REGENERATING OAK DOMINATED STANDS:
DESCRIPTIONS, PREDICTIVE MODELS, AND GUIDELINES

A Thesis in
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by
Peter Jay Gould

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The thesis of Peter Jay Gould was reviewed and approved* by the following:

Kim C. Steiner  
Professor of Forest Biology  
Thesis Advisor  
Chair of Committee

James C. Finley  
Professor of Forest Resources

Marc E. McDill  
Associate Professor of Forest Management

Alan H. Taylor  
Professor of Geography

Susan L. Stout  
Adjunct Professor of Forest Resources

Charles H. Strauss  
Professor of Forest Economics  
Director of the School of Forest Resources

*Signatures are on file in the Graduate School
ABSTRACT

Regenerating oak-dominated forests is a major challenge faced by forest managers in the eastern United States. Even-aged silvicultural systems are considered the best systems for regenerating oaks, but in the central Appalachians (and elsewhere) oaks are nevertheless often replaced by other species after timber harvests. The present work addresses several aspects of the oak regeneration problem. The post-harvest development of 90 formerly oak-dominated stands (> 50 percent oak before harvest) is described in terms of "developmental pathways." The developmental pathways link stand conditions around the time of harvest to stand compositions and forest structures in the "third decade" (20 - 32 yrs) following harvest. Pathways were described by first identifying four outcome classes (based on third-decade compositions) using cluster analysis. Differences between outcome classes in stand compositions before harvest (overstory and advance regeneration compositions) and two years after harvest were then identified. Of the four pathways, only the OAK pathway resulted in the regeneration of oak-dominated stands. The loss of oak dominance in the other pathways corresponded with poor oak regeneration potential at the time of harvest. The RED MAPLE pathway featured a rapid post-harvest transition to dominance by red maple (*Acer rubrum* L.), a shade-tolerant species that established as advance regeneration in the pre-harvest stands. Stand compositions in the MIXED pathway changed markedly after harvest with the establishment of black birch (*Betula lenta* L.) and other pioneer species. Regeneration failure occurred in the UNSTOCKED pathway, which featured pre-harvest mortality and a post-harvest loss of regeneration. The pathways reflect several ecological models of forest succession. More importantly, they highlight the importance of stand conditions around the time of harvest to subsequent development.

Models are presented to measure oak regeneration potential, expressed as expected third-decade oak stocking (i.e., the percentage of growing space occupied by oaks in the third decade after harvest). The models were created primarily using a long-term dataset developed from operational data collected in the course of timber sales, and a short-term research dataset collected as part of an on-going project examining
regeneration development in Pennsylvania. A plot-level model was developed to measure the regeneration potential of advance oak regeneration sampled on milacre plots. The model uses plot aggregate height, the sum of oak seedling heights, to estimate the probability that an oak will occupy the plot in the third decade after harvest. Inverse modeling was employed to fit the plot-level model using both the long-term and short-term datasets. A second model estimates the contribution of oak stump sprouts to third-decade oak stocking, based on the species and diameter of parent trees.

The two models are incorporated into comprehensive guidelines designed to aid forest managers in the regeneration of oaks. The guidelines recommend regeneration prescriptions based on management goals, expected third-decade oak stocking, and other stand conditions. Decision charts to assign prescriptions were developed using expert opinion and emerging information. Overstory removals are recommended when the current oak regeneration potential is adequate to meet management goals. When the current potential is lacking, treatments are to improve the seed-origin regeneration potential are recommended.

The effects of competition on the development of individual oak seedlings following clearcutting are evaluated to test whether competition terms can significantly improve individual tree regeneration models. Current oak regeneration models do not explicitly consider competitive effects when predicting oak regeneration development. An unusual dataset from the Missouri Ozarks that tracks 405 naturally-established oak seedlings from before harvest to about 20 yrs after harvest was used. Models were fit to predict 20-yr success (reaching a dominant or codominant crown class) based on pre-harvest seedling height (size model) and pre-harvest height plus an index of local competition (competition model). The competition model produced predictions that better matched observations across a range of competitive conditions. The results suggest that including competition terms can significantly improve future oak regeneration models.
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Chapter 1

Introduction: Oak Silviculture and Research Needs

Forest regeneration is arguably the single most important aspect of sustainable forest management. Forests are renewable natural resources only because they have the capacity to regenerate and produce usable materials within a reasonable time period. The level of investment in regeneration is a key factor in formulating a silvicultural system (Smith et al. 1997). In more intensive silvicultural systems, the regeneration process is carefully controlled and often includes site preparation to eliminate or reduce competitors, followed by artificial regeneration to establish highly uniform new stands. Less intensive silvicultural systems typically rely on natural regeneration and exert much less control on the regeneration process (Nyland 2002). In these situations, the regeneration process more closely resembles what would occur following a natural disturbance and a wider range of ecological factors influences outcomes, which can greatly vary.

Oak-dominated forests in the eastern United States are often managed under low-intensity silvicultural systems that rely on natural regeneration to restock harvested stands (Rogers et al. 1993). Even-aged regeneration methods are typically employed. Many of today's oak stands initiated within a relatively short period following industrial logging around the end of the 19th century and through the beginning of the 20th century. Maturing stands were often selectively harvested as some individual trees reached commercial size. Forest managers soon realized the difficulty of perpetuating moderately shade-tolerant oaks under selective harvesting, which favors more tolerant associated species. The adoption of even-aged regeneration methods was spurred, in part, by this dissatisfaction with regeneration under the selection method (Roach and Gingrich 1968). Although even-aged regeneration methods likely provide the best opportunities for regenerating oaks, they are often not successful and oak regeneration is a major concern in the eastern United States (Lorimer 1993).
The commonwealth of Pennsylvania sits on the ecotone between oak-dominated forests and northern hardwood forests (Bailey 1995). Oak forests occupy about one-half of Pennsylvania's forestland (Alerich 1993) and are common throughout the central Appalachians. Given the importance of oaks in the region and their uncertain prospects for regeneration, there is a critical need for research in this area. This dissertation focuses on several aspects of oak regeneration. Chapter 2 is a descriptive study examining outcomes to complete overstory removals in 90 oak-dominated stands on Pennsylvania State Forest lands. Even-aged management was adopted by the Pennsylvania Department of Land and Water (the precursor of today's Bureau of Forestry) in 1965 (Hench 1970). Stands in the study were harvested as part of a "first wave" of even-aged regeneration treatments on State Forest lands. Outcomes of these treatments, and how they relate to conditions before and just after harvest, have not been thoroughly examined. In this study, outcomes are related to earlier conditions by identifying and describing "developmental pathways."

Chapters 3, 4, and 5 describe the development of regeneration guidelines for central Appalachian oak forests. The regeneration guidelines were developed to be an easy-to-use tool for measuring regeneration potential in advance of harvest and identifying appropriate treatments when regeneration is found to be lacking. Essential to the guidelines are methods for assessing oak regeneration potential in advance of harvest. Simple, research-based models were developed to estimate seed-origin and sprout-origin regeneration potentials. Models were constructed using several datasets describing oak regeneration development in Pennsylvania. The guidelines employ the models to estimate oak regeneration potential and then rely on expert opinion and emerging information to assign treatments. Model development is described in Chapters 3 and 4. The regeneration guidelines are described in Chapter 5 and presented in Chapter 6. Note that SI units are used in all chapters except Chapters 5 and 6. Chapters 5 and 6 are written for an audience that routinely employs English units (i.e., inches, feet, etc.). Other chapters are intended for publication in scientific journals where SI units are standard.
Chapter 7 addresses the influence of competition on the development of individual oak stems. Individual stem success models, which assign a probability of success to individual stems based on their pre-harvest attributes, have been developed to predict oak regeneration development following clearcutting (Sander et al. 1984, Loftis 1990). However, the influence of competition has not been directly addressed. The study uses the best longitudinal dataset in existence to examine the influence of competition on individual stem success. The data track about 400 stems of advance oak regeneration in the Missouri Ozarks from before harvest to 20 yrs after harvest. This period of stand development is poorly understood and the results of the study contribute to a more informed conceptual model of early stand development.

In total, this work provides much needed information concerning the status of oak regeneration in the central Appalachians. Furthermore, the ideas and methodologies presented here can be applied to other forest types. Silvicultural systems that rely on natural regeneration are practiced throughout the world. These systems share similar challenges -- securing adequate regeneration, maintaining desirable species, and making outcomes more predictable. Research to address these challenges elsewhere can benefit from the present work.

The following pages are intended to provide a general description of factors shaping contemporary oak forests in the eastern United States. Subsequent chapters review literature relevant to their individual topics.

History of Eastern Oak Forests

The oldest known oak, or oak-like, megafossils date to the Late Cretaceous period (70 - 65 mya) (Arnold 1947: pg 361, Axelrod 1983). Early megafossil remains are sparse in the eastern United States and the best-preserved communities are in the West. Remnants of a forest community containing oaks are preserved in the Fort Union formation in the northern Rocky Mountains, which dates to the Paleocene epoch (65 - 56 mya) of the Tertiary period (Graham 1999: pg 164). Interestingly, the community is composed of both modern temperate genera (Betula, Castanea, Ulmus) and extirpated
groups, some of which are tropical (palms, araucarias) or found only in Asia (*Ginkgo, Metasequoia*). The community appears to have occurred at the northern margin of the tropical forests that occupied much of North America and were expanding northward as temperatures increased (Graham 1999: pg. 165). Specimens for *Quercus* sections *Leucobalanus* and *Erythrobalanus* appear in fossil beds dated to the late Eocene (35 mya) (Axelrod 1983), demonstrating the ancient origins of these lineages.

The development of extensive oak-dominated forests in the eastern United States coincided with the acceleration of a long-term shift towards a cooler and more arid climate during the middle Miocene (15 mya). Modern temperate forests containing oaks became more common first in the northeast and then spread south as tropical and exotic genera disappeared (Graham 1999: pg 246). Eastern vegetation was modernized, in the sense that now extinct genera had essentially disappeared and extant genera were present, by the beginning of the Pliocene (5 mya) (Graham 1999: pg. 268).

