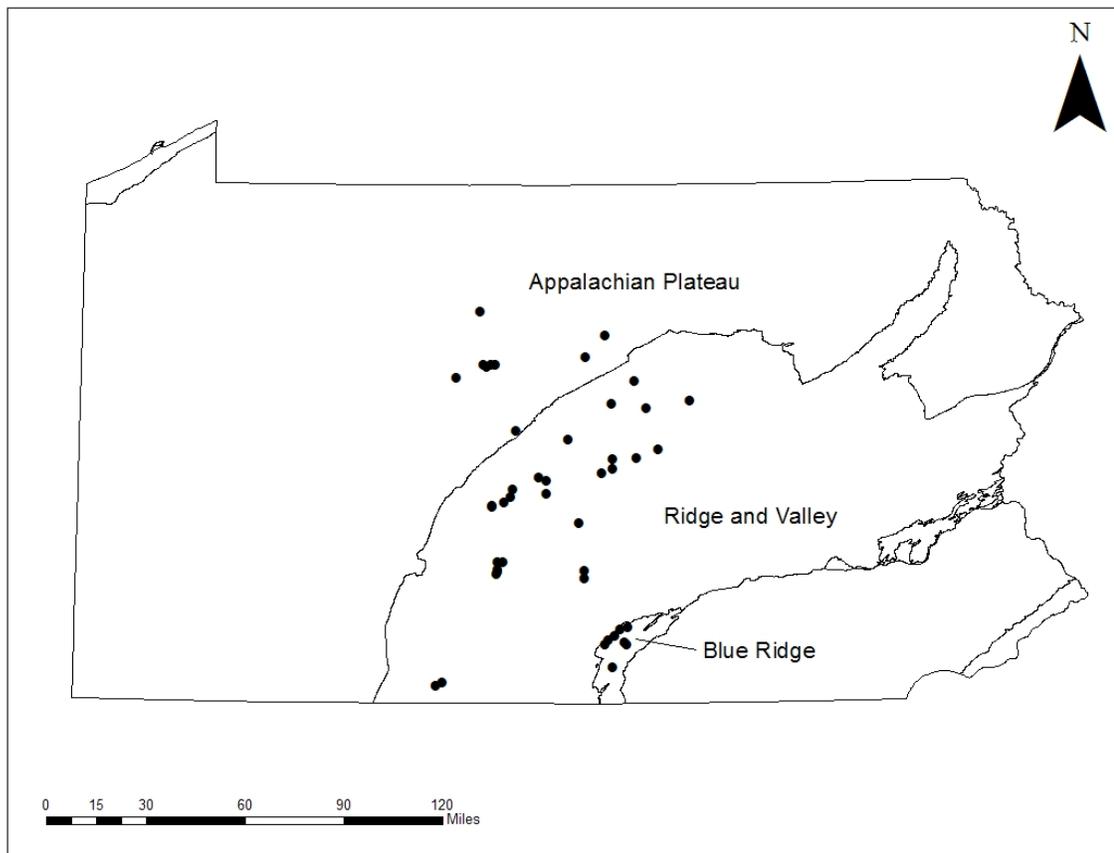


Figure 1: Physiographic provinces and the locations of stands used in this study

Nine of the study stands are on the Appalachian Plateau. This region covers most of the western portion of the state and extends over the north through to the northeast

corner. The Appalachian Plateau region originates primarily from fluvial and glacial erosion and consists of broad flat uplands with deep angular valleys. The well developed, highly weathered soils are generally rich and mesic, and tend to be naturally dominated by the “Alleghany hardwoods” (i.e., black cherry, tulip-poplar, red and sugar maples, and other mesic species), but oak is common as well and has been historically dominant in some stands. During the late 1960s portions of this province were subject to an oak leaf roller outbreak. Using Geographic Information System data acquired from the Pennsylvania Department of Conservation and Natural Resources (DCNR) Bureau of Forestry, it was determined that all of our stands in the Appalachian Plateau province occurred in areas of moderate to severe defoliation, some for multiple years.

The Ridge and Valley province curves across the central and southeastern portions of the state in a northeast/southwest direction. Twenty-nine of the study stands are located in this province. The unique topography of this region consists of linear sandstone ridges and parallel limestone and shale valleys. This region originates primarily from fluvial erosion and the majority of the soils are not advanced in terms of weathering and development. The soils are much drier in the Ridge and Valley making it more suitable for species that are adapted to slightly xeric conditions, such as many of the oaks.

The Blue Ridge province, whose northern tip extends into south central Pennsylvania, contains eight study stands. The relatively small portion of this province in Pennsylvania is sometimes included in the Ridge and Valley, which it resembles in many characteristics including species composition. The parallel ridges and deep valleys of this region originate from fluvial erosion of variable rocks. The underlying rock type

consists of metavolcanic rocks, quartzite and dolomite. While the topography is similar to the Ridge and Valley, the soils are strongly to highly weathered and akin to those of the Appalachian Plateau (Cuff et al. 1989, DCNR website).

Across central Pennsylvania and the mid-Atlantic region, oak has been historically dominant over the many parts of the landscape (Abrams and Downs 1990, Abrams and Nowacki 1992, Ruffner and Abrams 1998). This dominance dates back to pre-European settlement and is linked to times of frequent fire, most likely initiated by lightning and Native American practices (Abrams 1992). Prior to settlement, chestnut oak was common component of the coves and sandstone ridges of central Pennsylvania (Abrams 2003). White oak was well represented in the limestone valleys and well drained hill slopes of the region but had a poor association with the calcareous till of northwestern Pennsylvania. Following European settlement, oak's continued dominance in the region is associated with land clearing and fire occurrence related to charcoal production for iron furnaces. Contemporary loss of oak dominance in this region may be related to a reduction in fire because there is an apparent historical association between the two.

Data Collection

This study took place on state forest land managed by the Pennsylvania DCNR Bureau of Forestry. The majority of the data was gathered by Bureau of Forestry personnel for operational purposes, and stands that met our criteria were selected from this large collection of operational data. The 46 stands used in this study are a subset of 90 regenerating stands used in previous research and publications by Gould and others (2005, 2006). These 46 stands were selected using two criteria: (1) they had to have reached B-level (58%) stocking (Gingrich 1967) by the time of the 3rd decade measurement, and (2) they had to have some overstory component of oak by that time. While all 90 stands contained red maple by the 3rd decade, not all of them contained a significant oak component at that point and some had effectively failed to regenerate.

Prior to harvesting between 1968 and 1972, these 46 stands were largely dominated by one or more of five principal species of oak common to central Pennsylvania, with oaks accounting for an average of 80% of total basal in all stands and at least 45% in every stand. Red maple accounted for about half (9%) of the remaining balance of the basal, on average. The main oak species encountered in this data collection were northern red oak, white oak, chestnut oak, black oak (*Quercus velutina* Lam.) and scarlet oak (*Quercus coccinea* Muenchh.). The stands prescribed harvests were clearcuts where all stems greater than 2 inches in diameter at breast height were removed, with the exception that softwood-species were left as a residual conifer component. The conifer component was most often eastern white pine (*Pinus strobus* L.)

or eastern hemlock (*Tsuga canadensis* L.) but occasionally pitch pine (*Pinus rigida* Mill.) or Table Mountain pine (*Pinus pungens* Lamb.).

We have complete records of pre-harvest overstory, pre-harvest regeneration composition, and post-harvest regeneration composition. Regeneration composition was assessed using the Bureau of Forestry FMT-24 protocol, a commonly used regeneration assessment during that time period. This protocol consisted of establishing 60 1/1000th acre plots evenly across the stand and recording up to three seedling stems with the highest vigor on each plot. Vigorous stems were free of defects and likely competitive for dominant growing space. The maximum regeneration stocking level was 300% because a plot with 1 stem was considered to be 100% stocked.

Stand overstory examinations were made in the 3rd and 4th decades after harvest using the FMT-20 protocol. For our purposes, the 3rd decade refers to measurements taken between 1995 and 2001, when the stands averaged 24.7 years of age (range 21-33 years). All 4th decade measurements were made in 2011, when the stands averaged 37.8 years of age (range 35-43 years).

For all overstory measurements, a point sampling design was used in which the number of points was determined by the size of the sample area. If the stand was less than 21 acres, then one point per acre was taken. Similarly, 25 points were taken for stands of 21-50 acres, 30 points for 51-75 acres, and 35 points for 76-125 acres. Another plot was added to the sample for each additional ten acres over 125 acres. Five to six parallel cruise lines were laid out with sample points equidistant along the lines. Cruise lines were laid perpendicular to contour lines to capture as much variability as possible. At each point, tally trees were determined using a 10 BAF prism with variable radius plot

sampling, where the probability of selection is a function of size and distance from plot center. The inclusion area of a 10 BAF prism is calculated as 2.75 multiplied by the tree diameter in inches which yields the radius of the inclusion zone in feet (Avery and Burkhart 2002). All “in” trees greater than one inch DBH were recorded by one inch classes and the species was recorded.

Because each tallied tree represents 10ft²/acre of basal area, the number of tallied trees was multiplied by 10 and divided by the number of plots to obtain an average basal area for the entire stand and for individual species. Relative basal area (RBA) was calculated as the proportion of a stand’s total basal area by each species, and changes in a species’ relative basal area between the 3rd and 4th decade measurements were examined by calculating the difference in RBA between measurement periods.

To estimate the number of trees per acre represented by each sample tree, we calculated the “inclusion area” for that tree (the product of π and the square of the tree’s inclusion radius) and divided that value into the area of an acre. This was done for all trees in a stand, summed and divided by the number of plots to obtain the estimated number of trees per acre for a stand. Quadratic mean diameter (QMD), the diameter of a tree of average basal area, was calculated on the stand and the species level using the respective estimates of basal area and trees per acre.

Stocking, or relative density, is a composite metric that describes the “adequacy” of stand density with respect to the total available growing space within a stand. Stocking is a measure of crowding in a stand and stocking values for individual species indicate how much space is occupied by a species relative to the potential maximum. The maximums are based on a range of observed values from a given forest type. A

tree's maximum growing space is the area used when grown free of competition. If the total space in a stand is less than the sum of the maximum growing space for all trees, then a stand is said to be competing and is overstocked. This stocking was calculated by using the tree area (in milacres) equation:

$$\text{Stocking} = -.0507N + .1698\sum D + .0317\sum D^2,$$

where N is the number of trees and D is the individual tree diameter (Gingrich 1967).

This calculation extrapolates to a per acre level using fixed area sampling, but it is more difficult when using variable radius plots. To calculate stocking with the variable radius plot data, we calculated the estimated contribution to stand stocking of all trees represented by a sampled tree. For our purposes, N was equal to the average number of trees per acre that each sampled tree represented across the entire stand. The sum of the diameters, $\sum D$, was calculated as the average number of trees a sampled tree represents multiplied by the diameter of that sampled tree. The stocking equation produces stocking in milacres therefore the final value must then be divided by 1000 to scale up to stocking percentage on a per acre basis. All of these individual stocking values were then summed to attain a stand level stocking estimate.

Each sampled tree crown was classified based on its height and canopy dimensions relative to neighboring trees. Crown classes were designated as follows: dominant (crown extending well above crowns of surrounding trees), co-dominant (crown that is a component of the general layer of the canopy), intermediate (crown

within the canopy receiving little light from above), and suppressed (crown entirely below the surrounding canopy and receiving no direct light) (Avery and Burkhart 2002).

To examine changes in canopy class between measurement periods, we used a summative variable: the number of dominant and co-dominant trees of a given species as a proportion of the total number of dominant and co-dominant trees for all species. This was calculated for oaks and red maple separately and compared between 3rd and 4th decade measurements

Differences in mean levels of measurements were determined using Tukey-Kramer multiple comparison test for unbalanced designs. Significance of changes between the 3rd and 4th decade measurement were determined using a paired t-test in R statistical computing software. Analysis of variance was also performed to detect significant differences between pre-harvest and 4th decade measurements, and between 3rd decade and 4th decade measurements. ANOVAs were performed using the GLM procedure in SAS Version 9.3.

Results

Changes from Pre- to Post-Harvest (Fourth Decade) Stand Conditions

Prior to harvest between 1968 and 1972, the regenerating stands contained an average basal area of 95.7 ft²/acre (range 70-127) (Table 1) and an average stocking of 77.8% (range 24-111) (Table 3). After four decades of growth (mean=37.8 years), the stands had reached 117.3 ft²/acre basal area (range 71-144) with an average stocking of 127.5% (range 71-144).

Pre-harvest basal area was similar for the Blue Ridge and Ridge and Valley but much higher in the Appalachian Plateau. After four decades of regrowth, BA in each of the three provinces was similar. Before harvest, total stand BA averaged 91.2 for the Blue Ridge, 92.2 for the Ridge and Valley, and 110.4 ft²/acre for the Appalachian Plateau (Table 1). By the 4th decade, total basal area averaged 120.6, 119.2, and 108.2 ft²/acre, respectively.