Quaternary glaciations radically and repeatedly altered distributions and probably promoted speciation within North American oaks. Successive glacial advances erased much of the evidence from previous Quaternary glaciations, so most evidence of vegetation response is from the most recent (Wisconsin) glacial period (Graham 1999: pg 281). Cooling climates and advancing glaciers pushed eastern temperate tree species southward and possibly into more moderate coastal refugia. The Wisconsin glaciation reached about 40° N around 18 kya and then began to melt and retreat. According to palynological evidence, oaks were restricted to the southeastern United States (below 33° N) during full glaciation, where they were part of a mixed broadleaf community (Delcourt and Delcourt 1987). As the climate warmed, oaks expanded northward and reached their current northern distribution by about 6 kya. The importance of oaks later decreased in the southeast as they were displaced by southern pines (Delcourt and Delcourt 1987). Farther north, oak importance appears to have been fairly stable at a regional scale over the past 6000 yrs (Delcourt and Delcourt 1987).

The warming Holocene climate coincided with an increase in fire frequency in the eastern United States (Clark et al. 1996). Human impacts, often through fire (Pyne 1983), also became more important at this time. Fire is widely viewed as a key factor
that promoted and maintained oak dominance into the modern era (Abrams 1992). The Holocene climate of the past 12,000 yrs has not been stable, and a hypsithermal period, featuring a warmer and more arid climate than today, occurred between 8 and 4 kya (Graham 1999: pg 306). Fires became more common during this period in both the western (Graham 1999: pg 306) and eastern United States (Clark et al. 1996). It is intriguing, though speculative, to consider how climatic fluctuations in the recent past have influenced the modern distribution of oaks.

Though Native American practices undoubtedly had manifold impacts on eastern oak forests, Euro-American practices are most evident today. Virtually the entire eastern United States was logged at least once by the early 20th century. At first, logging was localized near settlements and water bodies that provided transportation of felled logs (Abrams 2001). Railroad logging beginning in the late 1800s allowed loggers to reach virtually every part of the region. Harvests then proceeded rapidly. Complete overstory removals over large areas, often followed by wildfires, appear to have created conditions that favored the regeneration of oaks (Abrams 1992, Lorimer 1993), leading to oak dominance in regenerated forests. The loss of the American chestnut (Castanea dentata (Marsh.) Borkh.) and removal of old field eastern white pine (Pinus strobus L.) during the first half of the 20th century further increased the predominance of oak in the region (Oliver 1975, Hibbs 1983, Stephenson 1986). However, conditions that had favored oak regeneration began to change as land use practices shifted in the latter part of the 20th century.

**Contemporary Conditions**

Oak dominance is declining in many contemporary eastern forests. As mature oak die from a variety of causes (e.g. wind, disease, harvesting), they are often replaced by other species (Lorimer 1993). Oak regeneration failures appear somewhat incongruous given the predominance of oaks in contemporary overstories. However, the conditions that promoted extensive oak regeneration following turn-of-the-century logging have changed markedly. Oak dominance in some pre-settlement forests appears
to have been perpetuated by a regime of frequent, low- to moderate-intensity fires, which
worked to exclude regeneration of less fire-tolerant species (Abrams 1992). Effective
fires suppression in the eastern United States was a major achievement of the
conservation organizations that emerged around the turn of the century. Wildfires, which
appear to have promoted oak dominance in the past, are now relatively rare in much of
the region. Many white-tailed deer populations were decimated by market hunting prior
to the logging era, which allowed forests to regenerate without intense browsing. Deer
populations have rebounded and are now at historically high levels (McCabe and
McCabe 1984). Deer browsing is now a major obstacle to successful forest regeneration,
particularly in Pennsylania (Jordan 1967, Marquis and Brenneman 1981).

Oak regeneration depends on advance regeneration, which are seedlings that
Contemporary understory conditions influence regeneration establishment and contribute
to the oak regeneration problem. The conversion from oaks to other species begins in
many cases with the establishment of shade-tolerant advance regeneration beneath oak
canopies (Lorimer 1984). Shade-tolerant species, such as red maple (Acer rubrum L.)
and sugar maple (Acer saccharum Marsh.), are often also fire-intolerant, and frequent
fires likely limited their establishment in the past (Huddle and Pallardy 1999). Once
established, shade-tolerant advance regeneration can take advantage of canopy
disturbances and replace oaks (Clinton et al. 1994). Shade cast by these seedlings can
also limit the capacity for oak seedlings to establish and survive in the understory
(Lorimer et al. 1994). Other understory vegetation, such as mountain-laurel (Kalmia
latifolia L.) and hayscented fern (Dennstaedtia punctilobula (Michx.) Moore) has also
expanded due to fire and/or deer browsing and may present a barrier to oak regeneration
(George and Bazzaz 1999, Clinton et al. 1994).

Selective timber harvests, such as diameter-limit cutting, also contribute to the
oak regeneration problem. The selective removal of sawtimber-size trees is a common
practice in the central Appalachians (Fajvan et al. 1998). Most commercial oak species
are intermediate in shade tolerance (Baker 1949). In the central Appalachians, oaks often
grow in mixtures with more shade-tolerant species that are better adapted to regenerate in
the small canopy gaps created by selective harvests (Heiligmann et al. 1985, Jenkins and Parker 1998, Schuler 2004). Selective harvests in oak-dominated stands remove potential seed trees, while creating environmental conditions that promote the regeneration of non-oak species.

In summary, the oak regeneration problem is rooted in a contemporary disturbance regime that is less suitable for oak regeneration than in the past. The contemporary disturbance regime is characterized by a lack of fire, high deer browsing, and low-intensity canopy disturbances. In combination, these factors are promoting a regional shift away from oak-dominated forests. The loss of oak appears to mark a major change in the composition of the forests that developed following the Holocene glacial retreat.
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Chapter 2

Developmental Pathways Following the Harvest of Oak-Dominated Stands

Abstract

The post-harvest development of 90 formerly oak-dominated stands in Pennsylvania was examined to identify developmental pathways that led to a range of stand compositions and structures in the third decade after harvest. Operational data collected through the course of timber sale administration were used to quantify pre-harvest overstory composition and the distribution and composition of advance regeneration and regeneration two years after harvest. Stands were remeasured during their third decade of development. Based on their third-decade compositions, stands were grouped into four distinct classes. The development of each class was then traced by comparing pre-harvest overstory, advance regeneration, and post-harvest regeneration compositions between classes. Stands in the OAK class maintained dominance by oaks throughout stand development, resulting in an average of 83.8 percent oak stocking in the third-decade after harvest. Stands in the MIXED and RED MAPLE classes began with lower levels of advance oak regeneration and lost oak dominance relative to pre-harvest stand compositions. The MIXED class experienced recruitment of pioneer species after harvest, resulting in stands where black birch (*Betula lenta* L.) and other species are important components, despite being poorly represented as advance regeneration. The RED MAPLE class had abundant red maple (*Acer rubrum* L.) advance regeneration and lacked post-harvest recruitment of oaks or pioneer species, leading to the development of red maple-dominated stands. Stands in the UNSTOCKED class suffered pre-harvest mortality and regeneration (primarily red maple) declined after harvest, resulting in regeneration failures. The four developmental pathways demonstrate the importance of specific stand conditions at the time of harvest and, to a lesser extent, just after harvest to future stand development.
Introduction

Regenerating oak-dominated forests is a major challenge facing forest managers in the eastern United States (Lorimer 1993). Many mature oak stands are "second-generation" stands that initiated after a period of extensive logging of presettlement-origin forests (Johnson et al. 2002). Complete overstory removals over large areas, often followed by wildfires, appear to have created conditions that favored the regeneration of oaks (Abrams 1992, Lorimer 1993). The loss of the American chestnut (*Castanea dentata* (Marsh.) Borkh.) and removal of old field eastern white pine (*Pinus strobus* L.) during the first half of the 20th century further increased the predominance of oak in the region (Oliver 1975, Hibbs 1983, Stephenson 1986). However, conditions that favored oak dominance in second-generation forests have changed dramatically, contributing to a regional oak regeneration problem (Lorimer 1993). Partial overstory removals and the exclusion of fire have favored the development of shade-tolerant species that limit the establishment, growth, and survival of oaks (Lorimer 1984, Abrams and Downs 1990, Abrams 1992, de la Cretaz and Kelty 2002). Browsing by white-tailed deer, which have reached historically high population levels in recent decades, reduces the accumulation of advance regeneration of oaks and other species (Jordan 1967, Marquis and Brenneman 1981). Under current conditions, the continued dominance of oaks in eastern forests appears unlikely without intensive management (Abrams 2003, Gould et al. 2003).

A range of outcomes to complete overstory removals in second-generation oak-dominated stands has been reported. Typically, the most desirable outcome is the regeneration of a "third-generation" oak-dominated stand. The self-replacement of oak stands depends in large part on the capacity of advance oak regeneration to capture and retain growing space after harvest (Larsen and Johnson 1998). The potential for oaks to capture growing space has been quantified and incorporated into several oak regeneration models (Sander et al. 1984, Dey et al. 1996). These models predict future oak stocking based on the distribution, density, and size of advance oak regeneration and the expected contribution of stump sprouts. These models predict whether a stand will continue to be occupied by oaks, or its composition will shift towards other species.
Without adequate advance oak regeneration, the composition of oak-dominated stands is likely to change after a stand-replacing disturbance. This change in composition represents one or more alternative outcomes to the self-replacement of oaks. Dominance by pioneer species is an alternative outcome that best follows a Clementsian model of secondary forest succession (Barnes et al. 1998). Under this model of forest succession, one or more pioneer species, which are typically not well represented in the pre-harvest overstory or as advance regeneration, invade the stand after harvest and dominate early stand development. This outcome has been reported in the southern Appalachians where yellow-poplar (*Liriodendron tulipifera* L.) invades and dominates stands after oaks are harvested (Beck and Hooper 1986, Loftis 1990). A similar outcome was reported in New England where paper birch (*Betula papyrifera* L.), pin cherry (*Prunus pensylvanica* L.f.), and black birch (*Betula lenta* L.) invaded an oak stand after harvest and remained dominant through the first three decades of stand development (Liptzin and Ashton 1999). Stand dominance by pioneers, however, may be short lived if even a relatively small number of oaks emerge to form an upper stratum later in stand development (Oliver 1975).

A second alternative outcome may result from “disturbance mediate accelerated succession” (Abrams and Scott 1989). Under this model of succession, advance regeneration of “late-successional” (i.e., more shade-tolerant) species become established under an oak overstory and then quickly captures growing space after harvest. The acceleration of succession from oak to red maple (*Acer rubrum* L.), a more shade-tolerant species, has been hypothesized based on the frequent occurrence of advance red maple regeneration under oak overstories (Lorimer 1984, Abrams and Nowacki 1992). A similar scenario has been reported in Wisconsin where advance sugar maple (*Acer saccharum* Marsh.) regeneration captured growing space released by the harvest of oaks (Hix and Lorimer 1991).