Table 1. Basal area for each species group by physiographic province and measurement period. Different letters within columns indicate significant differences at the 5% confidence level.

| Physiographic Province | Basal area (ft ² /acre) | | | | | Total |
|--|------------------------------------|-------------|-------------|--------------|-------------|--------------|
| | Oak | Red maple | Black birch | Black cherry | Others | |
| --Stands prior to harvest-- | | | | | | |
| Blue Ridge (n=8) | 78.5a | 4.1b | n/a | n/a | 8.5a | 91.2b |
| Ridge and Valley (n=28) | 73.2a | 6.6b | n/a | n/a | 12.4a | 92.2b |
| Appalachian Plateau (n=9) | 85.7a | 17.7a | n/a | n/a | 7.0a | 110.4a |
| Mean (n=45) | 76.6 | 8.4 | n/a | n/a | 10.6 | 95.7 |
| --Stands in 3 rd decade of regeneration-- | | | | | | |
| Blue Ridge (n=8) | 40.1a | 23.0b | 4.1a | 3.0a | 14.5ab | 84.7ab |
| Ridge and Valley (n=29) | 30.2a | 27.1b | 11.4a | 8.8a | 16.5a | 87.9a |
| Appalachian Plateau (n=9) | 5.1b | 45.1a | 3.2a | 8.7a | 5.7b | 67.8b |
| Mean (n=46) | 27.0 | 29.9 | 8.5 | 3.9 | 14.0 | 83.4 |
| --Stands in 4 th decade of regeneration-- | | | | | | |
| Blue Ridge (n=8) | 66.1a | 26.3b | 7.8a | 2.4b | 18.1a | 120.6a |
| Ridge and Valley (n=29) | 45.5b | 35.9b | 11.8a | 4.8b | 21.3a | 119.2a |
| Appalachian Plateau (n=9) | 7.5c | 60.6a | 9.6a | 16.4a | 14.2a | 108.2a |
| Mean (n=46) | 41.6 | 39.0 | 10.6 | 6.6 | 19.3 | 117.3 |

Average basal area levels in the 4th decade exceeded pre-harvest levels for the Blue Ridge and the Ridge and Valley, but the Appalachian Plateau simply recovered the pre-harvest basal area. Compositions in these 4th decade stands are significantly different from what existed prior to harvest (Appendix). On average, oak barely regained more than half of its pre-harvest basal area (41.6 vs. 76.6 ft²/acre), while red maple more than quadrupled its pre-harvest basal area by the 4th decade relative to pre-harvest BA (39.0 vs. 8.4 ft²/acre) and all other species in aggregate more than tripled (36.5 vs. 10.6 ft²/acre). Prior to harvest, the oak basal areas were similar in each province and after four decades of regeneration the basal areas of oak were quite different among provinces.

These changes are mirrored in changes of RBA. Oak regained less than half of its relative basal area from pre-harvest to 4th decade (35.3 vs. 80.5%), red maple recovered four times as much relative basal area (34.0 vs. 8.4%) and other species collectively almost tripled their RBA (30.6 vs. 11.1%)(Table 2). Again, the RBAs were similar among provinces before harvest, and four decades post-harvest the relative basal areas were very different among provinces.

Table 2. Percentage of total basal area accounted for by each species group by physiographic province and measurement period. Different letters within columns indicate significant differences at the 5% confidence level.

| Physiographic Province | Relative basal area (%) | | | | |
|--|-------------------------|-------------|-------------|--------------|-------------|
| | Oak | Red maple | Black birch | Black cherry | Others |
| --Stands prior to harvest-- | | | | | |
| Blue Ridge (n=8) | 86.5a | 4.5b | n/a | n/a | 9.0a |
| Ridge and Valley (n=28) | 79.7a | 7.1b | n/a | n/a | 13.2a |
| Appalachian Plateau (n=9) | 77.8a | 15.8a | n/a | n/a | 6.4a |
| Mean (n=45) | 80.5 | 8.4 | n/a | n/a | 11.1 |
| --Stands in 3 rd decade of regeneration-- | | | | | |
| Blue Ridge(n=8) | 48.7a | 27.0b | 5.0a | 3.5a | 15.8a |
| Ridge and Valley(n=29) | 34.1a | 30.4b | 14.2a | 2.9a | 18.4a |
| Appalachian Plateau (n=9) | 6.0b | 70.5a | 3.6a | 11.9a | 8.1a |
| Mean (n=46) | 31.1 | 37.6 | 10.5 | 4.8 | 15.9 |
| --Stands in 4 th decade of regeneration-- | | | | | |
| Blue Ridge (n=8) | 55.4a | 21.8b | 6.3a | 1.9ab | 14.5a |
| Ridge and Valley (n=29) | 38.7b | 30.0b | 9.8a | 4.1b | 17.4a |
| Appalachian Plateau (n=9) | 6.5c | 57.7a | 8.3a | 14.6a | 12.9a |
| Mean (n=46) | 35.3 | 34.0 | 8.9 | 5.7 | 16.0 |

Prior to harvest, average stocking levels were similar in the Blue Ridge and Ridge and Valley, but significantly lower in Appalachian Plateau stands (Table 3). By the 4th decade the average stocking was similar for all provinces. Pre-harvest average stocking

was 81.0 for the Blue Ridge, 83.3 for the Ridge and Valley, and 57.7% for the Appalachian Plateau. By the 4th decade the average stocking was 139.2, 125.5, and 123.5%, respectively.

Average stocking levels in the 4th decade far exceeded pre-harvest levels, particularly in the Appalachian Plateau where stocking more than doubled. The composition, as measured by stocking, changed significantly from the pre-harvest to the 4th decade measurement period (Appendix). While 4th decade oak stocking is only three-quarters of its pre-harvest level (57.1 vs. 43.1%), red maple's is more than 5 times greater than pre-harvest levels (8.2 vs. 45.9%) and black birch's stocking is 14 times greater than it was prior to harvest (0.8 vs. 11.9%). In each province, stocking levels were similar before harvest and became different after four decades following the regeneration harvest.

Table 3. Stocking percentages for each species group by physiographic province and measurement period. Different letters within columns indicate significant differences at the 5% confidence level.

| Physiographic Province | Stocking (%) | | | | | Total |
|--|--------------|-------------|-------------|--------------|-------------|--------------|
| | Oak | Red maple | Black birch | Black cherry | Others | |
| --Stands prior to harvest-- | | | | | | |
| Blue Ridge (n=8) | 68.7a | 4.2b | 0.2a | 0.0a | 7.9a | 81.0a |
| Ridge and Valley (n=28) | 64.0a | 7.4b | 1.1a | 0.1a | 10.7a | 83.3a |
| Appalachian Plateau (n=9) | 25.2b | 14.4a | 0.2a | 0.3a | 17.5a | 57.7b |
| Mean (n=45) | 57.1 | 8.2 | 0.8 | 0.1 | 11.5 | 77.8 |
| --Stands in 3 rd decade of regeneration-- | | | | | | |
| Blue Ridge (n=8) | 52.0a | 36.8b | 5.6a | 4.0a | 16.8ab | 115.2a |
| Ridge and Valley (n=29) | 36.7a | 36.2b | 16.3a | 3.1a | 19.7a | 112.0a |
| Appalachian Plateau (n=9) | 6.1b | 66.7a | 3.9a | 9.8a | 6.2b | 92.6b |
| Mean (n=46) | 33.3 | 42.3 | 12.0 | 4.5 | 16.6 | 108.8 |
| --Stands in 4 th decade of regeneration-- | | | | | | |
| Blue Ridge (n=8) | 72.7a | 34.8b | 8.8a | 3.0ab | 19.8a | 139.2a |
| Ridge and Valley (n=29) | 46.0b | 40.4b | 13.2a | 4.6b | 21.3a | 125.5a |
| Appalachian Plateau (n=9) | 7.7c | 73.5a | 10.4a | 17.8b | 14.1a | 123.5a |
| Mean (n=46) | 43.1 | 45.9 | 11.9 | 6.9 | 19.6 | 127.5 |

* Stocking percentages are calculated using only live stems which resulted in significantly lower pre-harvest levels in the Appalachian Plateau due to oak leaf roller mortality.

Changes from Third to Fourth Decade Stand Conditions

From the 3rd to 4th decade stand measurements, an average period of 13.1 years, basal area increased across the provinces by an average of 31.3 to 40.4 ft²/acre; however, there were no significant differences between provinces (Table 5). Stocking levels across provinces increased by an average of 13 to 31% (Table 6). Lastly, QMD increased by 1 to 2 inches and increases were similar in all three provinces (Table 8).

Between the 3rd and 4th decade and across all stands, basal area increases differed among species: For all stands average increases were 14.6 (SE=1.8) ft²/acre for oak, 9.1 (SE=1.7) for red maple, 2.1 (SE=1.2) for black birch, 2.7 (SE=1.2) for black cherry and 5.3 (SE=1.5) for the others (Table 4). Oak increases in basal area were much greater in the Blue Ridge (25.9 ft²/acre, SE=4.1, P<.001) and the Ridge and Valley (15.3 ft²/acre, SE=2.1, P<.001) compared to the Appalachian Plateau which showed no statistically detectable increase in basal area. By contrast, red maple basal area growth was greatest on the Appalachian Plateau (15.5 ft²/acre, SE=6.1, P=.034), intermediate in the Ridge and Valley (8.8 ft²/acre, SE=1.6, P<.001) and not statistically different from zero in the Blue Ridge province. Basal area increases for black birch, black cherry and other species were strongest on the Plateau but accounted for less than a third of the total growth. Oak grew more than the red maple in the Blue Ridge (P<.001) and the Ridge and Valley (P=.043). Red maple outgrew oak on the Appalachian Plateau but the difference was not statistically significant.

Table 4. Net changes in basal area between 3rd and 4th decades by physiographic province and species group. Different letters within rows indicate significant differences at the 5% confidence level. Asterisk indicates significant change within species from 3rd to 4th decade.

| Physiographic Province | Change in basal area (ft ² /acre) | | | | | Total |
|---------------------------|---|----------------|--------------|---------------|----------------|---------------|
| | Oak | Red maple | Black birch | Black cherry | Others | |
| | --Changes between 3 rd and 4 th decades-- | | | | | |
| Blue Ridge (n=8) | +25.9a* | +3.3b | +3.6b | -0.7b | +3.6b* | +35.8* |
| Ridge and Valley (n=29) | +15.3a* | +8.8ab* | +0.4c | +2.1c* | +4.8bc* | +31.3* |
| Appalachian Plateau (n=9) | +2.3a | +15.5a* | +6.4a | +7.7a | +8.5a | +40.4* |
| Mean (n=46) | +14.6a* | +9.1ab* | +2.1c | +2.7c* | +5.3bc* | +33.9* |

Considering all stands, changes in RBA were significantly different among species (Table 5). The proportion of total basal area increased by 4.2% (SE=1.1) for oak, decreased 3.6% (SE=1.6) for red maple, decreased 1.6% (SE=1.6) for black birch and increased 1% (SE=0.5) for black cherry (Table 6). Oak relative basal area significantly increased in the Blue Ridge (6.8%, SE=1.9, P=.011) and the Ridge and Valley province (4.6%, SE=1.6, P=.007). Changes for red maple were uniformly negative, suggesting a lower basal area growth relative to other species. A significant decrease for red maple occurred in the Blue Ridge province (-5.2%, SE=1.1, P=.002). Also, there was a large decrease in the Appalachian Plateau province (average 12.7% loss in RBA, SE=6.1), but the change was not statistically significant. Red maple experienced substantial increases in basal area on the Plateau between 3rd and 4th decades (Table 2), but its loss in relative position can be explained by large gains in BA for black birch, black cherry and other species. Black birch had marginal increases except in the Ridge and Valley where it experienced a significant decrease (-4.4%, SE=0.5, P=.023). Although oak gained

relative basal area compared to red maple in all provinces, the advantage was significant only in the Blue Ridge province ($P=.001$).

Table 5. Net change in relative basal area between 3rd and 4th decades by physiographic province and species group. Different letters within rows indicate significant differences at the 5% confidence level. Asterisk indicates significant change within a species from 3rd to 4th decade.

| Physiographic Province | Net change in relative basal area (%) | | | | |
|---|---------------------------------------|---------------|--------------|---------------|---------------|
| | Oak | Red maple | Black birch | Black cherry | Others |
| --Changes between 3 rd and 4 th decades-- | | | | | |
| Blue Ridge (n=8) | +6.8a* | -5.2c* | +1.3ab | -1.7bc | -1.2bc |
| Ridge and Valley (n=29) | +4.6a* | -0.3ab | -4.4b* | +1.2ab* | -1.0ab |
| Appalachian Plateau (n=9) | +0.5ab | -12.7b | +4.7a | +2.7a | +4.8a |
| Mean (n=46) | +4.2a* | -3.6b* | -1.6b | +1.0ab | +0.1ab |

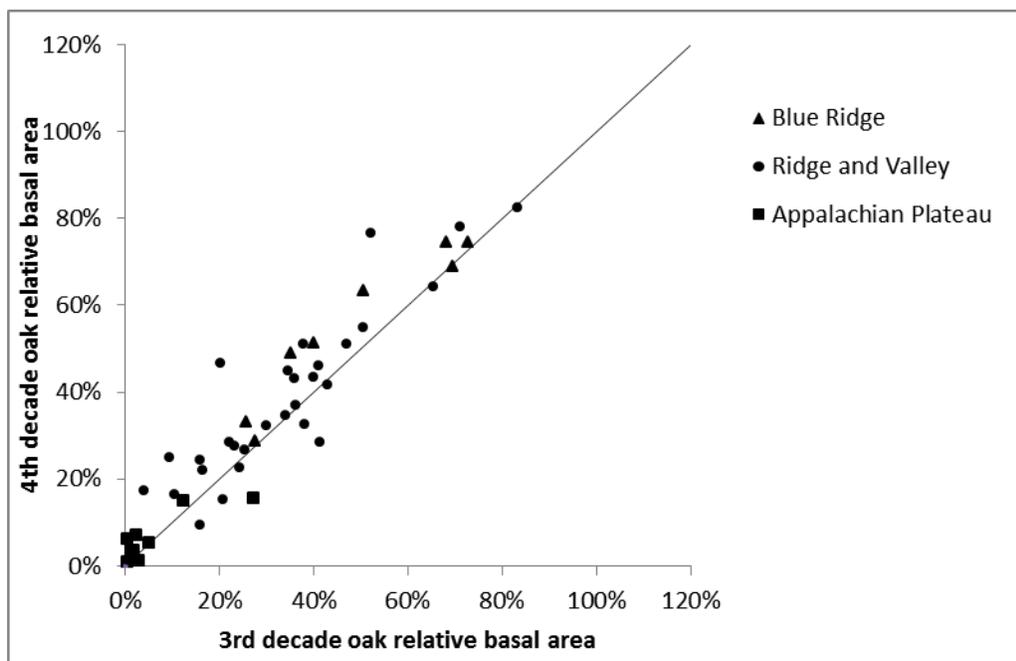


Figure 2. Comparison of 3rd and 4th decade oak relative basal area

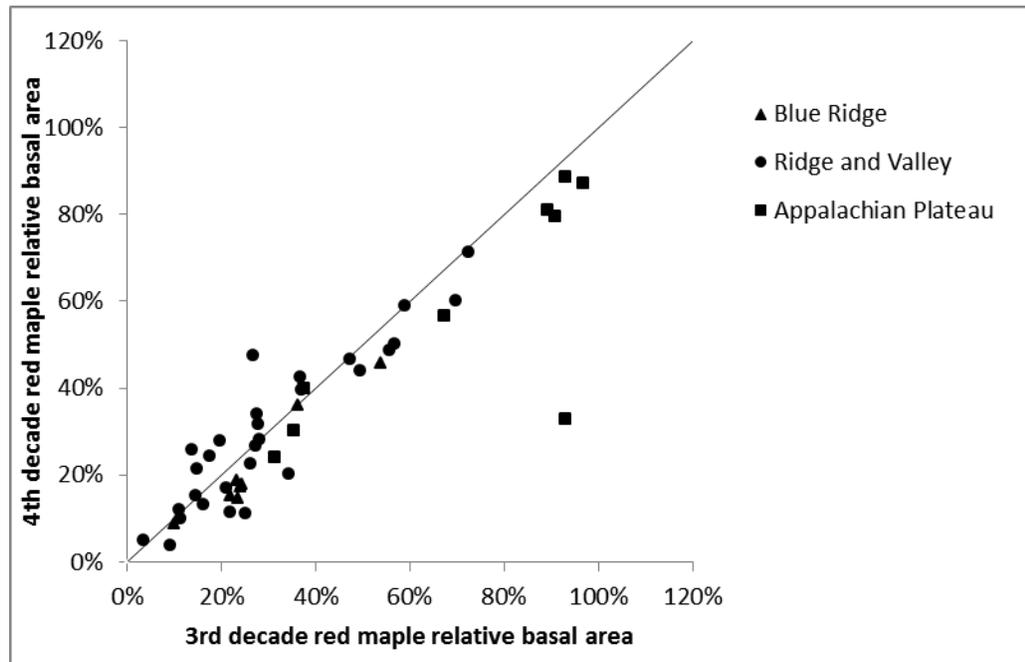


Figure 3. Comparison of 3rd and 4th decade red maple relative basal area

Total stocking changes between 3rd and 4th decades were not significantly different among provinces, but across all stands there were significant differences among species. Looking at all stands, stocking increased 9.8% (SE=1.9) for oak, 3.6% (SE=2.1) for red maple, 0% (SE=1.9) for black birch, 2.4% (SE=1.1) for black cherry, and 3.1% (SE=1.6) for others (Table 6). Oak stocking significantly increased by 20.8% in the Blue Ridge (SE=5.4, P=.006) and 9.3% in the Ridge and Valley (SE=2.3, P<.001). Red maple changes in stocking were not statistically different among provinces but increases were largest in Appalachian Plateau. The Ridge and Valley had intermediate increases in red maple stocking, and the Blue Ridge had decreases in red maple stocking (Figure 3). Significant changes occurred only in the Ridge and Valley province which had a 4.2% increase (SE=1.8, P=.025). A comparison of the 3rd and 4th decade stocking is shown for

oak and red maple in Figures 3 and 4, respectively. Changes in other species were typically small and not significant. For oak and red maple stocking growth, the only significant advantage occurred in the Blue Ridge province where the change in oak stocking was significantly greater than in red maple stocking ($P < .001$).

Table 6. Change in stocking between 3rd and 4th decades by physiographic province and species group. Different letters within rows indicate significant differences at the 5% confidence level. Asterisk indicates significant change within a species from 3rd to 4th decade.

| Physiographic Province | Change in stocking (%) | | | | | Total |
|---|------------------------|---------------|--------------|---------------|--------------|--------------|
| | Oak | Red maple | Black birch | Black cherry | Others | |
| --Changes between 3 rd and 4 th decades-- | | | | | | |
| Blue Ridge (n=8) | +20.8a* | -2.1b | +3.2b | -0.9b | +3.0b | +24.0* |
| Ridge and Valley (n=29) | +9.3a* | +4.2ab* | -3.1b | +1.6b* | +1.6b | +13.5* |
| Appalachian Plateau (n=9) | +1.6a | +6.8a | +6.5a | +8.0a | +7.9a | +30.9* |
| Mean (n=46) | +9.8a* | +3.6ab | -0.1b | +2.4b* | +3.1b | +18.7 |

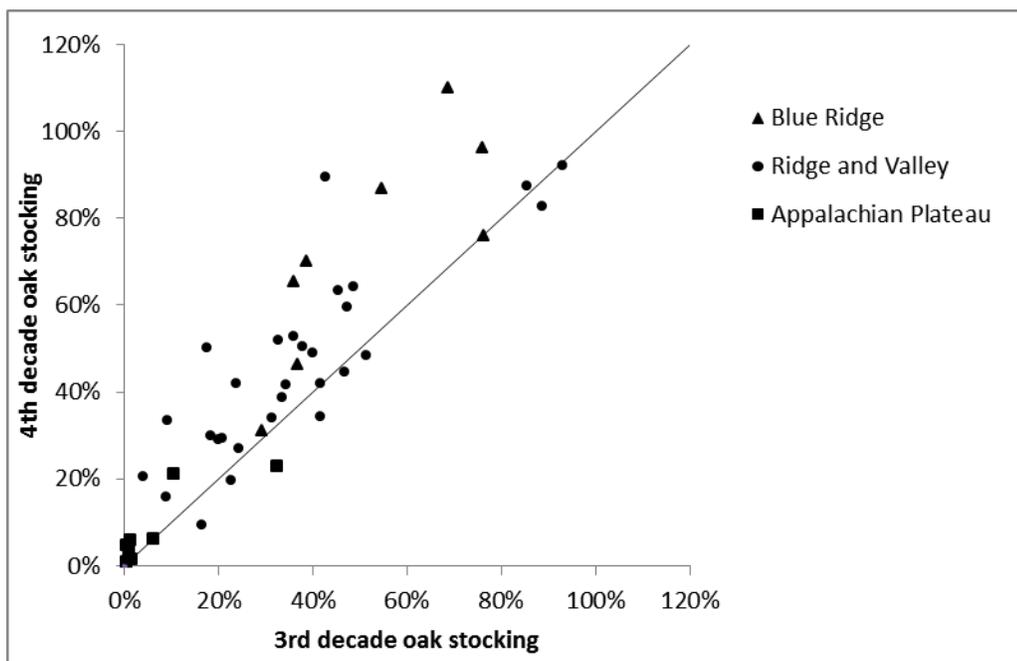


Figure 4. Comparison of 3rd and 4th decade oak stocking

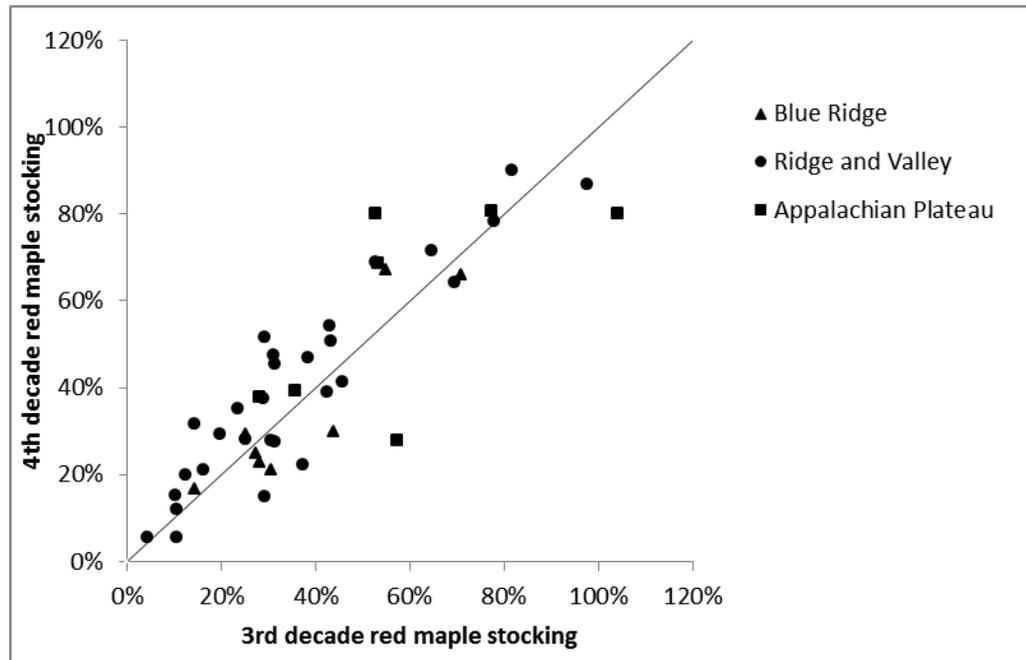


Figure 5. Comparison of 3rd and 4th decade red maple stocking

At the 3rd decade after harvest, the QMD was similar for all provinces, but by the time of the 4th decade measurements the average diameters for all species combined in the Ridge and Valley had become significantly larger than the other two provinces (Table 7). The average QMD by the 3rd decade was 2.9 inches for stands in the Blue Ridge, 3.6 inches for the Ridge and Valley, and 3.3 inches for the Appalachian Plateau. After four decades, the average QMD was 4.2, 5.6 and 4.6 inches, respectively.

Table 7. Quadratic mean diameter by physiographic province and decade of measurement.**Different letters within columns indicate significant differences at the 5% confidence level.**

| Physiographic Province | Quadratic mean diameter (inches) | | | | | Total |
|---------------------------|--|------------|-------------|--------------|------------|------------|
| | Oak | Red maple | Black birch | Black cherry | Others | |
| | --Stands in 3 rd decade of regeneration-- | | | | | |
| Blue Ridge (n=8) | 3.4b | 2.4b | 4.3a | 4.5a | 3.5a | 2.9a |
| Ridge and Valley (n=29) | 4.4ab | 3.4a | 3.7a | 5.7a | 4.2a | 3.6a |
| Appalachian Plateau (n=9) | 5.5a | 3.0ab | 3.3a | 6.0a | 4.7a | 3.3a |
| Mean (n=46) | 4.4 | 3.2 | 3.8 | 5.4 | 4.1 | 3.4 |
| | --Stands in 4 th decade of regeneration-- | | | | | |
| Blue Ridge (n=8) | 5.4b | 3.2b | 4.5a | 7.1a | 4.7a | 4.2b |
| Ridge and Valley (n=29) | 6.7ab | 4.8a | 6.0a | 8.3a | 5.7a | 5.6a |
| Appalachian Plateau (n=9) | 8.1a | 4.3ab | 6.6a | 8.3a | 6.2a | 4.6b |
| Mean (n=46) | 6.7 | 4.4 | 5.8 | 8.1 | 5.6 | 5.1 |

Changes in QMD were similar among provinces, but different among species. It increased across all stands 2.3 inches (SE=0.2) for oak, 1.2 inches (SE=0.2) for red maple, 1.8 inches (SE=0.3) for black birch, 2.3 inches (SE=0.3) for black cherry, and 1.5 inches (SE=0.3) for others, but the differences among species or species groups were not significant (Table 8). Changes in QMD were similar for all species within the three provinces, but individually not all species exhibited significant increases between measurements. Oak increased significantly in each province; 1.9 inches in the Blue Ridge (SE=0.4, P=.003), 2.3 inches in the Ridge and Valley (SE=0.2, P<.001), and 2.6 inches in the Appalachian Plateau (SE=0.7, P=.005). Increases in the QMD of red maple were significant in the Blue Ridge (0.9, SE=0.1, P<.001) and the Ridge and Valley (1.3, SE=0.1, P<.001), but not significant in the Appalachian Plateau. The remaining species in the Ridge and Valley also had significant increases in QMD. Black birch increased 1.9

inches (SE=0.4, P<.001), black cherry increased 2.4 inches (SE=0.3, P<.001) and the others increased 1.7 inches (SE=0.4, P<.001). Increases in oak diameters were significantly greater than the increases in red maple diameters in the Blue Ridge (P=.030), Ridge and Valley (P<.001), and Appalachian Plateau (P=.010).