Although the cases cited above offer alternative descriptions of post-harvest stand development, they all underscore the importance of stand conditions around the time of harvest to future development. In a broader context, patterns of stand initiation following
major disturbances are a product of often complex aggregates of stump sprouts, advance regeneration, invading and buried seeds, and competing non-tree vegetation (Oliver and Larson 1996, p. 144). Distinctly different conditions at the onset of stand initiation can set the stage for divergent developmental “pathways” in stands with previously similar composition. The establishment of advance oak regeneration before harvest, for example, sets a stand on a pathway towards self-replacement by oaks. Similarly, advance regeneration of later successional species may result in the loss of oaks and the acceleration of succession after harvest. In both cases, the pre-harvest overstory composition and structure affect the potential contribution of stump sprouts to regeneration and modify the growing environment of advance regeneration (Lorimer et al. 1994, Weigel and Peng 2002). Changes in the understory environment created by harvests or other disturbances may favor the establishment and growth of pioneer and fugitive species (Marks 1974). Growth, competition, and shade tolerance control the composition of the stand as a new forest canopy develops (Oliver 1980).

The purpose of this chapter is to examine developmental pathways leading to a range of outcomes to complete overstory removals in second-growth oak-dominated stands. The concept of pathways of vegetation response to disturbance has been used in ecological studies to contrast observed variability against the deterministic model of Clementsian succession (Abrams et al. 1985, Halpern 1988). The concept is used here to summarize the range of outcomes observed in the third decade following the harvest of 90 second-generation oak-dominated stands in Pennsylvania. Differences in the species composition and regeneration success of these stands was expected to correspond with differences in initial conditions, namely the pre-harvest overstory, advance regeneration, and post-harvest composition of the stands.
Methods

Study Area

The study was conducted in 90 stands covering 6485 acres of Pennsylvania State Forest land (Figure 2.1). The study area spans three physiographic provinces (Cuff et al. 1989). The Appalachian Plateaus province is an uplifted region deeply dissected by stream and river valleys. The Ridge and Valley province is a folded and faulted region characterized by steep, nearly parallel ridges oriented northeast to southwest. Ridges are covered by forest and valleys are primarily under agricultural production. The Blue Ridge province is a single ridge that marks the northern tip of the Blue Ridge, extending from North Carolina into southern Pennsylvania. Soils in our study areas are derived from sandstone, siltstone, and shale and are typically well-drained. Stand elevations range from 300 m above MSL in the Ridge and Valley province to 730 m on the Appalachian Plateaus. Precipitation and frost-free periods vary with elevation and topography. Mean annual precipitation ranges from 965 to 1143 mm and frost-free periods range from 140 to 160 days (Cuff et al. 1989). Oak forests are the dominant natural vegetation in the Ridge and Valley and Blue Ridge provinces. Oak forests transition into Allegheny hardwoods moving from south to north on the Appalachian Plateaus, though oaks continue to be locally dominant (Stout 1991, Bailey et al. 1994). All 90 stands were oak-dominated (>50% basal area in oak) prior to harvest. Although specific histories are unknown, most stands in the region regenerated following turn-of-the-century logging (Stout 2000). Stands were primarily composed of chestnut oak (Quercus prinus L.), white oak (Quercus alba L.), northern red oak (Quercus rubra L.), black oak (Quercus velutina Lam.), scarlet oak (Quercus coccinea Muenchh.), and red maple. All stands were harvested between 1968 and 1978.
Figure 2.1. Locations of the 90 formerly oak-dominated stands included in the study.

Data Collection and Summary

Operational data describing the pre-harvest overstory, advance regeneration composition, and post-harvest regeneration composition were retrieved from timber sale records collected and maintained by individual forest district offices. A stand was included in the analysis if 1) a complete set of records could be located, 2) the stand had >50% basal area in oaks before harvest, and 3) the stand was regenerated by silvicultural clearcutting (all stems > 2" dbh were felled) at least twenty years before the initiation of the study in 2000. Additional effort was made to identify stands in poorly represented portions of the study area to produce a geographically balanced dataset.

Pre-harvest overstory data were collected approximately one year before harvest on ten variable-radius plots using a 2.3 m² ha⁻¹ basal area factor (BAF) prism (Avery and Burkhart 1994, pg 217). Trees that fell within the plots were tallied by species into four size classes: 5.0 to 15.2 cm, 15.3 to 30.5 cm, 30.6 to 40.6 cm, and over 40.6 cm. High levels of mortality caused by oak leaf roller (Archips semiferana Walker) defoliation were noted in 31 stands during the pre-harvest overstory exam. In 26 of these stands, live
and dead basal area were tallied separately, while in the remaining stands, a percentage estimate of mortality was recorded.

Advance regeneration and post-harvest regeneration data were collected using identical data collection protocols. Advance regeneration data were collected approximately one year before harvest and post-harvest regeneration data were collected two growing seasons after harvest. Data were collected on sixty 4.05 m² (1/1000-acre) plots. On each plot, up to three species exhibiting acceptable regeneration were recorded. For a species to be recorded, at least one acceptable stem less than 10.2 cm dbh had to fall on the plot. An acceptable stem was defined as a vigorous stem, at least two years old, which was a competitor for dominance on the plot. In the post-harvest regeneration exam, stump sprouts were considered acceptable stems if they were less than 15.2 cm dbh. The presence or absence of competing vegetation was recorded for each plot, but specific criteria for defining competing vegetation were not recorded.

Stands were re-measured at least twenty years after harvest (mean = 24.3 yrs, range 20 to 32 yrs). Thirty variable-radius plots were measured with a 2.3 BAF prism in stands of 12.1 hectares or more and one plot was measured for each 0.4 hectares in stands of less than 12.1 hectares. A minimum of 10 plots was measured per stand. The diameters of “in” trees were measured to the nearest 2.5 cm and crown classes were recorded (Smith et al. 1997). Data collected at this point in stand development are hereafter referred to as “third-decade data” to reflect the range of ages of the sampled stands.

The importance of each individual species was summarized in each measurement period by calculating measures of stand-level stocking (Gingrich 1967). Stocking was selected for two reasons. First, it allows for a conceptual connection, based on the occupation of area, between advance regeneration, regeneration shortly after harvest, and overstory trees. When a 100-percent-stocked upland oak stand on a medium quality site reaches the age of 20 years, the average tree occupies approximately 4.05 m² of stand area (Sander 1977). Therefore, a successful stem of advance or post-harvest regeneration that is measured on a 4.05 m² plot is expected to fully occupy that area at a stand age of 20. Second, Gingrich’s stocking diagram provides a threshold for objectively identifying
understocked stands. Stands that fall below the B-line have area unoccupied by trees (Gingrich 1967). This property of stocking was used to quantify the effect of mortality before harvest and the failure to reach a closed-canopy condition in the third decade after harvest.

Pre-harvest and third-decade stocking were calculated for live trees by species for each stand using Gingrich’s (1967) stocking equation for upland oak stands. Stocking is a robust measure of species importance across a wide range of size and age classes (Gingrich 1967). To apply this equation, estimates of density by diameter class are needed. For the third-decade data, densities were calculated from diameter measurements based on variable plot radii (Avery and Burkhart 1994, pg 221). For the pre-harvest data, where trees were tallied into four size classes, diameters were set at the midpoints of the three size classes with both upper and lower bounds, and densities were calculated using the same method as for the third-decade data. For the largest size class (> 40.6 cm), the diameter was set at 45.7 cm. While this selection of diameter was arbitrary, it had little influence on the calculation of pre-harvest stocking due to the negative relationship between size and density estimates on variable radius plots (Avery and Burkhardt 1994). Increasing the upper diameter produced an approximately compensatory decline in density (and vice-versa), resulting in little net change in stocking. In stands where a percentage estimate of mortality was recorded, but live and dead trees were not tallied separately, the stocking of each species was reduced by the mortality estimate.

An open condition was calculated in addition to stocking. A stand was considered to have open area if stocking by all species failed to reach the B-line (57 percent of maximum stocking) of Gingrich’s stocking diagram. The difference between total observed stocking and 57 percent stocking was used to quantify openness in stands that fell below the B-line in stocking (stands without any trees = 57 percent “open”). Advance regeneration and post-harvest regeneration stocking were calculated for each stand, by species, as the percentage of sample plots where the species was observed. If multiple species were observed on a plot, all species were considered equally likely to fully occupy the plot; thus stocking by all species could sum to 300 percent. This
approach was used to reflect the uncertainty associated with a lack of information on the density and size of regeneration (Rogers and Johnson 1998). Stocking by any oak species was calculated as the percentage of plots where any oak species was recorded. The percentage of plots that lacked regeneration of any species was calculated as the “open” condition, indicating a lack of stocking. The percentage of plots with competing vegetation (presence / absence) before and after harvest was calculated for each stand. The data developed from the pre-harvest overstory, advance regeneration, post-harvest regeneration, and third-decade data consisted of a set of four stocking values for 48 species in 90 stands. The data represent a developmental sequence where one generation of trees was harvested, advance and post-harvest regeneration were released, and new forest stands developed.

Data Analysis

The ten most common species in the third-decade stands were identified based on the proportion of stands in which they occurred. The data for each stand was summarized to include stocking by the 10 most common species, the open condition, and an “other” category – total stocking by the less common species. Further analysis was based on these 12 variables.

Developmental pathways were identified by grouping stands with similar third-decade compositions and retracing the development of these groups. Grouping was done with cluster analysis using Ward’s hierarchical clustering method. Ward’s method groups observations into clusters with a minimum square error between the observations and cluster means (Ward 1963). Computations were done using the CLUSTER procedure in SAS version 8.02 (SAS Institute 1999).

Mean stocking levels of the 10 most common species, the five common oak species combined, other species, and the open condition were calculated for each group and measurement period. Analysis of variance could not be used for means separation due to heterogeneity of variances that persisted after transformations were applied to the data (Neter et al. 1996, pg 763). Instead, means were separated using a series of two-
sample t-tests, corrected as necessary for non-homogenous variances (Ott 1993, pg 340). The family-wide error rate for multiple comparisons between pathways was held at $\alpha = 0.05$ for each set of comparisons using a Bonferroni correction (Neter et al. 1996, pg 736).