Table 8. Change in quadratic mean diameter between 3rd and 4th decades by physiographic province and species group. Different letters within rows indicate significant differences at the 5% confidence level. Asterisk indicates significant change from 3rd to 4th decade.

| Physiographic Province | Quadratic mean diameter (inches) | | | | | Total |
|---|----------------------------------|---------------|---------------|---------------|---------------|--------------|
| | Oak | Red maple | Black birch | Black cherry | Others | |
| --Changes between 3 rd and 4 th decades-- | | | | | | |
| Blue Ridge (n=8) | +1.9a* | +0.9a* | +0.2a | +2.6a | +1.2a | +1.3* |
| Ridge and Valley (n=29) | +2.3a* | +1.3a* | +1.9a* | +2.4a* | +1.7a* | +2.0* |
| Appalachian Plateau (n=9) | +2.6a* | +1.3a | +3.1a | +0.5a | +1.5a | +1.3 |
| Mean (n=46) | +2.3a* | +1.2a* | +1.8a* | +2.3a* | +1.5a* | +1.7* |

At the 3rd decade measurement, the percentage of dominant or co-dominant oak stems was 34.1% and the maple percentage was 40.4% (Table 9). By the 4th decade, the percentages had virtually switched. 40.1% percent of dominant/co-dominant stems were oak and 33.6% were red maple. 3rd decade oak values were significantly higher in the Blue Ridge (57.1%), followed by the Ridge and Valley (36.9%) and lastly, the Plateau (4.8%). 3rd decade red maple values were always highest in the Plateau (79.5%), and lower in the Ridge and Valley (32.5%) and Blue Ridge provinces (24.8%).

Table 9. Percentage of stems in the upper canopy (dominant/co-dominant) represented by each species by physiographic province and decade of measurement. Different letters within columns indicate significant differences at the 5% confidence level.

| Physiographic Province | Canopy dominants and co-dominants (%) | | | | |
|--|---------------------------------------|-------------|-------------|--------------|-------------|
| | Oak | Red maple | Black birch | Black cherry | Others |
| --Stands in 3 rd decade of regeneration-- | | | | | |
| Blue Ridge (n=8) | 57.1a | 24.8b | 7.4a | 5.7ab | 9.3a |
| Ridge and Valley (n=29) | 36.9b | 32.5b | 19.4a | 3.7b | 12.4a |
| Appalachian Plateau (n=9) | 4.8c | 79.5a | 11.1a | 14.7a | 5.5a |
| Mean (n=46) | 34.1 | 40.4 | 16.7 | 5.8 | 10.5 |
| --Stands in 4 th decade of regeneration-- | | | | | |
| Blue Ridge (n=8) | 68.5a | 15.4b | 11.7a | 3.5ab | 6.7a |
| Ridge and Valley (n=29) | 42.5b | 30.2b | 12.7a | 5.1b | 12.5a |
| Appalachian Plateau (n=9) | 6.8c | 60.6a | 17.4a | 20.8a | 9.0a |
| Mean (n=46) | 40.1 | 33.6 | 13.2 | 7.6 | 10.8 |

Tree composition in the upper canopy changed significantly over the measurement period. Across all stands, dominant and co-dominant oaks as a proportion of all upper canopy trees increased by 5.9% (SE=1.7). By contrast, the proportion comprised of red maples decreased by 6.8% (SE=2.3), black birch decreased by 1.8% (SE=1.9), black cherry increased by 2.4% (SE=1.4) and others showed no noteworthy change (Table 10). Examining the percentage of upper canopy (dominant and co-dominant) stems by species or species group for the two measurement periods and three provinces, oak increased in the dominant and co-dominant layer in all three provinces (Figure 2). Oak experienced significant increases in the Blue Ridge (11.4%, SE=3.4, P=.013) and the Ridge and Valley (5.6%, SE=2.5, P=.038). But, red maple generally decreased its upper canopy occupancy, especially so in the Appalachian Plateau. The Blue Ridge province experienced a 9.4% decrease in red maple in the upper canopy

(SE=3.9, P=.048) and the Appalachian Plateau had an 18.9% decrease (SE=8.0, P=.047). Black birch decreased significantly in upper canopy occupancy in the Ridge and Valley province (-5.5%, SE=2.2, P=.027). The percentage change in upper canopy stems was significantly greater for oak than red maple in the Blue Ridge (P=.019) and Appalachian Plateau (P=.033), and not significant in the Ridge and Valley (P=.070).

Table 10. Net change in percentage of stems in the upper canopy occupied by each species group within physiographic province. Different letters within rows indicate significant differences at the 5% confidence level. Asterisk indicates significant change from 3rd to 4th decade.

| Change in percentage of canopy dominants and co-dominants (%) | | | | | |
|---|---------------|---------------|---------------|---------------|---------------|
| Physiographic Province | Oak | Red maple | Black birch | Black cherry | Others |
| --Changes between 3 rd and 4 th decades-- | | | | | |
| Blue Ridge (n=8) | +11.4a* | -9.4c* | +2.7ab | -2.1bc | -2.6bc |
| Ridge and Valley (n=29) | +5.6a* | -2.4b | -5.5b* | +2.1a* | +0.2ab |
| Appalachian Plateau (n=9) | +2.0ab | -18.9b* | +6.0a | +7.4a | +3.5a |
| Mean (n=46) | +5.9a* | -6.8c* | -1.8bc | +2.4ab | +0.3ab |

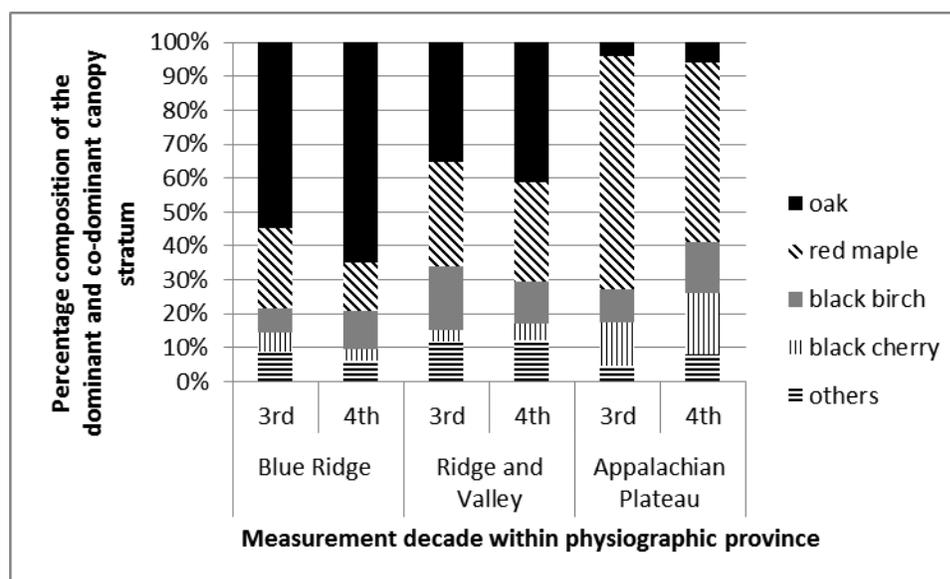


Figure 6. Average percentage of stems in upper canopy (dominants and codominants) for various species and species groups in three physiographic provinces. Values were calculated by averaging individual stand percentages, and the bars were scaled to 100% to facilitate comparisons between stand ages and provinces.

The provinces experienced varying degrees of change in trees per acre. The Ridge and Valley lost the greatest proportion of trees (41.5%) relative to 3rd decade densities while the Appalachian Plateau had the smallest, showing a minor increase (Table 11). Changes were not significantly different between species, when considering all stands. In individual provinces, oak generally decreased in number of stems per acre except for a two-thirds increase in the Appalachian Plateau, but this increase represents only a few dozen more stems per acre in the 4th decade and is most likely a sampling error. Red maple lost stems in every province with greatest losses in the Blue Ridge province. Within any province, oak changes were not significantly different from red maple changes in the percentage of stems lost.

Table 11. Percentage change in trees per acre relative to 3rd decade, by province and species.**Different letters within rows indicate significant differences at the 5% confidence level.**

| Physiographic Province | Change in trees per acre (%) | | | | | Total |
|---------------------------|---|-----------|-------------|--------------|--------|-------|
| | Oak | Red maple | Black birch | Black cherry | Others | |
| | --Changes between 3 rd and 4 th decades-- | | | | | |
| Blue Ridge (n=8) | -21.9a | -36.5a | +48.8a | +4.5a | +21.7a | -25.5 |
| Ridge and Valley (n=29) | -24.5a | -26.3a | -35.4a | +14.3a | +80.0a | -41.5 |
| Appalachian Plateau (n=9) | +67.3a | -13.5a | +193.3a | +12.6a | +77.6a | +1.3 |
| Mean (n=46) | -6.1a | -25.6a | +5.0a | +12.0a | +69.4a | -30.4 |

Discussion

The stands we chose to represent the three physiographic provinces had similar oak basal areas and relative basal areas prior to harvest, but oak stocking was significantly lower in the Appalachian Plateau, most likely due to oak leaf roller mortality, which was prevalent on the Plateau at that time. After four decades of stand re-growth, oak basal area, relative basal area, and stocking had differentiated among the three provinces: average measurements were highest in the Blue Ridge, intermediate in the Ridge and Valley and lowest in the Appalachian Plateau. Prior to harvest, red maple values, as measured by the same three density metrics, were significantly higher in the Appalachian Plateau and were similar for the Blue Ridge and the Ridge and Valley. Four decades after clearcutting, the differences are identical for each metric; significantly higher values in Appalachian Plateau than the other two provinces. 4th decade oak differences among provinces are likely a result of both composition differences following harvest and environmental influences imposed by unique growing conditions. The average oak regeneration stocking one year following harvest was 37.7% and 44.9% in the Blue Ridge and Ridge and Valley, respectively, compared to 20.3% in the Appalachian Plateau province. After four decades of stand development, the disadvantage on the Plateau remains; average 4th decade oak stocking was 72.7 in the Blue Ridge, 46.0 in the Ridge and Valley, and 7.7% on the Appalachian Plateau. Low oak stocking on the Plateau may also be a result of oaks competitive disadvantage on mesic sites (Lorimer 1984). Areas with site characteristics similar to the Blue Ridge have sometimes been referred to as intrinsic accumulator, which means the site characteristics predispose them

to accumulate relatively large amounts of oak regeneration with little to no effort by resource managers. These sites are described as beneficial to the development of oak (Johnson et al. 2009). In regards to red maple, the advantage exhibited in the Appalachian Plateau prior to harvest was maintained after harvest and through the 4th decade of re-growth. The relative advantage sustained by the Appalachian Plateau supports the description of red maple as a “super-generalist,” able to compete across a variety of sites and conditions (Abrams 1998). If red maple favored one site over another then we would expect to see a disproportionate increase in red maple growth among provinces. The relative development of different species between the 3rd and 4th decades suggests that shifts in species composition are continuing as stands approach mid-rotation age.

In the Blue Ridge province, changes between the 3rd and 4th decades strongly favored oak over red maple. The advantage exists not only because oak had such large gains, but also because red maple experienced decreases in key measurements. The relative basal area of oak significantly increased by an average of 6.8% across the eight Blue Ridge stands. In the same eight stands red maple significantly decreased by an average of 5.2%. The Blue Ridge had strong increases in oak partly at the expense of red maple judging by its decrease. Relative density, or stocking, is a measure of crowding in a stand. It is a more precise measure of density than basal area alone and incorporates trees per acre and diameter to describe how much competition-free growing space is available in a stand relative to a potential maximum (Gingrich 1967). The stocking changes in our stands were similar to changes in basal area. Stocking increases for oak were very strong and statistically significant in the Blue Ridge province. In addition, oak

out-grew red maple in QMD and further displaced red maple in canopy dominance. On average, oak diameter growth was a full inch greater than red maple (1.9 vs. 0.9in.). Regarding canopy dominance, oak increased its share of canopy dominants and co-dominants by 11.4% while red maple decreased by 9.4%. At the fourth decade, 69% of oak stems in this province were chestnut oak, and any other individual oak species comprised no more than 10%.