Analysis of variance was used to test for differences between groups in the percentage of plots with competing vegetation. The percentage of plots with competing vegetation was first calculated at the stand level, and each stand was then considered an observation. Means were separated using Tukey’s studentized range test (Neter et al. 1996, pg 725).

Differences between developmental pathways were illustrated by creating a two-dimensional plot of the multidimensional developmental pathways. Detrended correspondence analysis (DCA) was used to summarize the high-dimensional data (12 variables) in two-dimensional space (Hill and Gauch 1980). DCA, like other ordination techniques, is designed to project high dimensional data onto a lower dimensional space while minimizing distortion between observations (Johnson and Wichern 1999, pg 761). DCA is superior to other ordination techniques (e.g., principal components analysis), in that it removes distortion caused by the “arching” of axes and simultaneously fits sites into species space and species into site space (Gauch 1989, pg 152, Peet et al. 1988). DCA coordinates were calculated for each of the 90 stands in each of the four time periods ($n = 360$ observations). Mean values of the first two DCA axes were calculated by third-decade cluster to yield four pairs of coordinates for each pathway (representing, respectively, the mean species composition of the pre-harvest overstory, advance regeneration, post-harvest regeneration, and third-decade overstory). Computations were done using DECORANA (Hill 1979) implemented in the R programming environment (Ihaka and Gentlemen 1996).
Results

Data Summary

The data were summarized to include stocking by the 10 species most commonly observed in the third-decade stands, the total stocking of the less common species (OTHER), and an open condition (UNSTOCKED) (Table 2.1). Red maple and black birch were the most common non-oak species in the regenerated stands (88.9 and 63.3 percent of stands, respectively) and red maple had the highest mean stocking in the stands where it occurred of any species (34.7 percent). Among oaks, chestnut oak was the most common (63.3 percent of stands) and had the greatest mean stocking (19.2 percent) in stands where it was present. Northern red oak (62.2 percent of stands), black oak (55.6 percent), scarlet oak (48.9 percent), and white oak (38.9 percent) were common species, but individually had less than 10 percent stocking in the stands where they occurred. Black cherry (*Prunus serotina* Ehrh.) (47.8 percent of stands), hickories (*Carya* spp.) (44.4 percent of stands), and blackgum (*Nyssa sylvatica* Marsh.) (36.7 percent of stands) were the other common species. Less common species were widespread, occurring in 84.4 percent of stands, where they averaged 14.4 percent stocking. Eastern white pine, black locust (*Robinia pseudoacacia* L.), striped maple (*Acer pensylvanicum* L.), sassafras (*Sassafras albidum* (Nutt.) Nees), and yellow-poplar were the most important of the less common species. Stands that were understocked (28.9 percent) had 42.6 percent open area indicating that these stands were severely understocked.

Identification of Outcome Classes

Third-decade stands clustered into four rather well-defined groups, which together accounted for 67 percent of the total variation in stand compositions (Figure 2.2). Clustering the stands into three groups would have shifted an additional 11 percent of the total variation from between groups to within groups.
Table 2.1. Frequency of occurrence (percentage of stands) and mean stocking of common species in 90 formerly oak-dominated stands during the third-decade after harvest. Stocking by less common species (Others) and unstocked area (Open) are included.

<table>
<thead>
<tr>
<th>Species</th>
<th>Frequency (percent)</th>
<th>Stocking¹ (percent)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer rubrum</td>
<td>88.9</td>
<td>34.7</td>
</tr>
<tr>
<td>Quercus prinus</td>
<td>63.3</td>
<td>19.2</td>
</tr>
<tr>
<td>Betula lenta</td>
<td>63.3</td>
<td>14.7</td>
</tr>
<tr>
<td>Querus rubra</td>
<td>62.2</td>
<td>6.9</td>
</tr>
<tr>
<td>Quercus velutina</td>
<td>55.6</td>
<td>4.9</td>
</tr>
<tr>
<td>Quercus coccinea</td>
<td>48.9</td>
<td>4.9</td>
</tr>
<tr>
<td>Prunus serotina</td>
<td>47.8</td>
<td>6.0</td>
</tr>
<tr>
<td>Carya spp.</td>
<td>44.4</td>
<td>7.0</td>
</tr>
<tr>
<td>Quercus alba</td>
<td>38.9</td>
<td>1.9</td>
</tr>
<tr>
<td>Nyssa sylvatica</td>
<td>36.7</td>
<td>2.7</td>
</tr>
<tr>
<td>Others</td>
<td>84.4</td>
<td>14.5</td>
</tr>
<tr>
<td>Open</td>
<td>28.9</td>
<td>42.6</td>
</tr>
</tbody>
</table>

¹Mean stocking among stands where the species or stand condition occurred.

Figure 2.2. Dendrogram of cluster analysis on third-decade species compositions in 90 formerly oak-dominated stands. Names reflect dominant stand compositions (see text).
Due to the wide range of ages at which third-decade stands were measured, differences in stand age between groups were examined. Mean group ages ranged from 24.0 to 24.9 yrs. Analysis of variance failed to detect a significant difference in mean age between groups (F = 0.51, p = 0.67). These results suggest stand age did not influence stand composition or the grouping of stands.

Third-decade compositions of the four groups of stands are shown in Table 2.2. The groups represent four distinct classes of outcomes to regeneration harvest in oak stands. The OAK class consists of stands with the highest mean levels of oak stocking (83.8 percent) and chestnut oak stocking (54.9 percent). Chestnut oak was the most important oak species in these stands, with five to ten times more stocking than the other individual oak species. Average stocking levels of oaks other than chestnut oak were greatest in stands in the OAK class, but differences between classes were not statistically significant.

As a group, the stands in the MIXED class lacked a clearly dominant species in the third-decade after harvest, but had significantly more stocking of black birch (21.3 percent) and the less common species (21.5 percent) than the other classes (Table 2.2). Black cherry stocking was also somewhat greater in these stands (6.7 percent) versus the stands in the other classes (0.0 – 2.3 percent). Chestnut oak was the most important oak species in the MIXED class, but it was far less abundant that in the OAK class. Stocking of other oak species did not differ significantly between the two classes. Red maple stocking did not significantly differ between stands in the OAK (18.3 percent) and MIXED (27.3 percent) classes.

The RED MAPLE class contains stands with the greatest stocking of red maple (70.1 percent) (Table 2.2). Stocking of black birch and less common species did not significantly differ between stands in the RED MAPLE and OAK classes. Stocking by all oak species or any individual oak species did not differ between the stands in the MIXED and RED MAPLE classes. In short, the RED MAPLE class differed from the MIXED class in having far more red maple stocking and far less black birch, and it differed from the OAK class in having far more red maple stocking and far less oak.
Table 2.2. Average third-decade composition, by outcome class, of 90 formerly oak-dominated stands. Different superscripts within rows indicate significant differences at the 0.05 confidence level.

The UNSTOCKED class represents regeneration failure. Total stocking reached an average of only 14.6 percent (range = 0.0 to 44.9 percent) in this class (Table 2.2). In contrast, virtually all of the stands in the other classes were fully stocked in the third-decade after harvest. Red maple (4.8 percent) and less common species (4.6 percent) were the most important species in this class. Northern red oak was the most important oak, although stocking of all oak species was only 1.8 percent.

The MIXED class was the most common outcome class (34.4 percent of stands) and the OAK class (12.2 percent of stands) was the least common (Table 2.3). The RED MAPLE and UNSTOCKED classes were almost equally common (25.6 and 27.8 percent of stands, respectively). The OAK class occurred with equal frequency in the Ridge and Valley and the Blue Ridge provinces, but did not occur on the Appalachian Plateaus. The
Table 2.3. Distribution of subject stands by outcome class and physiographic province.

<table>
<thead>
<tr>
<th>Physiographic Prov.</th>
<th>OAK</th>
<th>MIXED</th>
<th>RED MAPLE</th>
<th>UNSTOCKED</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Appalachian Plateaus</td>
<td>0.0 (0)</td>
<td>3.3 (3)</td>
<td>11.1 (10)</td>
<td>24.4 (22)</td>
<td>38.9 (35)</td>
</tr>
<tr>
<td>Blue Ridge</td>
<td>5.6 (5)</td>
<td>2.2 (2)</td>
<td>2.2 (2)</td>
<td>0.0 (0)</td>
<td>10.0 (9)</td>
</tr>
<tr>
<td>Ridge and Valley</td>
<td>6.7 (6)</td>
<td>28.9 (26)</td>
<td>12.2 (11)</td>
<td>3.3 (3)</td>
<td>51.1 (46)</td>
</tr>
<tr>
<td>Total</td>
<td>12.2 (11)</td>
<td>34.4 (31)</td>
<td>25.6 (23)</td>
<td>27.8 (25)</td>
<td>100.0 (90)</td>
</tr>
</tbody>
</table>

MIXED class was most common in the Ridge and Valley province and the UNSTOCKED class was most common on the Appalachian Plateaus and absent from the Blue Ridge. The RED MAPLE class was equally common on the Appalachian Plateaus and Ridge and Valley provinces, but rare in the Blue Ridge.

**Development Pathways**

Figure 2.3 shows the average composition of each class of stands (defined by their third-decade post-harvest compositions) at four points in development, from pre-harvest overstory through third-decade post-harvest overstory, on a two-dimensional DCA plot. The relative distances between the numeric labels (points 1-4, representing the pre-harvest overstory, advance regeneration, post-harvest regeneration, and third-decade overstory compositions, respectively) and species labels (e.g., ACRU) reflect the importance of the species within the class at each point in development. The trajectory of stand conditions associated with each outcome class defines the developmental pathway of the class. Figure 2.4 shows the positions of individual stands on the same DCA plots to illustrate within-class variation.
Figure 2.3. Detrended correspondence analysis (DCA) plot illustrating sequences of stand development by outcome class. Outcome classes (defined by third-decade compositions) are labeled with boxed text. The four points in each sequence represent the average compositions of the pre-harvest overstory (1), advance regeneration (2), post-harvest regeneration (3), and third-decade overstory (4). The distances between points and species names reflect the relative importance of the species at a given stage of development (a point would fall on a species label if only that species was represented in the class). Species are red maple (ACRU), black birch (BELE), hickories (CAXX), blackgum (NYSY), white oak (QUAL), scarlet oak (QUCO), chestnut oak (QUPR), n. red oak (QURU), and black oak (QUVE). Other species (OTHER) and unstocked area (UNSTOCKED) are also shown. Black cherry was included in the analysis but was excluded from the plot to improve scale. The dashed line divides the plot between an oak-dominated condition (lower, left side) and a condition where oaks are not dominant.
Figure 2.4. DCA plots illustrating pre-harvest overstory, advance regeneration, post-harvest regeneration and third-decade overstory compositions for individual stands in the OAK, MIXED, RED MAPLE, and UNSTOCKED classes. Species positions are identical to Figure 2.3.
Stands in the OAK, MIXED, and RED MAPLE classes were similar to one another in pre-harvest overstory composition, but they differed sharply as a group from the UNSTOCKED class (Figure 2.3). Pre-harvest stocking by all oaks in the UNSTOCKED class (30.2 percent) was lower than in the OAK and MIXED classes (69.0 and 62.2 percent, respectively) (Table 2.4). This difference is attributable almost entirely to low stocking of chestnut oak in the UNSTOCKED class (5.6 percent) versus the other classes (40.9 to 22.5 percent). Commensurate with low oak stocking, stands in the UNSTOCKED class had significantly more unoccupied area before harvest than those in the other three classes (19.6 percent, versus 0.0 to 6.8 percent). The UNSTOCKED class had moved from an oak-dominated condition towards an open condition in advance of harvest, reaching a starting point in its developmental pathway that was markedly different from the other classes.

Smaller differences in pre-harvest overstory compositions occurred between stands in the OAK, MIXED, and RED MAPLE classes (Table 2.4). Stocking by all oaks was greater in the OAK class as compared to the RED MAPLE class. Although chestnut oak was the most important oak species in all three classes, chestnut oak stocking was significantly greater in the OAK class (40.9 percent) versus the MIXED and RED MAPLE classes (22.5 and 21.2 percent, respectively). Pre-harvest stocking by red maple was significantly higher in the RED MAPLE class (11.8 percent) than in the OAK and MIXED classes (2.8 and 6.9 percent, respectively). Pre-harvest overstory compositions in the OAK class appear to have been less variable than in the other classes, as reflected by a more compact set of data points in Figure 2.4.

The advance regeneration composition of stands in the MIXED, RED MAPLE, and UNSTOCKED classes differed from the OAK class, presaging a shift in species composition towards red maple (Figure 2.3). An inverse relationship between oak and red maple stocking is apparent, with oaks becoming progressively less well-stocked from the OAK through, respectively, the MIXED, RED MAPLE, and UNSTOCKED classes, and red maple becoming progressively better stocked. A similar trend is illustrated in Figure 2.4, with the OAK class remaining, for the most part, entirely in an oak-dominated
Table 2.4. Average pre-harvest overstory composition, by outcome class, of 90 formerly oak-dominated stands. Different superscripts within rows indicate significant differences at the 0.05 confidence level.

<table>
<thead>
<tr>
<th>Species</th>
<th>Percentage Stocking by Outcome Class</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>OAK</td>
</tr>
<tr>
<td>All Quercus spp.</td>
<td>69.0\textsuperscript{a}</td>
</tr>
<tr>
<td>Q. alba</td>
<td>9.3</td>
</tr>
<tr>
<td>Q. coccinea</td>
<td>7.1</td>
</tr>
<tr>
<td>Q. prinus</td>
<td>40.9\textsuperscript{a}</td>
</tr>
<tr>
<td>Q. rubra</td>
<td>8.2</td>
</tr>
<tr>
<td>Q. velutina</td>
<td>3.4\textsuperscript{b}</td>
</tr>
<tr>
<td>Acer rubrum</td>
<td>2.8\textsuperscript{c}</td>
</tr>
<tr>
<td>Betula lenta</td>
<td>0.2</td>
</tr>
<tr>
<td>Carya spp.</td>
<td>1.2\textsuperscript{ab}</td>
</tr>
<tr>
<td>Nyssa sylvatica</td>
<td>0.4</td>
</tr>
<tr>
<td>Prunus serotina</td>
<td>0.0</td>
</tr>
<tr>
<td>Others</td>
<td>7.9\textsuperscript{a}</td>
</tr>
<tr>
<td>Open</td>
<td>0.0\textsuperscript{c}</td>
</tr>
</tbody>
</table>

condition, while a progressively greater proportion of stands in the MIXED, RED MAPLE, and UNSTOCKED classes moved away from an oak-dominated condition.

Advance regeneration of any oak species was significantly greatest in the OAK class (75.3 percent) and lowest in the UNSTOCKED class (14.3 percent) (Table 2.5). Advance chestnut oak regeneration was significantly greater in the oak class than in any other (51.1 percent versus 18.0 to 5.4 percent). Advance red maple regeneration was significantly greater in the RED MAPLE and UNSTOCKED classes (69.8 and 79.1 percent respectively), versus the MIXED (45.8 percent) and the OAK classes (20.6 percent). Surprisingly, there were no significant differences between classes in the percentage of plots that lacked advance regeneration (12.4 to 15.7 percent open).
Table 2.5. Average advance regeneration composition, by outcome class, of 90 formerly oak-dominated stands. Different superscripts within rows indicate significant differences at the 0.05 confidence level.

<table>
<thead>
<tr>
<th>Species</th>
<th>OAK</th>
<th>MIXED</th>
<th>RED MAPLE</th>
<th>UNSTOCKED</th>
</tr>
</thead>
<tbody>
<tr>
<td>All Quercus spp.</td>
<td>75.3a</td>
<td>52.7b</td>
<td>30.4c</td>
<td>14.3d</td>
</tr>
<tr>
<td>Q. alba</td>
<td>5.8ab</td>
<td>11.5a</td>
<td>6.7ab</td>
<td>2.1b</td>
</tr>
<tr>
<td>Q. coccinea</td>
<td>10.0a</td>
<td>7.2a</td>
<td>0.3b</td>
<td>0.5b</td>
</tr>
<tr>
<td>Q. prinus</td>
<td>51.1a</td>
<td>18.0b</td>
<td>14.4bc</td>
<td>5.4c</td>
</tr>
<tr>
<td>Q. rubra</td>
<td>22.7a</td>
<td>17.3a</td>
<td>8.5ab</td>
<td>4.1b</td>
</tr>
<tr>
<td>Q. velutina</td>
<td>10.6ab</td>
<td>18.8a</td>
<td>4.5b</td>
<td>3.1b</td>
</tr>
<tr>
<td>Acer rubrum</td>
<td>20.6c</td>
<td>45.8b</td>
<td>69.8a</td>
<td>79.1a</td>
</tr>
<tr>
<td>Betula lenta</td>
<td>2.7b</td>
<td>10.0a</td>
<td>8.7ab</td>
<td>3.1b</td>
</tr>
<tr>
<td>Carya spp.</td>
<td>6.7a</td>
<td>4.9a</td>
<td>0.9b</td>
<td>0.5b</td>
</tr>
<tr>
<td>Nyssa sylvatica</td>
<td>2.7</td>
<td>0.3</td>
<td>1.5</td>
<td>0.0</td>
</tr>
<tr>
<td>Prunus serotina</td>
<td>0.2</td>
<td>1.5</td>
<td>0.3</td>
<td>1.9</td>
</tr>
<tr>
<td>Others</td>
<td>15.3</td>
<td>13.3</td>
<td>6.5</td>
<td>8.5</td>
</tr>
<tr>
<td>Open</td>
<td>12.4</td>
<td>13.1</td>
<td>13.8</td>
<td>15.7</td>
</tr>
</tbody>
</table>

Stands in the MIXED, RED MAPLE, and UNSTOCKED classes exhibited no evidence, either individually (Figure 2.4) or as classes (Figure 2.3), of returning towards an oak-dominated condition two years after harvest. At this point in the chronology, the MIXED class had sharply diverged from a trajectory similar to the RED MAPLE class and moved towards black birch and less common species, indicating that these species established within the two years after harvest (although black birch stocking was already highest in the MIXED class before harvest). Post-harvest stocking of black birch was significantly greater in the MIXED class (22.7 percent) than in the others (1.1 to 5.4 percent) (Table 2.6). Stocking by less common species was greatest in the OAK and MIXED classes (21.1 and 26.2 percent respectively) and least in the UNSTOCKED class (6.1 percent). The post-harvest regeneration composition of the RED MAPLE class was...
Table 2.6. Average post-harvest regeneration composition, by outcome class, of 90 formerly oak-dominated stands. Different superscripts within rows indicate significant differences at the 0.05 confidence level.

<table>
<thead>
<tr>
<th>Species</th>
<th>OAK</th>
<th>MIXED</th>
<th>RED MAPLE</th>
<th>UNSTOCKED</th>
</tr>
</thead>
<tbody>
<tr>
<td>All Quercus spp.</td>
<td>85.9\textsuperscript{a}</td>
<td>47.3\textsuperscript{b}</td>
<td>31.9\textsuperscript{b}</td>
<td>14.6\textsuperscript{c}</td>
</tr>
<tr>
<td>Q. alba</td>
<td>10.8\textsuperscript{a}</td>
<td>8.8\textsuperscript{a}</td>
<td>3.3\textsuperscript{b}</td>
<td>3.9\textsuperscript{b}</td>
</tr>
<tr>
<td>Q. coccinea</td>
<td>18.3\textsuperscript{a}</td>
<td>8.0\textsuperscript{a}</td>
<td>1.6\textsuperscript{b}</td>
<td>0.5\textsuperscript{a}</td>
</tr>
<tr>
<td>Q. prinus</td>
<td>52.4\textsuperscript{a}</td>
<td>19.6\textsuperscript{b}</td>
<td>16.7\textsuperscript{b}</td>
<td>2.8\textsuperscript{c}</td>
</tr>
<tr>
<td>Q. rubra</td>
<td>26.7\textsuperscript{a}</td>
<td>9.5\textsuperscript{b}</td>
<td>8.4\textsuperscript{b}</td>
<td>5.9\textsuperscript{b}</td>
</tr>
<tr>
<td>Q. velutina</td>
<td>13.6\textsuperscript{ab}</td>
<td>15.5\textsuperscript{a}</td>
<td>5.7\textsuperscript{bc}</td>
<td>3.3\textsuperscript{c}</td>
</tr>
<tr>
<td>Acer rubrum</td>
<td>20.5\textsuperscript{c}</td>
<td>46.9\textsuperscript{b}</td>
<td>66.9\textsuperscript{a}</td>
<td>62.6\textsuperscript{ab}</td>
</tr>
<tr>
<td>Betula lenta</td>
<td>1.7\textsuperscript{b}</td>
<td>22.7\textsuperscript{a}</td>
<td>5.4\textsuperscript{b}</td>
<td>1.1\textsuperscript{b}</td>
</tr>
<tr>
<td>Carya spp.</td>
<td>3.9\textsuperscript{a}</td>
<td>3.4\textsuperscript{a}</td>
<td>0.7\textsuperscript{b}</td>
<td>0.1\textsuperscript{b}</td>
</tr>
<tr>
<td>Nyssa sylvatica</td>
<td>2.0</td>
<td>1.5</td>
<td>0.9</td>
<td>0.3</td>
</tr>
<tr>
<td>Prunus serotina</td>
<td>1.2</td>
<td>4.6</td>
<td>0.3</td>
<td>0.7</td>
</tr>
<tr>
<td>Others</td>
<td>21.1\textsuperscript{ab}</td>
<td>26.2\textsuperscript{a}</td>
<td>13.0\textsuperscript{bc}</td>
<td>6.1\textsuperscript{c}</td>
</tr>
<tr>
<td>Open</td>
<td>4.4\textsuperscript{c}</td>
<td>10.5\textsuperscript{bc}</td>
<td>14.6\textsuperscript{ab}</td>
<td>28.6\textsuperscript{a}</td>
</tr>
</tbody>
</table>