Shifts between oak and red maple during the last decade of development were also apparent in the Ridge and Valley, but less striking than in the Blue Ridge province. Gains by oak were smaller and more variable, and red maple appeared to fare better in the Ridge and Valley than in the Blue Ridge. Despite significant basal area increases by both groups, oak had a significant advantage over red maple (15.3 vs. 8.8 ft²/acre). The RBA of oak in the Ridge and Valley province increased by 4.6% and red maple's was effectively unchanged. The Ridge and Valley is a region with considerable soil and topographical variability as well as advance oak regeneration at the time of harvest (post-harvest regeneration stocking ranged from 3-125%), which no doubt led to variable success in the establishment and growth of oak following harvest. Oak still showed significant gains in RBA. Oak increases in stocking were moderate but significant in the Ridge and Valley, and stocking increases for red maple were small but also significant. Similar to the Blue Ridge province, the oak outgrew red maple in diameter by a full inch on average, a statistically significant advantage in favor of oak. Oak also had significant increases in its percentage of upper canopy trees occupied, and red maple had no real change, but the oak advantage was not significant ($P=.070$). At the fourth decade, the

composition of oak in this province was 49% chestnut oak, 18% northern red oak, and 17% white oak.

Over the measurement interval between 3rd and 4th decades, red maple accumulated more than five times as much BA as oak on the Appalachian Plateau. Even though red maple had a significant increase in BA between 3rd and 4th decades, changes in the RBA of red maple were not significant and were negative on average (-12.7%). Oak had small and insignificant increases in basal area, but maintained its RBA. Non-significant changes suggest that RBA remained constant across species between the 3rd and 4th decade measurements, or perhaps that stands differed so much in development that a common trend for the province could not be detected. Initially, at harvest the Appalachian plateau stands had very low levels of oak; that, oak maintained its relative basal area between the 3rd and 4th decade measurement is encouraging. Both species groups had small and statistically similar increases in stocking despite differing changes in basal area. Once again, oak had a statistically significant advantage over red maple in diameter growth, growing more than an inch greater (2.6 vs. 1.3in.). Oak had small and insignificant increases in the percentage of upper canopy occupied with its stems (2.0%) but red maple had large, significant decreases (-18.9%) giving oak a significant advantage over red maple. Fourth decade oak composition in this province was 65% red oak and 27% white oak

Basal area growth is highly dependent on the initial composition because tree diameter is highly correlated with canopy size (Krajicek et al. 1961), and the larger the canopy, the greater is growth in basal area. Composition of oak/red maple is highly uneven in the Blue Ridge and Appalachian Plateau; biased toward oak or red maple,

respectively. The most convincing evidence of oak's ability to attain dominance during mid-rotation appears in the Ridge and Valley province where the compositions were approximately even at the time of the 3rd decade measurements: 30.2 ft²/acre for oak and 27.1ft²/acre for red maple. Between the 3rd and 4th decades, oak had grown an average of 15.3ft²/acre and red maple had only grown an average 8.8 ft²/acre. This is also supported by differing diameter growth, discussed later. The basal area growth is significantly greater for oak than red maple suggesting differing growth rates at this point in the rotation favor oak. Furthermore, oak accumulated more growth and obtained significant advantage with fewer stems. In the Ridge and Valley, the average number of trees in the 4th decade was 210 for oak and 296 for red maple per acre (Appendix). So, oak accounted for 38% of the 4th decade basal area but only 29% of the trees, and red maple accounted for only 29% of the basal area with 41% of the trees.

Stand 572050 in the Ridge and Valley is an instance where the 3rd decade basal area and trees per acre were approximately equal. Red maple had an average of .5 more trees per acre and oak had 2.8 ft²/acre more basal area at the 3rd decade measurement. At the time of the fourth decade, red maple had increased its advantage in trees per acre to 77, but oak had increased its basal area advantage to 6.6 ft²/acre. Despite oak losing more trees per acre than red maple, oak was able to increase the magnitude of difference in basal area. Oak's relative basal area increased from 41 to 46% and red maple's increased from 37 to 39%.

Additional clarity can be provided by partitioning the species basal area growth by canopy classification (Table 12). A species group that accumulates most of its growth in dominant and co-dominant trees is more successful at competing for dominance than a

group that accumulates growth in subordinate classes. The average growth of oak in upper canopy classes was greater than red maple, but was insignificant in the Appalachian Plateau province, where growth was very low because of the general paucity of oaks in those stands. Oak also accumulated significantly more basal area in its upper class than in its lower class in all stands but those in the Plateau. Red maple accumulated the same amount of growth in the lower and the upper classes for the Ridge and Valley and Blue Ridge provinces but accumulated all its growth in the lower crown class in the Plateau province.

Table 12. Average changes between 3rd and 4th decade in basal area by physiographic province and canopy stratum; upper (dominant and codominant) and lower (intermediate and suppressed). Different letters (a or b) for upper and lower canopy class means within the same column indicate significant differences at the 5% confidence level. Different letters (y or z) for oak and red maple means within the same row indicate significant differences at the 5% confidence level.

| Physiographic Province | Canopy Class | Changes in basal area (ft ² /acre) by canopy class | | | | | Total |
|------------------------|--------------|---|-----------|-------------|--------------|-------|-------|
| | | Oak | Red maple | Black birch | Black cherry | Other | |
| Blue Ridge | Upper | 19.9a,y | 0.6a,z | 2.4 | -1.1 | 0.8 | 22.7 |
| | Lower | 6.0b,y | 2.7a,y | 1.2 | 0.4 | 2.8 | 13.1 |
| Ridge and Valley | Upper | 12.3a,y | 3.7a,z | -0.9 | 1.9 | 3.1 | 20.0 |
| | Lower | 3.0b,y | 5.2a,y | 1.3 | 0.2 | 1.8 | 11.4 |
| Appalachian Plateau | Upper | 1.5a,y | -1.5b,y | 3.3 | 4.1 | 3.8 | 11.1 |
| | Lower | 0.9a,z | 17.1a,y | 3.1 | 3.6 | 4.7 | 29.4 |

Red maple growth appears to have slowed relative to oak resulting in uniform decreases in its RBA in all provinces. A portion of the RBA relinquished by red maple

appears to be displaced by oak as its RBA increases. The amount of RBA gained increases with increasing oak abundance. Oak only had an advantage in RBA in one province, but considering all stands together, the advantage of oak is highly significant ($P < .001$).

Oak and red maple had varying levels of change in stocking from 3rd to 4th decade. The higher the 3rd decade stocking, the larger the stocking increase. Oak increases were largest in the Blue Ridge and red maple increases were largest in the Appalachian Plateau. In the Ridge and Valley, the average 3rd decade stocking levels for oak and red maple were nearly identical. After a decade of growth, oak had significantly increased its stocking by 9.3% and red maple had significantly increased its stocking by 4.3%. These increases were not significantly different from each other; however, if the trajectories continue, oak will gain a significant advantage. In addition, if all stands are considered, oak's increase in stocking (9.3%) is significantly greater ($P = .045$) than red maple's (3.6%).

While basal area and other measures of density are strongly influenced by the species abundance, QMD accounts for broad ranges of diameters and densities between stands and among species. That is, QMD compares tree sizes of the different species irrespective of abundance. Simple, within stand comparisons between the oak and red maple QMD can yield insights into relative dominance irrespective of abundance.

Oliver (1978) working in New England found that by age 15 mean diameter of oak was significantly larger than the mean diameter of red maple. In the present study, the mean diameter of oak was significantly larger than maple across all stands as early as the 3rd decade measurement (age 24.7) ($P < .001$) and continued to be significantly larger

at the 4th decade measurement (age 37.8) ($P < .001$). A plausible explanation for this distinct difference in diameter is differing shade tolerances; where oak experiences higher mortality in smaller size classes while red maple persists as suppressed trees (Arthur et al. 1997, Ward and Stephens 1994). Lower mortality rates, particularly in the lower diameter and crown classes, would result in a lower mean diameter for red maple.

In this study, all stems are of the same cohort, and the smaller stems do not reflect ingrowth because our stands are still in stem exclusion phase where new individual establishment does not occur (Oliver and Larson 1996). Nevertheless, to partially correct for this, suppressed trees were excluded from the mean diameter calculations. Excluding the suppressed trees decreased bias against red maple because it has a relatively larger number of suppressed trees and oak has relatively few. Using only the dominant, co-dominant, and intermediate stems, the average diameter of oak in the 3rd decade was 4.9 inches and red maple was 3.8 inches, which remained a significant difference ($P < .001$). The 4th decade diameters for oak and red maple were 7.3 and 5.6 inches, respectively, also a significant difference ($P < .001$). At this point, approximately halfway through the stand rotations, it appears that the diameter growth of red maple is significantly lower than that of oak.

A likely explanation for the diameter difference is different growth characteristics and life history traits of oak and red maple. Each species has its own way to deal with constraints imposed by the environment and competition. The responses to constraints create various levels of ecological organization (Tilman 1990). In trees, these responses are manifest in shade tolerance, height and diameter growth, and lifespan, which are partially responsible for the organization of trees within the canopy and through

successional time (Oliver 1980, Hibbs 1983). Red maple grows rapidly following disturbance and is often numerically dominant in regenerating stands; however, when the young stand reaches crown closure red maple growth slows as competition for light increases (Walters and Yawny, *Silvics of NA*). Oak, on the other hand, is less shade tolerant than red maple and can prove more difficult to accumulate as advance regeneration. Despite initial dominance by red maple, both numerically and in height, oak has the ability to eventually outgrow other species and establish a competitive canopy position (Oliver 1978, 1980). Oliver (1978) found that all oaks dominant by the end of rotation had achieved that position not at a young age but during mid-rotation. Although, oak did not make up a large number of the overall stems, it did comprise a large proportion of the stems in the upper canopy, suggesting a stronger ability to attain a competitive canopy position. Hibbs (1983) also found that oak, despite a disadvantage in the number of stems, made up a disproportionately large number of trees in the dominant canopy position. Also, 60 years after a stand replacing disturbance in West Virginia, red and white oak controlled more basal area than red maple on both dry and mesic sites despite the numerical dominance by red maple, and the oaks had a higher number of stems in the dominant and co-dominant canopy classes compared to red maple (Tift and Fajvan 1999). Johnson and Krinard (1988) tracked the growth of young southern red oak and sweetgum up to age 29 and found similar trends; oak was capable over time of achieving crown positions competitive with sweetgum beginning around age 18 when oak had “steady, if not spectacular” height growth. Red oak diameter growth rate increased from age 18 to 29 while the growth rate of associated sweetgum decreased over the same interval, and the oak diameter grew twice as fast as sweetgum during the last six

year interval. On that trajectory, southern red oak was expected to surpass sweetgum in height by age 30 to 35. Another Pennsylvania study found it was common for oaks to be shorter than associated species through at least the first decade of growth, only to attain a dominant canopy position later in the rotation (Zenner et al., in-press). Our study supports claims that oak has a latent ability to achieve canopy dominance following initial suppression by red maple.

After the first decade or so of stand development following a clearcut harvest, few if any new trees become established to the canopy during the next many decades (Oliver and Larson 1996). Furthermore, as stands mature, trees are annually lost due to natural mortality and competition. As the stands in this study mature they are showing varying degrees of mortality, but, in most cases, oak and red maple experienced percentage equal relative mortality rates between the 3rd and 4th decades. No species had a statistically detectable difference in percentage change of trees per acre in any province (Table 11). This similarity in mortality rates, provides a stronger understanding of how changes in canopy classification are occurring.

With the exception of the Appalachian Plateau province, where pre-harvest perturbations from oak leaf roller had likely affected composition and oak seedling recruitment, there were significant increases in the percent of upper canopy occupied by oak stems (11.4% in Blue Ridge and 5.4% in Ridge and Valley). This could represent oak's relatively low mortality within the dominant/co-dominant class compared to other overstory tree species. Oak could be maintaining its overstory presence and abundance while associated species are experiencing higher mortality, but due to the lack of difference in mortality of each species, it seems more likely oak is exhibiting an innate

ability to achieve dominance. For example, oak has the ability to produce large spreading crowns and endure physical abrasion between its own twigs and those of competing species (Oliver 1978). At the same time oak is increasing its competitive position in the canopy, red maple is experiencing significant decreases in its canopy presence, with the exception of the Ridge and Valley province (9.4% in Blue Ridge and 18.9% in the Appalachian Plateau).

At the 3rd decade in the Ridge and Valley, the composition of oak in the upper canopy was 4% higher (36.9 vs. 32.5%), and by the 4th decade, the margin between oak and red maple compositions had increased to 12% (42.5 vs. 30.2%), but the difference was not significant. Given the way oak has increased its percentage of the overstory, it is possible that oak will, in a relatively short time, have significantly more trees than red maple in a dominant/co-dominant position. That may never be true for stand studies on the Appalachian Plateau, where oak occurs much less frequently. Fortunately, the majority of them are already in dominant positions, which could be related to a lack of competition inter-oak competition because higher oak densities have a negative effect on growth of individual oaks (Kittredge 1988).

Uniform increases in the percentage of oak stems occupying positions in the upper canopy and uniform decreases in the percentage of red maple stems demonstrate distinctly different species growth processes during stand development. Differences between the two groups give oaks a statistically significant advantage in two of the three provinces. The marginal decrease in red maple in the Ridge and Valley prevents oak from having the clear advantage across all provinces. Also, the relatively low magnitude of oak increase on the Appalachian Plateau results in lack of significance in that region.