almost identical to the advance regeneration composition, reflected by a very small segment between advance regeneration and post-harvest regeneration on the DCA plot. The RED MAPLE and UNSTOCKED classes had the greatest post-harvest red maple stocking (66.9, 62.6 percent, respectively) of the four classes. The UNSTOCKED class showed movement towards an open condition two years after harvest and had the highest percentage of open area among the four classes (28.6 percent, versus 4.4 to 14.6 percent).

Stands in the OAK class remained nearly uniformly oak-dominated after harvest (Figures 2.3 and 2.4). Stocking by all oak species (85.9 percent), chestnut oak (52.4 percent), and northern red oak (26.7 percent), was significantly greater in the OAK class than in the three other classes (Table 2.6).
Table 2.7. Percentage of plots with competing vegetation, by outcome class, before and after harvest in 90 formerly oak-dominated stands. Different superscripts within rows indicate significant differences at the 0.05 confidence level.

<table>
<thead>
<tr>
<th>Period</th>
<th>Percentage of Plots by Outcome Class</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>OAK</td>
</tr>
<tr>
<td>Pre-harvest</td>
<td>7.3(^b)</td>
</tr>
<tr>
<td>Post-harvest</td>
<td>5.5(^c)</td>
</tr>
</tbody>
</table>

Competing vegetation was significantly more common before harvest in stands in the RED MAPLE and UNSTOCKED classes (45.0 and 69.9 percent, respectively) versus the OAK and MIXED classes (7.3 and 16.9 percent, respectively) (Table 2.7). Two years after harvest, the occurrence of competing vegetation increased in the MIXED, RED MAPLE, and UNSTOCKED classes. After harvest, competing vegetation was significantly greatest in the UNSTOCKED class (87.4 percent), followed by the RED MAPLE class (68.8 percent). Competing vegetation remained less common in the OAK and MIXED classes (5.5 and 30.7 percent, respectively).

**Discussion**

In the third decade after harvesting oak-dominated stands, regeneration (or lack of it) created new stands that sometimes differed markedly in species composition from their predecessors. The range of third-decade stand conditions falls into four distinct classes that reflect several models of forest succession (Finegan 1984, Abrams and Scott 1989, Laycock 1991). From the perspective of forest succession, the harvest of oak-dominated stands alternately resulted in the self-replacement of oaks (OAK class), the return to an early seral stage where pioneer species are prominent (MIXED class), the acceleration of succession from oak to red maple (RED MAPLE class), or the transition to a non-forested alternate stable state (UNSTOCKED class). The developmental pathways presented here demonstrate the importance of specific initial conditions to future stand development. The recognition of these pathways, and the conditions that
make each unique, provides the opportunity to better understand the results of timber harvests and tailor prescriptions to produce more desirable outcomes.

Of the four pathways, only the OAK pathway (i.e., the pathway resulting in the OAK outcome class; other pathways are similarly labeled) led to the successful regeneration of oak-dominated stands. The key factor separating this pathway from the others was the presence of abundant advance oak regeneration at the time of harvest. In contrast, the transition away from an oak-dominated condition was foreshadowed in the other three pathways by their lower levels of advance oak regeneration stocking. There is some evidence that less common species established after harvest in the OAK pathway, but their establishment does not appear to have influenced the composition of the third-decade stands.

Although a high level of advance oak regeneration stocking was the key factor separating the OAK pathway from the other three, it is unclear why abundant oak regeneration developed in this pathway. Johnson and others (2002) suggest that some oak stands are “intrinsic accumulators” of advance oak regeneration. These stands develop advance regeneration with little, if any, silvicultural manipulation. Intrinsic accumulators are typically found on more xeric sites with little competing vegetation (Johnson et al. 2002, pg 126). The average pre-harvest condition of the stands in the OAK pathway suggests that some of these stands fit the description of intrinsic accumulators. Pre-harvest chestnut oak overstory stocking was greater in the stands that developed along this pathway versus the other three. Chestnut oak is the predominant oak species on xeric sites in the central Appalachians, suggesting that the stands in the OAK pathway were generally located on drier sites (McQuilkin 1990). Other studies have demonstrated that dry chestnut oak stands can be regenerate successfully with little management before harvest (Ross et al. 1986, Weaver and Robertson 1981). In addition, the occurrence of competing vegetation was generally low in the OAK pathway, pointing towards favorable understory conditions for the establishment and survival of advance oak regeneration (Lorimer et al. 1994). Not all stands, however, were necessarily intrinsic accumulators. Factors such as variation in browsing intensity and past overstory disturbances may have contributed to the development of oak regeneration in these
stands. In addition, a fortuitous seed crop shortly before harvest may have shifted some stands to the OAK pathway (Johnson et al. 1989).

If the OAK pathway is representative of stable, self-replacing oak forests in Pennsylvania, then this condition is uncommon and limited in geographic extent. Only 12.2 percent of stands developed along the OAK pathway. Nearly one-half of these stands in our study were located in the Blue Ridge physiographic province, which occupies a relatively small area in the southern part of Pennsylvania. The pathway did not occur at all on the Appalachian Plateaus, in the northern part of the study area. These findings suggest that a minority of oak-dominated stands in our region will be replaced by oak-dominated stands after harvest without silvicultural manipulations that are different from those used to create these stands.

The RED MAPLE pathway featured a rapid transition from oak dominance to dominance by red maple. The transition away from an oak-dominated condition undoubtedly took place due in part to relatively low stocking of advance oak regeneration (30 percent of plots). The transition to a red maple-dominated condition occurred due to both the establishment of advance red maple regeneration and the exclusion of regeneration by other species before and after harvest. The development of advance red maple regeneration in oak-dominated stands is a widespread phenomenon (Lorimer 1981, 1984, Allen and Bowersox 1989). Effective fire suppression efforts in the eastern United States are thought to have allowed red maple to expand into upland sites where it had previously been excluded by frequent fires (Abrams 1998). In the absence of fire, red maple has the capacity to establish and survive in a wide range of habitats, from moist valleys to dry ridge tops (Walters and Yawney 1990). This ecological amplitude allows red maple to regenerate in stands where conditions previously favored other species (Abrams 1998).

Several pre-harvest stand conditions appear to have favored the establishment of advance red maple regeneration at the expense of other species in the RED MAPLE pathway. The occurrence of competing vegetation was higher in this pathway than in the OAK and MIXED pathways. Competing vegetation has been shown to inhibit the seedling growth of a number of species (Gottschalk 1985, de la Cretaz and Kelty 2002),
although it is unclear whether it specifically favors the development of red maple regeneration (see George and Bazzaz 1999a, 1999b). After harvest, the occurrence of competing vegetation increased in this pathway, probably inhibiting the recruitment of regeneration by pioneer species. Pre-harvest overstory stocking by red maple was greater in the RED MAPLE pathway than in the OAK and MIXED pathways. In mature stands, overstory red maple often forms a sub-stratum below oaks, increasing understory shade (Oliver 1978). This sub-stratum has been shown to reduce the growth and survival of oak regeneration (Lorimer et al. 1994, McDonald et al. 2003). In addition to shading the understory, overstory red maple provide a seed source for regeneration (Sakai 1990) and contribute to sprout-origin stocking after harvest (Kays et al. 1988).

The particular combination of pre-harvest overstory and understory conditions found in the RED MAPLE pathway suggests that some stands are highly inclined to succeed from oak to red maple after a timber harvest. This pattern of development is a widely recognized outcome of timber harvests in oak stands (Crow 1988, Lorimer 1993). The inclination may be particularly strong in oak stands located in the Appalachian Plateaus physiographic province. The RED MAPLE pathway was more common than the OAK and MIXED pathways in this region. The region contains the ecotone between the oak-hickory and northern hardwood forest types, and oak stands in the region are sometimes referred to as transition stands when they contain a significant red maple component (Stout 1991). The transition of these stands from oak to red maple may be indicative of a more general southward shift in this ecotone as a result of a modern disturbance regime that favors the regeneration of northern hardwood species over oaks as was suggested also by Abrams and Nowacki (1992).

The MIXED pathway, like the RED MAPLE pathway, was characterized by a transition away from an oak-dominated condition. In both pathways, the transition was probably encouraged by relatively low levels of advance oak regeneration stocking (53 percent of plots in the MIXED pathway, versus 75 percent in the OAK). But unlike the RED MAPLE pathway, the transition in the MIXED pathway did not result in dominance by a single species. The oaks, red maple, black birch, and the less common species (in the aggregate) are approximately equally well represented in the third-decade stands.
Post-harvest recruitment of regeneration appears to have had a strong effect on third-decade stand composition in only this pathway. Accordingly, the trajectory of the MIXED pathway appears to have been less predetermined in advance of harvest than the OAK and RED MAPLE pathways.

Pre-harvest stand conditions that characterized the MIXED pathway are intermediate between the OAK and RED MAPLE pathways. The stands in the MIXED pathway were not strong accumulators of advance oak regeneration. The lower level of pre-harvest overstory chestnut oak stocking in this pathway versus the OAK pathway suggests that the MIXED pathway occurred in stands located on a wider range of sites. Site conditions in some of these stands were probably unfavorable for the accumulation of advance oak regeneration. Although the stands in the MIXED pathway did not develop abundant advance oak regeneration, the recruitment of post-harvest regeneration of non-oak species was not inhibited as in the RED MAPLE pathway. Lower levels of competing vegetation and advance red maple regeneration were found in the MIXED pathway versus the RED MAPLE pathway. These conditions suggest that there was a greater post-harvest “window of opportunity” for the establishment of pioneer species in the MIXED pathway than in the RED MAPLE pathway.