Again, this is likely due to the lack of oak stems in these study stands, which is likely linked to low regeneration prior to harvest. Despite initial advantages for red maple, our data suggest that vigorous oaks in central Pennsylvania that survive initial stand development stages compete well against red maple for dominant canopy positions. Evidence supports that the mechanism for these changes is not differential mortality; rather, it is an enhanced ability of oak to achieve dominance during mid-rotation.

Conclusions

The evidence of oak's mid-rotation transition to dominance is most compelling where trends are similar across all physiographic provinces and all levels of oak regeneration. Strong trends across these variables provide robust support to the distinct developmental patterns of oak and red maple. QMD is one of these strong variables and it allowed us to compare the two species across varying oak densities in the 4th decade despite large variability in levels of oak regeneration. Irrespective of the amount of oak established as regeneration by the 4th decade, or even the 3rd, the diameter of oak was larger. This finding supports that of Oliver (1978), although, our earliest data is approximately 10 years later in stand development. Furthermore, in the Blue Ridge and the Ridge and Valley, oak accounted for a large portion (>40%) of the stems in the upper canopy, more than red maple; a trend that is significantly increasing for oak and decreasing for maple.

Results were almost always positive for oak in the Blue Ridge province. In this province, there is more likelihood of oak regenerating and becoming established; however, managers should monitor red maple encroachment. The results for oak in the Appalachian Plateau were fairly dismal, due to its lack of advance regeneration, which we attribute to an oak leaf roller outbreak prior to harvest. There may also be issues related to the inability of oak to compete on good sites or with aggressive species (Hilt 1985, Brashears et al. 2004). Unfortunately, in the Appalachian Plateau, there is no

chance for these stands to naturally return to their former oak-dominated condition as they are so devoid of oak.

Due to the fact that most of these stands are overstocked, the majority of stands could be entered and thinned to favor further oak development for the remainder of the rotation. Four decades after harvest, there were twelve stands (6 Blue Ridge and 6 Ridge and Valley) that have at least 60% stocking in oak, and twenty-four stands (7 Blue Ridge and 17 Ridge and Valley) that had at least 40% stocking in oak. At this time in the stands rotation, when we believe oak to be increasing its dominance, it may be an appropriate time to enter many of these stands and further increase oak's dominance. For example, depending on the spacing, stands with greater than 60% oak stocking could be heavily thinned, selecting against red maple, to ensure an oak dominated stand by the end of the rotation. Stands with 40-60% oak could be greatly influenced by a thinning to produce a stand that is mostly oak with a smaller component of red maple and others.

The protocol used to measure regeneration in these stands prior to harvest was adequate to determine amounts of competitive oak regeneration. A species was tallied if it was a competitor for dominance on the plot, but in the "Oak Type" protocol a plot was acceptably stocked if it had two, competitive red maple. Since these sites were harvested, much has been learned about development of shade tolerant species and their inhibiting effect on oak (Lorimer 1983, 1984; Abrams 1998, 2003). In light of this research, a manager seeking to replace oak should exclude red maple as acceptable stems. Of course, there are more robust oak regeneration guidelines available; Oak SILVAH, ORSPA (Marquis et al. 1992, Steiner et al. 2008, respectively).

To successfully regenerate oak, emphasis must be maintained on quality advance oak regeneration with established root systems. Even regeneration distribution across the harvest area is also important. Furthermore, fire as a management tool should be used whenever possible because of its ability to create favorable conditions for oak and to control competing trees and vegetation (VanLear et al. 2000). However, fire is not applicable at all stages of development. Regeneration cutting or thinning are more effective than fire to manage understory light, and significant fire free periods (10-30 years) are needed for mature oak to develop fire resistance (Arthur et al. 2012). In central Pennsylvania, oak that survives the first three decades after harvest appears to perform well as it transitions into the 4th decade while facing varying levels of competition.

References

- Abrams, M.D. 1992. Fire and the development of oak forests. *Bioscience* 42: 346-353.
- Abrams, M.D. 1998. The red maple paradox. *Bioscience* 48: 355-364.
- Abrams, M.D. 2003. Where has all the white oak gone? *Bioscience* 53: 927-939.
- Abrams, M.D. and J.A. Downs. 1990. Successional replacement of old-growth white oak by mixed mesophytic hardwoods in southwestern Pennsylvania. *Canadian Journal of Forest Research* 20: 1864-1870.
- Abrams, M.D. and G.J. Nowacki. 1992. Historical variation in fire, oak recruitment and post logging accelerated succession in central Pennsylvania. *Bulletin of the Torrey Botanical Society* 119: 19-28.
- Arthur, M.A., R.N. Muller and S. Costello. 1997. Composition in a central hardwood forest in Kentucky 11 years after clear-cutting. *American Midland Naturalist* 137: 274-281.
- Arthur, M.A., H.D. Alexander, D.C. Dey, C.J. Schweitzer and D.L. Loftis. 2012. Refining the oak-fire hypothesis for management of oak-dominated forests of the eastern United States. *Journal of Forestry* 110: 257-266.
- Avery, T.E.; Burkhart, H.E. 2002. *Forest measurements* (5th edition). New York: McGraw-Hill. 456 p.
- Beck, D.E. and R.H. Hooper. 1986. Development of a Southern Appalachian hardwood stand after clearcutting. *Southern Journal of Applied Forestry* 10: 168-172.
- Brose, P. and D.H. Van Lear. 1998. Response of hardwood advance regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. *Canadian Journal of Forest Research* 28: 331-339.
- Brose, P., T. Schuler, D.H. Van Lear and J. Berst. 2001. Bringing Fire Back: The Changing Regimes of the Appalachian Mixed-Oak Forests. *Journal of Forestry* 99: 30-35.
- Cuff, D.J., W.J. Young, E.K. Muller, W. Zelinsky and R.F. Abler. 1989. *The Atlas of Pennsylvania*. Temple University Press. Philadelphia, PA. 288p.
- Department of Conservation and Natural Resources, Pennsylvania Bureau of Forestry. Map 13. Available: http://www.dcnr.state.pa.us/topogeo/pub/map/map_online.aspx Accessed on January 18th, 2012.

- Fei, S. and K.C. Steiner. 2007. Evidence for increasing red maple abundance in the eastern United States. *Forest Science* 53: 473-477.
- Fei, S. and K.C. Steiner. 2009. Rapids capture of growing space by red maple. *Canadian Journal of Forest Research* 39: 1444-1452.
- Fei, S., N. Kong, K.C. Steiner, W.K. Moser and E.B. Steiner. 2011. Change in oak abundance in the eastern United States from 1980 to 2008. *Forest Ecology and Management* 262: 1370-1377.
- Gingrich, S.F. 1967. Measuring and evaluating stocking and stand density in Upland Hardwood forests in Central States. *Forest Science* 13: 38-53.
- Gould, P.J., K.C. Steiner, J.C. Finley and M.E. McDill. 2005. Developmental pathways following the harvest of oak dominated stands. *Forest Science* 51: 76-90.
- Hardin, J.W., D.J. Leopold and F.M. White. 2001. Harlow & Harrar's Textbook of Dendrology. 9th ed. McGraw-Hill. New York, NY. 534p.
- Hibbs, D.E. 1983. Forty years of forest succession in central New England. *Ecology* 64: 1394-1401.
- Hix, D.M. and C.G. Lorimer. 1991. Early stand development on former oak sites in southwestern Wisconsin. *Forest Ecology and Management* 42: 169-193.
- Johnson, R.L. and R.M. Krinard. 1988. Growth and development of two sweet gum-red oak stands from origin through 29 years. *Southern Journal of Applied Forestry* 12: 29-34.
- Johnson, P.S., S.R. Shifley and R. Rogers. 2009. *The Ecology and Silviculture of Oaks*. CABI Publishing. 2nd ed. New York, NY. 580p.
- Kittredge, D.B. 1988. The influence of species composition on the growth of individual red oaks in mixed stands in southern New England. *Canadian Journal of Forest Research* 18: 1550-1555.
- Krajicek, J.E., K.A. Brinkman and S.F. Gingrich. 1961. Crown competition- A measure of density. *Forest Science* 7: 35-42.
- Loftis, D.L. 1983. Regenerating southern appalachian mixed hardwood stands with the shelterwood method. *Southern Journal of Applied Forestry* 7:212-217.
- Loftis, D.L. 1990. Predicting post-harvest performance of advance northern red oak reproduction in the Southern Appalachians. *Forest Science* 36: 908-916.

- Lorimer, C.G. 1983. Eighty-year development of northern red oak after partial cutting in a mixed species Wisconsin forest. *Forest Science* 29: 371-383
- Lorimer, C.G. 1984. Development of the red maple understory in northeastern oak forests. *Forest Science* 30: 3-22.
- Lorimer, C.G. 1993. Causes of the oak regeneration problem. In: *Oak Regeneration: Serious problems practical recommendations*. U.S. Department of Agriculture, Forest Service. General Technical Report. SE-84: 14-39.
- Marquis, D.A., R.L. Ernst and S.L. Stout. 1992. Prescribing silvicultural treatments in hardwood stands of the Alleghenies. U.S. Department of Agriculture, Forest Service. General Technical Report. NE-96: 108p.
- Nowacki, G.J. and M.D. Abrams. 2008. The demise of fire and the “mesophication” of forests in the eastern United States. *Bioscience* 58: 123-138.
- Oliver, C.D. 1978. The development of northern red oak in mixed stands in central New England. *Yale University School of Forestry and Environmental Studies Bulletin*. 91: 63p.
- Oliver, C.D. 1980. Even-aged development of mixed species stands. *Journal of Forestry* 78: 201-203.
- Oliver, C.D. and E.P. Stephens. 1977. Reconstruction of a mixed species forest in central New England. *Ecology* 58: 562-572.
- Oliver, C.D. and B.C. Larson. 1996. *Forest Stand Dynamics*. John Wiley & Sons, Inc. New York, NY. 519p.
- Palik, B.J. and K.S. Pregitzer. 1991. The relative influence of establishment time and height-growth rates on species vertical stratification during secondary forest succession. *Canadian Journal of Forest Research* 21: 1481-1490.
- Palik, B.J. and K.S. Pregitzer. 1993. The vertical development of early successional forests in northern Michigan, USA. *Journal of Ecology* 81: 271-285.
- Powell, D.S. and T.J. Considine, Jr. 1982. An analysis of Pennsylvania’s forest resources. U.S. Department of Agriculture, Forest Service. *Resource Bulletin*. NE-69: 103p.
- Ruffner, C.M. and M.D. Abrams. 1998. Relating land-use history and climate to the dendroecology of a 326-year-old *Quercus prinus* talus slope forest. *Canadian Journal of Forest Research*. 28: 347-358.

- Steiner, K.C., J.C. Finley, P.J. Gould, S. Fei and M.E. McDill. 2008. Oak regeneration guidelines for the central Appalachians. *Northern Journal of Applied Forestry* 25: 5-16.
- Thirgood, J.V. 1971. The historical significance of oak. In: *Oak Symposium Proceedings*. 1971 August 16-20; U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: Upper Darby, PA. 1-18.
- Tift, B.D. and M.A. Fajvan. 1999. Red maple dynamics in Appalachian hardwood stands in West Virginia. *Canadian Journal of Forest Research* 29: 157-165.
- Van Lear, D.H., P.H. Brose and P.D. Keyser. 2000. Using prescribed fire to regenerate oaks. In: Yaussy, Daniel A., comp. 2000. *Proceedings: workshop on fire, people, and the central hardwoods landscape*; 2000 March 12-14; Richmond, KY. Gen. Tech. Rep. NE-274. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station: 97-102.
- Ward, J.S. and G.R. Stephens. 1994. Crown class transition rates of maturing northern red oak (*Quercus rubra* L.). *Forest Science* 40: 221-237.
- Zenner, E.K., D.J. Heggenstaller, P.H. Brose, J.E. Peck and K.C. Steiner. (in press). Reconstructing the competitive dynamics of mixed-oak neighborhoods. *Canadian Journal of Forest Research*.