The common occurrence of the MIXED pathway suggests that many oak-dominated stands in Pennsylvania lack a clear future trajectory in advance of harvest. This appears to be especially true in the Ridge and Valley physiographic province, where most of the stands that developed under the MIXED pathway are located. These stands are not stable, self-replacing oak stands, nor are they highly inclined to succeed to red maple. The indeterminate condition of the stands in this pathway may reflect the generally depauperate condition of advance regeneration in Pennsylvania (McWilliams et al. 1995) without the underlying conditions that favor the succession of oak stands to red maple.

The UNSTOCKED pathway resulted in the partial or complete loss of forest cover. The pathway appears to have been initiated by defoliation and mortality in the years preceding harvest. Most stands in the UNSTOCKED pathway are located in an area that experienced widespread defoliation by the oak-leaf roller beginning in the late
1960s (Frank 1974). In many cases, timber sale records indicate extensive mortality before harvest. This was evident in pre-harvest overstory stocking levels, which were lowest in the UNSTOCKED pathway and well below the point where complete crown closure is expected (Gingrich 1967). The poor condition of the overstory at the time of harvest probably reduced seed production and undoubtedly reduced the potential for stump sprouts to contribute to third-decade stocking (Weigel and Peng 2002). In addition, the increase in light reaching the understory appears to have led to an increase in potentially competitive non-tree vegetation.

Despite the pre-harvest mortality, the UNSTOCKED pathway appeared poised before harvest to transition to a red maple-dominated condition. Advance red maple regeneration stocking did not significantly differ between the UNSTOCKED and RED MAPLE pathways, nor did the pre-harvest occurrence of competing vegetation. After harvest, the shift towards an open condition became more apparent as regeneration stocking decreased and the occurrence of competing vegetation increased. It is unclear which factors shifted the UNSTOCKED pathway away from the trajectory of the RED MAPLE pathway. Anecdotal evidence suggests that intense browsing by white-tailed deer greatly contributed to the shift in the trajectory of the UNSTOCKED pathway. An earlier study that was located near several stands that developed under the UNSTOCKED pathway found that regeneration of woody species after an overstory removal was limited to areas protected from browsing by a deer-proof fence. Unfenced control sites, in contrast, became dominated by low vegetation unpalatable to white-tailed deer (Wood 1971). Moderate levels of deer browse may have favored the development of red maple regeneration in the RED MAPLE pathway, while heavy levels of deer browse inhibited regeneration of all woody species in the UNSTOCKED pathway (Kittredge et al. 1995, Horsley et al. 2003).

In the third decade after harvest, natural forest cover has failed to return to the stands that developed under the UNSTOCKED pathway. The low vegetation that now occupies these sites may represent an alternative stable state that will persist until a disturbance provides an opportunity for regeneration to become established (Stromayer
and Warren 1997). Even when a disturbance does occur, high deer densities would continue to favor the survival of the less palatable vegetation.

The four pathways present different sets of challenges for managers trying to sustain oaks on a site after harvest. The OAK pathway is clearly most favorable to oak regeneration success. In stands that develop abundant advance regeneration with little management effort, an overstory removal alone will successfully reproduce a new oak-dominated stand (Sander et al. 1984). This pathway, however, is uncommon and may generally be restricted to less productive sites.

The MIXED and RED MAPLE pathways present greater sets of challenges. Both pathways should be altered before final overstory removal. The recruitment of pioneer species after harvests and consistently low levels of competing vegetation in the MIXED pathway suggests stand conditions are generally suitable for regeneration establishment. Other limiting factors (e.g., light, deer browsing) may be altered through shelterwood treatment and fencing to encourage the establishment of oak seedling before final harvest (Marquis and Brenneman 1981, Loftis 1990). Shelterwood treatments alone may not be appropriate for stands developing along the RED MAPLE pathway. Competing vegetation and red maple regeneration would likely increase with increased light, further inhibiting oak regeneration. Treatments should reduce red maple and other vegetation to create conditions suitable for oak establishment (Lorimer et al. 1994). Prescribed fire shows promise for this objective (Brose et al. 1999).

Land managers may consider stands that develop along the MIXED and RED MAPLE pathways to be acceptable if they contain at least a small number of well-distributed oaks. Oliver (1975) found oaks in New England stands emerged above black birch and red maple after the third decade of stand development to form an upper stratum. Similarly, Ward and others (1999) reported an increase in oak dominance during this period in oak-red maple-black birch stands. Although oak dominance may be delayed in the MIXED and RED MAPLE pathways, oaks may become more important parts of these stands closer to the end of their rotations.

The OPEN pathway represents the greatest challenge to successful oak regeneration. In most cases, the composition of the future stand will be secondary to the
Figure 2.5. Conceptual model of four pathways of stand development after the harvest of oak-dominated stands. Stand development begins at the top of the model with oak-dominated overstories. Advance regeneration differs between pathways and regeneration is modified after harvest by the establishment or exclusion of pioneer species. Pathways end at the bottom of the model with different stand compositions in the third-decade after harvest.

goal of maintaining forest cover on the site. Reductions in deer browse and competing vegetation appear necessary after harvest to promote existing regeneration (Jordan 1967, McGill and Brenneman 2002). Artificial regeneration may ultimately be needed to reestablish oaks.

Figure 2.5 is a conceptual model summarizing the four developmental pathways. All pathways begin in oak-dominated stands. Stands that develop along the OAK pathway remain oak-dominated throughout early development, resulting in the self-replacement of oaks. The MIXED pathway diverges from the OAK pathway due to
lower advance oak regeneration and the establishment of black birch and other pioneer species after harvest. The resulting stands lack a clear dominant species and, on average, contain equal parts oak, black birch, and red maple. Stands that develop along the RED MAPLE pathway begin with a relatively large red maple component in the overstory and abundant advance red maple regeneration. After harvest, the recruitment of pioneer species is inhibited and red maple retains its dominance. Stands in the UNSTOCKED pathway experience pre-harvest mortality and advance regeneration dominated by red maple. Post-harvest recruitment is inhibited and regeneration declines, ultimately resulting in regeneration failure.

A detailed understanding of forest stand dynamics is essential to successful silviculture. Although general models of forest succession appear adequate to describe the range of developmental patterns observed in this study, they provide little insight into why stands develop along one pathway, rather than another. The developmental pathways emphasize the importance of specific stand conditions at the time of harvest and, to a lesser extent, immediately after harvest to future development. The suite of factors that contributed to differences in initial conditions is not entirely clear, but variations in site quality and recent disturbance histories appear to have played strong roles.

The methods employed in this chapter may prove useful for addressing similar research questions in other vegetation types. Developmental pathways offer a flexible framework for contrasting the development of two or more classes of stand. Pathways similar to those reported here are likely to be found following stand-replacing disturbances in stands containing species with different modes of regeneration (i.e., sprouting, advance regeneration, post-disturbance germination) and a range of shade-tolerances. In other stands, the type and severity of disturbance will likely be more important determinants of future development (Halpern 1989).
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Chapter 3

A Quantitative Seed-Origin Oak Regeneration Model for the Central Appalachians

Abstract

A model is presented to quantify seed-origin oak regeneration potential in advance of complete overstory removal in central Appalachian oak-dominated stands. Oak regeneration potential, expressed as expected oak stocking in the third decade after harvest, is estimated from the size, density, and distribution of advance oak regeneration. The model incorporates several modeling elements developed elsewhere. The effect of regeneration distribution is accounted for in the model by linking regeneration development to a model stand that reflects the expected stand structure at the end of the regeneration period. Regeneration size and density are accounted for in a plot-level model that summarizes the probability that at least one stem of advance oak regeneration present before harvest will occupy a given plot at the end of the regeneration period. A negative exponential function \((1 - e^{-\alpha x})\) is used for the plot-level model to simplify the calculation of multiple seedling success probabilities. A "top down" modeling approach was used. A stand-level base model was first fit to long-term data describing the relationship between the distribution of advance oak regeneration and third-decade seed-origin oak stocking. Inverse modeling was then used to fit a plot-level model to short-term data. Silvicultural systems that rely on natural regeneration are often faulted for producing inconsistent and seemingly unpredictable results. Although the present model is focused on central Appalachian oak forests, the methods outlined here may prove useful for modeling regeneration in other forest types.
Introduction

Successful natural regeneration is critical to silvicultural systems applied throughout the world. Natural regeneration is often the best method for restocking harvested forests, as it requires relatively little investment, promotes native species, and conserves locally-adapted genotypes (Smith et al. 1997, Finkeldey and Ziehe 2004). However, there are some clear challenges to successful natural regeneration. Forest managers have relatively little control over species mixtures and cannot always achieve acceptable stocking rates. Valuable species may be lost or poorly represented in naturally-regenerated stands and regeneration failures are a real possibility (Bertault et al. 1995, Kozlowski 2002). Stands that were harvested with little consideration for future development are sometimes labeled "naturally regenerates." Dissatisfaction with natural regeneration in these cases can be attributed, in part, to poor forest management (Timoney and Peterson 1996). However, even under careful management, silvicultural systems that employ natural regeneration can produce inconsistent and seemingly unpredictable results.

Predictive models can provide forest managers with useful tools for better understanding and controlling natural regeneration. Even-aged silvicultural systems are perhaps the most straightforward to model. Much of the regeneration potential in even-aged stands is in place before final harvest in the form of advance regeneration, stored seeds, and sprouting potential. The challenge is measuring these sources of regeneration and translating the measurements into useful information, such as future stocking. In forest types where sufficient regeneration is not assured, this information can alert forest managers to the need for remedial measures.

Adequate natural regeneration of oaks (**Quercus** spp.) under even-aged silvicultural systems in eastern North America is often difficult to obtain. Oaks are frequently replaced by other species after timber harvests and other disturbances (Beck and Hooper 1986, Abrams and Nowacki 1992). The oak regeneration problem emerged in the latter-half of the 20th century throughout much of the eastern United States and has been linked to (among other causes) fire suppression, lack of overstory disturbance in
maturing stands, and excessive browsing by white-tailed deer (*Odocolieus virginianus* Boddaert) (Lorimer 1993). Oaks are considered to be among the most desirable species in many eastern forests due to their high economic value and ecological importance (Johnson et al. 2002). Given the importance of oaks and the difficulties encountered in regenerating them, there is a need for predictive models and regional research-based guidelines to aid forest managers in reaching regeneration goals.