Appendix

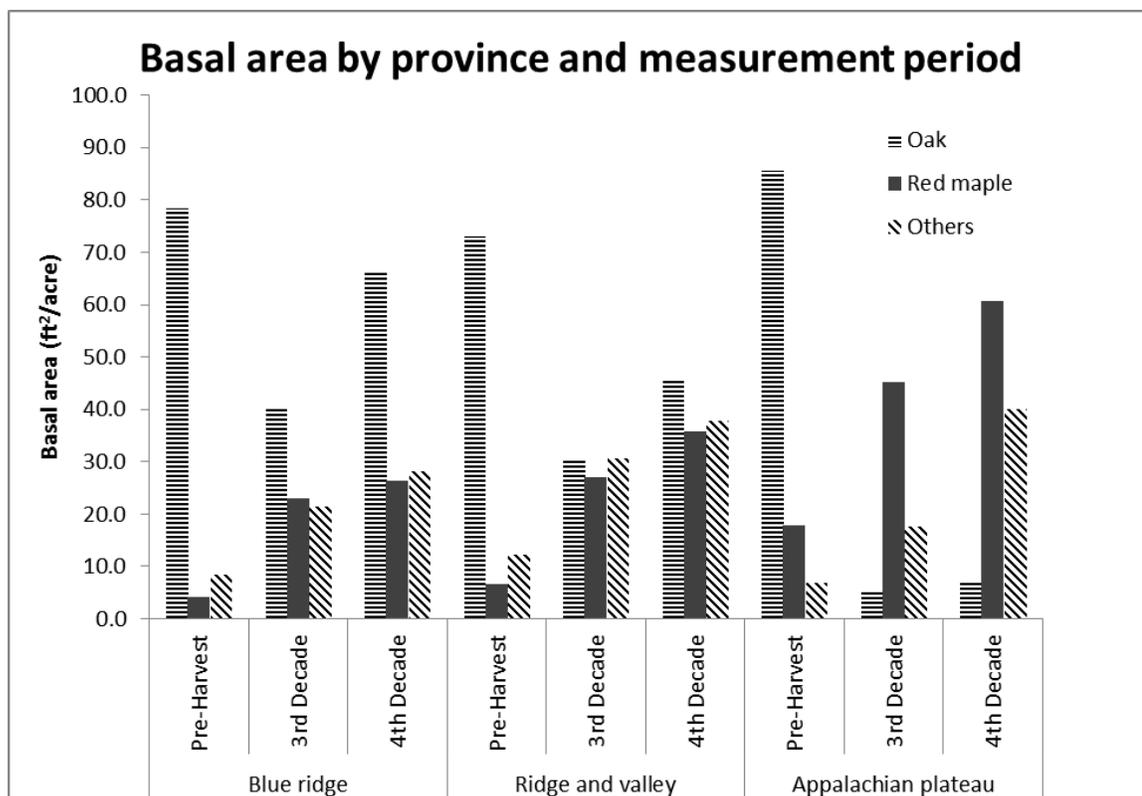


Table 7. Basal area by measurement period and province

Table 13 . Average number of trees per acre for each species by physiographic province and decade of measurement. Different letters within columns indicate significant differences at the .05 confidence level.

| Physiographic Province | Trees per acre | | | | | Total |
|--|----------------|--------------|--------------|--------------|--------------|---------------|
| | Oak | Red maple | Black birch | Black cherry | Others | |
| --Stands in 3 rd decade of regeneration-- | | | | | | |
| Blue Ridge (n=8) | 705.8a | 817.8ab | 70.6a | 50.9a | 180.4ab | 1825.5a |
| Ridge and Valley (n=29) | 361.5b | 473.6b | 269.4a | 22.6a | 265.5a | 1392.6a |
| Appalachian Plateau (n=9) | 53.8c | 1296.6a | 34.3a | 77.0a | 67.2b | 1528.9a |
| Mean (n=46) | 361.2 | 694.5 | 188.9 | 38.2 | 211.9 | 1494.5 |
| --Stands in 4 th decade of regeneration-- | | | | | | |
| Blue Ridge (n=8) | 512.5a | 490.2ab | 67.2a | 32.1a | 188.4a | 1290.4a |
| Ridge and Valley (n=29) | 210.7b | 296.7b | 81.7a | 17.0a | 119.8a | 725.9b |
| Appalachian Plateau (n=9) | 41.0c | 771.9a | 62.2a | 127.6a | 98.5a | 1101.2a |
| Mean (n=46) | 230.0 | 423.3 | 75.4 | 41.2 | 127.6 | 897.5 |

Table 14: Analysis of variance output for 3rd to 4th decade comparisons of basal area

Basal area ANOVA -3rd to 4th

The GLM Procedure

Dependent Variable: basal basal

| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
|-----------------|-----|----------------|-------------|---------|--------|
| Model | 287 | 197530.4490 | 688.2594 | 14.17 | <.0001 |
| Error | 172 | 8355.4834 | 48.5784 | | |
| Corrected Total | 459 | 205885.9324 | | | |

| R-Square | Coeff Var | Root MSE | basal Mean |
|----------|-----------|----------|------------|
| 0.959417 | 34.71824 | 6.969820 | 20.07539 |

| Source | DF | Type I SS | Mean Square | F Value | Pr > F |
|--------------------|-----|-------------|-------------|---------|--------|
| decade | 1 | 5276.34384 | 5276.34384 | 108.62 | <.0001 |
| prov | 2 | 686.15162 | 343.07581 | 7.06 | 0.0011 |
| spec | 4 | 69084.02033 | 17271.00508 | 355.53 | <.0001 |
| decade*prov | 2 | 61.26121 | 30.63060 | 0.63 | 0.5335 |
| prov*spec | 8 | 30940.03360 | 3867.50420 | 79.61 | <.0001 |
| decade*spec | 4 | 2467.45405 | 616.86351 | 12.70 | <.0001 |
| decade*prov*spec | 8 | 1817.03166 | 227.12896 | 4.68 | <.0001 |
| stand(prov) | 43 | 3019.32395 | 70.21684 | 1.45 | 0.0519 |
| spec*stand(prov) | 172 | 83208.46184 | 483.77013 | 9.96 | <.0001 |
| decade*stand(prov) | 43 | 970.36687 | 22.56667 | 0.46 | 0.9980 |

| Source | DF | Type III SS | Mean Square | F Value | Pr > F |
|--------------------|-----|-------------|-------------|---------|--------|
| decade | 1 | 4371.33705 | 4371.33705 | 89.99 | <.0001 |
| prov | 2 | 686.15162 | 343.07581 | 7.06 | 0.0011 |
| spec | 4 | 52660.22680 | 13165.05670 | 271.01 | <.0001 |
| decade*prov | 2 | 61.26121 | 30.63060 | 0.63 | 0.5335 |
| prov*spec | 8 | 30940.03360 | 3867.50420 | 79.61 | <.0001 |
| decade*spec | 4 | 1518.14270 | 379.53568 | 7.81 | <.0001 |
| decade*prov*spec | 8 | 1817.03166 | 227.12896 | 4.68 | <.0001 |
| stand(prov) | 43 | 3019.32395 | 70.21684 | 1.45 | 0.0519 |
| spec*stand(prov) | 172 | 83208.46184 | 483.77013 | 9.96 | <.0001 |
| decade*stand(prov) | 43 | 970.36687 | 22.56667 | 0.46 | 0.9980 |

Table 15: Analysis of variance output for pre harvest to 4th decade comparisons of basal area

Basal area ANOVA- Pre to 4th

The GLM Procedure

Dependent Variable: basal basal

| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
|-----------------|-----|----------------|-------------|---------|--------|
| Model | 188 | 205955.0392 | 1095.5055 | 2.91 | <.0001 |
| Error | 84 | 31594.8198 | 376.1288 | | |
| Corrected Total | 272 | 237549.8590 | | | |

R-Square Coeff Var Root MSE basal Mean
 0.866997 54.57047 19.39404 35.53944

| Source | DF | Type I SS | Mean Square | F Value | Pr > F |
|--------------------|----|-------------|-------------|---------|--------|
| decade | 1 | 3545.08593 | 3545.08593 | 9.43 | 0.0029 |
| prov | 2 | 60.34202 | 30.17101 | 0.08 | 0.9230 |
| spec | 2 | 74837.68489 | 37418.84245 | 99.48 | <.0001 |
| decade*prov | 2 | 1069.27876 | 534.63938 | 1.42 | 0.2471 |
| prov*spec | 4 | 11910.99907 | 2977.74977 | 7.92 | <.0001 |
| decade*spec | 2 | 61066.09309 | 30533.04655 | 81.18 | <.0001 |
| decade*prov*spec | 4 | 11542.55902 | 2885.63975 | 7.67 | <.0001 |
| stand(prov) | 43 | 3356.79163 | 78.06492 | 0.21 | 1.0000 |
| spec*stand(prov) | 86 | 35989.33820 | 418.48068 | 1.11 | 0.3123 |
| decade*stand(prov) | 42 | 2576.86660 | 61.35397 | 0.16 | 1.0000 |

| Source | DF | Type III SS | Mean Square | F Value | Pr > F |
|--------------------|----|-------------|-------------|---------|--------|
| decade | 1 | 1885.95096 | 1885.95096 | 5.01 | 0.0278 |
| prov | 2 | 63.30638 | 31.65319 | 0.08 | 0.9194 |
| spec | 2 | 57124.69907 | 28562.34954 | 75.94 | <.0001 |
| decade*prov | 2 | 1078.41448 | 539.20724 | 1.43 | 0.2442 |
| prov*spec | 4 | 11612.85685 | 2903.21421 | 7.72 | <.0001 |
| decade*spec | 2 | 51189.71960 | 25594.85980 | 68.05 | <.0001 |
| decade*prov*spec | 4 | 11705.40514 | 2926.35129 | 7.78 | <.0001 |
| stand(prov) | 43 | 3356.79163 | 78.06492 | 0.21 | 1.0000 |
| spec*stand(prov) | 86 | 35989.33820 | 418.48068 | 1.11 | 0.3123 |
| decade*stand(prov) | 42 | 2576.86660 | 61.35397 | 0.16 | 1.0000 |

Table 16: Analysis of variance output for 3rd to 4th decade comparisons of relative basal area

RBA ANOVA-3rd to 4th
The GLM Procedure

Dependent Variable: rba rba

| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
|-----------------|-----|----------------|-------------|---------|--------|
| Model | 287 | 20.01065824 | 0.06972355 | 17.33 | <.0001 |
| Error | 172 | 0.69185171 | 0.00402239 | | |
| Corrected Total | 459 | 20.70250995 | | | |

| R-Square | Coeff Var | Root MSE | rba Mean |
|----------|-----------|----------|----------|
| 0.966581 | 31.71117 | 0.063422 | 0.200000 |

| Source | DF | Type I SS | Mean Square | F Value | Pr > F |
|--------------------|-----|------------|-------------|---------|--------|
| decade | 1 | 0.00000000 | 0.00000000 | 0.00 | 1.0000 |
| prov | 2 | 0.00000000 | 0.00000000 | 0.00 | 1.0000 |
| spec | 4 | 7.03920496 | 1.75980124 | 437.50 | <.0001 |
| decade*prov | 2 | 0.00000000 | 0.00000000 | 0.00 | 1.0000 |
| prov*spec | 8 | 4.07252443 | 0.50906555 | 126.56 | <.0001 |
| decade*spec | 4 | 0.07836513 | 0.01959128 | 4.87 | 0.0010 |
| decade*prov*spec | 8 | 0.11284648 | 0.01410581 | 3.51 | 0.0009 |
| stand(prov) | 43 | 0.00000000 | 0.00000000 | 0.00 | 1.0000 |
| spec*stand(prov) | 172 | 8.70771725 | 0.05062626 | 12.59 | <.0001 |
| decade*stand(prov) | 43 | 0.00000000 | 0.00000000 | 0.00 | 1.0000 |

| Source | DF | Type III SS | Mean Square | F Value | Pr > F |
|--------------------|-----|-------------|-------------|---------|--------|
| decade | 1 | 0.00000000 | 0.00000000 | 0.00 | 1.0000 |
| prov | 2 | 0.00000000 | 0.00000000 | 0.00 | 1.0000 |
| spec | 4 | 5.93450566 | 1.48362641 | 368.84 | <.0001 |
| decade*prov | 2 | 0.00000000 | 0.00000000 | 0.00 | 1.0000 |
| prov*spec | 8 | 4.07252443 | 0.50906555 | 126.56 | <.0001 |
| decade*spec | 4 | 0.09043341 | 0.02260835 | 5.62 | 0.0003 |
| decade*prov*spec | 8 | 0.11284648 | 0.01410581 | 3.51 | 0.0009 |
| stand(prov) | 43 | 0.00000000 | 0.00000000 | 0.00 | 1.0000 |
| spec*stand(prov) | 172 | 8.70771725 | 0.05062626 | 12.59 | <.0001 |
| decade*stand(prov) | 43 | 0.00000000 | 0.00000000 | 0.00 | 1.0000 |

Table 17: Analysis of variance output for pre harvest to 4th decade comparisons of relative basal area

RBA ANOVA- Pre to 4th
The GLM Procedure

Dependent Variable: rba rba

| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
|-----------------|-----|----------------|-------------|---------|--------|
| Model | 188 | 20.20379230 | 0.10746698 | 4.05 | <.0001 |
| Error | 84 | 2.22983134 | 0.02654561 | | |
| Corrected Total | 272 | 22.43362364 | | | |

| R-Square | Coeff Var | Root MSE | rba Mean |
|----------|-----------|----------|----------|
| 0.900603 | 48.87847 | 0.162928 | 0.333333 |

| Source | DF | Type I SS | Mean Square | F Value | Pr > F |
|--------------------|----|------------|-------------|---------|--------|
| decade | 1 | 0.00000000 | 0.00000000 | 0.00 | 1.0000 |
| prov | 2 | 0.00000000 | 0.00000000 | 0.00 | 1.0000 |
| spec | 2 | 8.08528729 | 4.04264364 | 152.29 | <.0001 |
| decade*prov | 2 | 0.00000000 | 0.00000000 | 0.00 | 1.0000 |
| prov*spec | 4 | 1.35150715 | 0.33787679 | 12.73 | <.0001 |
| decade*spec | 2 | 7.02323244 | 3.51161622 | 132.29 | <.0001 |
| decade*prov*spec | 4 | 0.63050555 | 0.15762639 | 5.94 | 0.0003 |
| stand(prov) | 43 | 0.00000000 | 0.00000000 | 0.00 | 1.0000 |
| spec*stand(prov) | 86 | 3.11325987 | 0.03620070 | 1.36 | 0.0776 |
| decade*stand(prov) | 42 | 0.00000000 | 0.00000000 | 0.00 | 1.0000 |

| Source | DF | Type III SS | Mean Square | F Value | Pr > F |
|--------------------|----|-------------|-------------|---------|--------|
| decade | 1 | 0.00000000 | 0.00000000 | 0.00 | 1.0000 |
| prov | 2 | 0.00000000 | 0.00000000 | 0.00 | 1.0000 |
| spec | 2 | 5.89581434 | 2.94790717 | 111.05 | <.0001 |
| decade*prov | 2 | 0.00000000 | 0.00000000 | 0.00 | 1.0000 |
| prov*spec | 4 | 1.32749330 | 0.33187332 | 12.50 | <.0001 |
| decade*spec | 2 | 5.66626601 | 2.83313301 | 106.73 | <.0001 |
| decade*prov*spec | 4 | 0.64414218 | 0.16103555 | 6.07 | 0.0002 |
| stand(prov) | 43 | 0.00000000 | 0.00000000 | 0.00 | 1.0000 |
| spec*stand(prov) | 86 | 3.11325987 | 0.03620070 | 1.36 | 0.0776 |
| decade*stand(prov) | 42 | 0.00000000 | 0.00000000 | 0.00 | 1.0000 |

Table 18: Analysis of variance output for 3rd to 4th decade comparisons of stocking

Stocking ANOVA- 3rd to 4th

The GLM Procedure

Dependent Variable: stock stock

| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
|-----------------|-----|----------------|-------------|---------|--------|
| Model | 287 | 27.80343875 | 0.09687609 | 14.85 | <.0001 |
| Error | 172 | 1.12171036 | 0.00652157 | | |
| Corrected Total | 459 | 28.92514911 | | | |

| R-Square | Coeff Var | Root MSE | stock Mean |
|----------|-----------|----------|------------|
| 0.961220 | 34.18481 | 0.080756 | 0.236234 |

| Source | DF | Type I SS | Mean Square | F Value | Pr > F |
|--------------------|-----|-------------|-------------|---------|--------|
| decade | 1 | 0.16140954 | 0.16140954 | 24.75 | <.0001 |
| prov | 2 | 0.06292096 | 0.03146048 | 4.82 | 0.0092 |
| spec | 4 | 10.29971853 | 2.57492963 | 394.83 | <.0001 |
| decade*prov | 2 | 0.02349733 | 0.01174867 | 1.80 | 0.1681 |
| prov*spec | 8 | 4.63365307 | 0.57920663 | 88.81 | <.0001 |
| decade*spec | 4 | 0.12367380 | 0.03091845 | 4.74 | 0.0012 |
| decade*prov*spec | 8 | 0.14405537 | 0.01800692 | 2.76 | 0.0068 |
| stand(prov) | 43 | 0.35247012 | 0.00819698 | 1.26 | 0.1550 |
| spec*stand(prov) | 172 | 11.81787808 | 0.06870859 | 10.54 | <.0001 |
| decade*stand(prov) | 43 | 0.18416195 | 0.00428284 | 0.66 | 0.9471 |

| Source | DF | Type III SS | Mean Square | F Value | Pr > F |
|--------------------|-----|-------------|-------------|---------|--------|
| decade | 1 | 0.17477798 | 0.17477798 | 26.80 | <.0001 |
| prov | 2 | 0.06292096 | 0.03146048 | 4.82 | 0.0092 |
| spec | 4 | 8.74833912 | 2.18708478 | 335.36 | <.0001 |
| decade*prov | 2 | 0.02349733 | 0.01174867 | 1.80 | 0.1681 |
| prov*spec | 8 | 4.63365307 | 0.57920663 | 88.81 | <.0001 |
| decade*spec | 4 | 0.07789850 | 0.01947463 | 2.99 | 0.0205 |
| decade*prov*spec | 8 | 0.14405537 | 0.01800692 | 2.76 | 0.0068 |
| stand(prov) | 43 | 0.35247012 | 0.00819698 | 1.26 | 0.1550 |
| spec*stand(prov) | 172 | 11.81787808 | 0.06870859 | 10.54 | <.0001 |
| decade*stand(prov) | 43 | 0.18416195 | 0.00428284 | 0.66 | 0.9471 |

Table 19: Analysis of variance output for pre harvest to 4th decade comparisons of stocking

Stocking ANOVA- Pre to 4th

The GLM Procedure

Dependent Variable: stock stock

| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
|-----------------|-----|----------------|-------------|---------|--------|
| Model | 286 | 25.92503057 | 0.09064696 | 4.00 | <.0001 |
| Error | 168 | 3.80635526 | 0.02265688 | | |
| Corrected Total | 454 | 29.73138583 | | | |

| R-Square | Coeff Var | Root MSE | stock Mean |
|----------|-----------|----------|------------|
| 0.871975 | 73.13737 | 0.150522 | 0.205807 |

| Source | DF | Type I SS | Mean Square | F Value | Pr > F |
|--------------------|-----|-------------|-------------|---------|--------|
| decade | 1 | 1.12399681 | 1.12399681 | 49.61 | <.0001 |
| prov | 2 | 0.07299984 | 0.03649992 | 1.61 | 0.2028 |
| spec | 4 | 12.99496451 | 3.24874113 | 143.39 | <.0001 |
| decade*prov | 2 | 0.04544024 | 0.02272012 | 1.00 | 0.3690 |
| prov*spec | 8 | 3.51211401 | 0.43901425 | 19.38 | <.0001 |
| decade*spec | 4 | 3.10013765 | 0.77503441 | 34.21 | <.0001 |
| decade*prov*spec | 8 | 0.51511488 | 0.06438936 | 2.84 | 0.0055 |
| stand(prov) | 43 | 0.16997313 | 0.00395286 | 0.17 | 1.0000 |
| spec*stand(prov) | 172 | 4.20070473 | 0.02442270 | 1.08 | 0.3129 |
| decade*stand(prov) | 42 | 0.18958477 | 0.00451392 | 0.20 | 1.0000 |

| Source | DF | Type III SS | Mean Square | F Value | Pr > F |
|--------------------|-----|-------------|-------------|---------|--------|
| decade | 1 | 1.04182349 | 1.04182349 | 45.98 | <.0001 |
| prov | 2 | 0.07253799 | 0.03626900 | 1.60 | 0.2048 |
| spec | 4 | 8.87449320 | 2.21862330 | 97.92 | <.0001 |
| decade*prov | 2 | 0.04243848 | 0.02121924 | 0.94 | 0.3940 |
| prov*spec | 8 | 3.48505010 | 0.43563126 | 19.23 | <.0001 |
| decade*spec | 4 | 2.22556454 | 0.55639113 | 24.56 | <.0001 |
| decade*prov*spec | 8 | 0.53398924 | 0.06674865 | 2.95 | 0.0042 |
| stand(prov) | 43 | 0.16997313 | 0.00395286 | 0.17 | 1.0000 |
| spec*stand(prov) | 172 | 4.20070473 | 0.02442270 | 1.08 | 0.3129 |
| decade*stand(prov) | 42 | 0.18958477 | 0.00451392 | 0.20 | 1.0000 |

Table 20: Analysis of variance output for 3rd to 4th decade comparisons of quadratic mean diameter

QMD ANOVA- 3rd to 4th

The GLM Procedure

Dependent Variable: qmd qmd

| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
|-----------------|-----|----------------|-------------|---------|--------|
| Model | 255 | 1819.877883 | 7.136776 | 6.93 | <.0001 |
| Error | 138 | 142.048434 | 1.029336 | | |
| Corrected Total | 393 | 1961.926317 | | | |

| R-Square | Coeff Var | Root MSE | qmd Mean |
|----------|-----------|----------|----------|
| 0.927597 | 20.38016 | 1.014562 | 4.978186 |

| Source | DF | Type I SS | Mean Square | F Value | Pr > F |
|--------------------|-----|-------------|-------------|---------|--------|
| decade | 1 | 318.7998062 | 318.7998062 | 309.71 | <.0001 |
| prov | 2 | 55.5824959 | 27.7912479 | 27.00 | <.0001 |
| spec | 4 | 279.4481278 | 69.8620320 | 67.87 | <.0001 |
| decade*prov | 2 | 4.3228833 | 2.1614416 | 2.10 | 0.1264 |
| prov*spec | 8 | 45.0404327 | 5.6300541 | 5.47 | <.0001 |
| decade*spec | 4 | 18.8675613 | 4.7168903 | 4.58 | 0.0017 |
| decade*prov*spec | 8 | 14.2305973 | 1.7788247 | 1.73 | 0.0970 |
| stand(prov) | 43 | 445.0132806 | 10.3491461 | 10.05 | <.0001 |
| spec*stand(prov) | 140 | 501.4843081 | 3.5820308 | 3.48 | <.0001 |
| decade*stand(prov) | 43 | 137.0883896 | 3.1881021 | 3.10 | <.0001 |

| Source | DF | Type III SS | Mean Square | F Value | Pr > F |
|--------------------|-----|-------------|-------------|---------|--------|
| decade | 1 | 175.6693727 | 175.6693727 | 170.66 | <.0001 |
| prov | 2 | 47.9275463 | 23.9637732 | 23.28 | <.0001 |
| spec | 4 | 213.8889907 | 53.4722477 | 51.95 | <.0001 |
| decade*prov | 2 | 3.8435062 | 1.9217531 | 1.87 | 0.1585 |
| prov*spec | 8 | 42.2464687 | 5.2808086 | 5.13 | <.0001 |
| decade*spec | 4 | 14.8535522 | 3.7133881 | 3.61 | 0.0079 |
| decade*prov*spec | 8 | 5.5820569 | 0.6977571 | 0.68 | 0.7104 |
| stand(prov) | 43 | 445.0562015 | 10.3501442 | 10.06 | <.0001 |
| spec*stand(prov) | 140 | 491.6517811 | 3.5117984 | 3.41 | <.0001 |
| decade*stand(prov) | 43 | 137.0883896 | 3.1881021 | 3.10 | <.0001 |

Table 21: Analysis of variance output for 3rd to 4th decade comparisons of canopy classifications

Canopy class ANOVA- 3rd to 4th

The GLM Procedure

Dependent Variable: percent percent

| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
|-----------------|-----|----------------|-------------|---------|--------|
| Model | 268 | 23.17897492 | 0.08648871 | 9.93 | <.0001 |
| Error | 135 | 1.17599571 | 0.00871108 | | |
| Corrected Total | 403 | 24.35497062 | | | |

| R-Square | Coeff Var | Root MSE | percent Mean |
|----------|-----------|----------|--------------|
| 0.951714 | 40.98543 | 0.093333 | 0.227723 |

| Source | DF | Type I SS | Mean Square | F Value | Pr > F |
|--------------------|-----|------------|-------------|---------|--------|
| decade | 1 | 0.01284392 | 0.01284392 | 1.47 | 0.2268 |
| prov | 2 | 0.05092359 | 0.02546179 | 2.92 | 0.0572 |
| spec | 4 | 7.03709730 | 1.75927433 | 201.96 | <.0001 |
| decade*prov | 2 | 0.00228918 | 0.00114459 | 0.13 | 0.8770 |
| prov*spec | 8 | 5.70456623 | 0.71307078 | 81.86 | <.0001 |
| decade*spec | 4 | 0.21097063 | 0.05274266 | 6.05 | 0.0002 |
| decade*prov*spec | 8 | 0.17260901 | 0.02157613 | 2.48 | 0.0154 |
| stand(prov) | 43 | 0.15163855 | 0.00352648 | 0.40 | 0.9995 |
| spec*stand(prov) | 153 | 9.79516294 | 0.06402067 | 7.35 | <.0001 |
| decade*stand(prov) | 43 | 0.04087357 | 0.00095055 | 0.11 | 1.0000 |

| Source | DF | Type III SS | Mean Square | F Value | Pr > F |
|--------------------|-----|-------------|-------------|---------|--------|
| decade | 1 | 0.03357552 | 0.03357552 | 3.85 | 0.0517 |
| prov | 2 | 0.00003202 | 0.00001601 | 0.00 | 0.9982 |
| spec | 4 | 5.56636027 | 1.39159007 | 159.75 | <.0001 |
| decade*prov | 2 | 0.04680654 | 0.02340327 | 2.69 | 0.0718 |
| prov*spec | 8 | 5.60806479 | 0.70100810 | 80.47 | <.0001 |
| decade*spec | 4 | 0.32145246 | 0.08036312 | 9.23 | <.0001 |
| decade*prov*spec | 8 | 0.30108030 | 0.03763504 | 4.32 | 0.0001 |
| stand(prov) | 43 | 0.17888224 | 0.00416005 | 0.48 | 0.9969 |
| spec*stand(prov) | 153 | 9.77626842 | 0.06389718 | 7.34 | <.0001 |
| decade*stand(prov) | 43 | 0.04087357 | 0.00095055 | 0.11 | 1.0000 |