Successful oak regeneration depends on establishing oak seedlings in advance of final overstory removal (i.e., advance oak regeneration). These seedlings, combined with oak sprouts, must then compete successfully to occupy growing space in the regenerated stand. Promising methods have been developed to improve oak regeneration potential using the shelterwood regeneration method and prescribed burning (Loftis 1990a, Brose et al. 1999). Methods to evaluate the adequacy of existing sources of regeneration are needed to determine whether a final overstory removal is warranted or if remedial measures are needed. Research-based methods for evaluating seed-origin regeneration potential have been developed for the Missouri Ozarks (Sander et al. 1984, Dey 1991) and the southern Appalachians (Loftis 1990b), but little work has been done in oak stands in the central Appalachians.

This chapter describes the development of a seed-origin oak regeneration model using data from Pennsylvania. Although this chapter focuses on oak-dominated forests, there is a much larger need for predictive models to improve silvicultural systems that rely on natural regeneration, and the concepts and methodology used here can be applied to other forest types. Three goals guided model development: 1) the model should fit the best available data, 2) the model should be easy to use (minimal computations) and readily incorporated into comprehensive oak regeneration guidelines, and 3) the model should reflect current knowledge of the oak regeneration process and incorporate innovative elements of other models. To meet the third goal, other methods for assessing oak regeneration potential are reviewed.
Assessing Regeneration Potential

Oak regeneration originates from two sources – stump sprouts and seedlings. Rather than representing a clear biological distinction, these sources of regeneration reflect the conventional division of forest vegetation into an overstory and an understory component (Dey et al. 1996). Sprout-origin regeneration refers to new stems that arise from the stumps of overstory trees (defined by some minimum diameter; e.g., > 5 cm dbh) after they are severed near the ground line. Although oak stump sprouts typically occur at low densities (Johnson 1975) their rapid growth and high rate of survival make them an important source of regeneration (McIntyre 1936; Kays et al. 1988). The production of stump sprouts cannot be readily enhanced by known silvicultural treatments, and it declines with increasing stand age and average diameter (Johnson 1977; Weigel and Peng 2002).

Seedling regeneration refers to regeneration from smaller stems (e.g., < 5 cm dbh), which includes both true seedlings (stem and root collar are the same age) and seedling sprouts (stem is younger than the root collar) (Sander 1972). In general, seedling regeneration must be established in advance of an overstory removal to produce stems of sufficient size and in sufficient quantity to compete successfully after harvest (Sander et al. 1984; Crow 1988). Therefore, advance regeneration is generally considered the only reliable source of seedling oak regeneration.

Concepts of what constitutes adequate advance oak regeneration are evolving and reflect very different perspectives on the development of oak stands. Based on a retrospective study of oak stand development in New England, Oliver (1978) concluded that northern red oak (*Quercus rubra* L.) is typically a superior competitor in mixed-species stands in New England. Based on this conclusion, 150 stems ha⁻¹ of advance oak regeneration were suggested as adequate to reproduce oak-dominated stands 60 yrs after harvest (Oliver 1978). Arend and Scholz (1969) suggested 988 stems ha⁻¹ > 30 cm tall is adequate to regenerate northern red oak stands in Wisconsin. Their recommendation was based on the observation that advance regeneration of competing red maple (*Acer rubrum* L.) and black cherry (*Prunus serotina* Ehrh.) was generally around 30 cm tall and oaks
would have an advantage if they exceeded that height at the time of harvest. Sander and others (1976) suggested that 1070 stems ha\(^{-1}\) of advance oak regeneration \(\geq 137\) cm tall is adequate to reproduce oak stands in the Missouri Ozarks. This recommendation was based on the assumption that advance oak regeneration < 137 cm tall makes a negligible contribution to oak stocking in the future stand (Sander 1972). The preceding recommendations vary widely in their concepts of regeneration adequacy. I am not aware of any attempts to test these recommendations against large bodies of field data and, unfortunately, their usefulness remains unknown.

More recent efforts to describe adequate regeneration have focused on the probability of “success” of individual oak stems. Success typically refers to the expectation that an oak will reach a dominant or codominant crown position at the end of the regeneration period. A stem’s probability of success has been shown to depend on its size at the time of harvest and the environmental factors that influence the growth of oaks and other species (Sander 1971; Sander 1972; Loftis 1990b). Sander and others (1984) modeled fifth-year success to develop oak regeneration guidelines for the Missouri Ozarks. Oak stems were considered successful five years after harvest if they reached 2.7 m in height, which was 80 percent of the average height of five-year-old oak stump sprouts. These results were then extrapolated to 20 yrs after harvest by assuming a 1 percent annual mortality rate. Loftis (1990b) modeled regeneration success of northern red oaks in the southern Appalachians by modeling eighth-year success. A stem was considered successful if it reached a minimum height (4.2 – 5.7 m) and maintained a “free-to-grow” condition after eight years. These results were then extrapolated to 20 yrs after harvest by reducing the probability of success by one-half. Belli and others (1999) used a similar definition of success three years after harvest to refine regeneration guidelines for oaks in Mississippi bottomland forests.

The quantitative properties of individual tree success (ITS) models are useful, but scaling the success of individual trees to the stand level requires consideration of the density and distribution of advance regeneration, in addition to size (Johnson et al. 2002). Loftis (1993) illustrated a simple, "distribution-free" approach to scaling individual tree success to a stand-level. In this approach, the density of seedlings in each size class is
multiplied by the probability of success of the respective size class to yield an expected density 20 yrs after harvest. While this approach considers the density of seedlings, it does not take into account their distribution. Seedlings that are aggregated are more likely to compete with one another, possibly decreasing the number of successful stems (Leps and Kindlman 1987; Tome and Burkhart 1989).

Sander and others (1984) addressed the issue of distribution by considering stand structure at the end of the regeneration period. This is referred to as a "model stand." The model stand provides a context for predicting the importance of oaks in a future stand and serves as a template to link a soon-to-be-regenerated stand with a future stand. The template guides the sampling of advance regeneration and the modeling of stand development after harvest. Sander and others (1984) sampled advance regeneration in plots scaled to represent the crown area of average dominant or codominant 20-yr-old trees. The regeneration measured on the plot is assumed to have the potential to occupy only that plot, as opposed to a more general position within the stand. Concomitantly, each plot is expected to be occupied (or not) by a single oak at the end of the regeneration period. Plots that lack advance oak regeneration are assumed to have no chance of being occupied by an oak.

The plot-level approach proposed by Sander and others (1984) simplifies the regeneration process into a collection of plot-level "events", i.e., the occupation and eventual domination of a plot by a single tree. An event is a "success" if an oak occupies the plot and a "failure" if an oak fails to occupy the plot. The importance of oak in the future stand is expressed as the average probability of success across sampled plots. Interestingly, the system proposed by Sander and others (1984) does not consider advance regeneration density within plots, but rather calculated plot-level success using an ITS model as the probability that the largest stem of advance oak regeneration on a plot will succeed. Consequently, a plot that contains several stems of advance regeneration of a given size is considered to have the same probability of success as a plot that contains only a single stem. This approach can be characterized as "density-free" in the sense that only the size and distribution of regeneration directly influence model output.
Belli and others (1999) improved on the plot-level approach by estimating the probability of success as the probability that at least one stem within a plot will succeed. This approach uses size, density, and distribution of advance oak regeneration to predict the importance of oaks in the future stand. Like Sander and others (1984), Belli and other's (1999) plot-level model is based on an ITS model, but the probability of success is calculated for each oak stem on a plot. The ITS model output is the probability that an individual stem will fail, expressed as:

$$P(failure) = 1 - P(success)$$  \hspace{1cm} \text{eq. 1}$$

The probability that a plot will succeed is then expressed as

$$P(success)_{plot} = 1 - \prod_{j=1}^{n} P_j(failure)$$  \hspace{1cm} \text{eq. 2}$$

Where:

- $P_j(failure)$ = Probability that stem $j$ will fail
- $n$ = Number of stems in the plot

The probability of success (eq. 2) is equal to the probability that at least one stem of advance oak regeneration that falls on the plot will succeed. Each stem provides an additional "chance" for success, allowing the probability of plot-level success to increase with increasing regeneration density.

**Model Development**

**Model Stand**

The present model is structured around a model stand similar to the one employed by Sander and others (1984). It reflects stand structure during the third decade after a
complete overstory removal in a mixed-oak stand. This range of stand ages (20 – 30 yrs) allows for variable rates of development due to different initial stand conditions and rates of productivity. The period coincides with the point in mixed-oak stand development where the oak component is well established and is not expected to decline as a result of competitive exclusion by other species (Oliver 1978; Ward and Stephens 1994; Ward et al. 1999).

Gingrich's stocking chart and yield table for young upland mixed-oak stands indicate that stands on moderately productive sites (site index 20 to 23 m, base age 50 yrs) are expected to contain approximately 2470 stems ha⁻¹ (1000 stems acre⁻¹) during the third decade of stand development (Gingrich 1967, 1971). At this density, the expected average diameter is 9.4 cm (3.7 in) and each tree is expected to occupy 13.3 m² (1 milacre) of stand area. Thus the model stand contains 2470 stems ha⁻¹, each occupying 13.3 m² of stand area.

The validity of the model stand was tested by comparing the expected stand structure with the structure of 53 young stands in Pennsylvania. The stands were regenerated with silvicultural clearcuts in mixed-oak stands and were primarily in their third-decade of development (age range = 21 to 33 yrs). The stands were at least 90 percent stocked when they were measured (Gingrich 1967). The density and average diameter of dominant, codominant, and intermediate trees were calculated for each stand. Suppressed trees were not included in the analysis because these trees, by definition, do not occupy area in the upper canopy (Smith et al. 1997).

The overall structure of these 53 stands shows the model stand to be a reasonable estimate of stand structure during the third decade of development. A statistically significant relationship (P < 0.001) was found between stand age and stand density (Figure 3.1). Based upon this relationship, the average stand reaches a density of 2470 stems ha⁻¹ at an age of 21.0 yrs. In addition, all stands over 28 yrs old had < 2470 stems ha⁻¹, suggesting that most stands transition through the model stand density by the end of the third-decade. A similar, statistically significant relationship (P < 0.001) was found between stand age and average diameter (Figure 3.2). The average stand diameter
Figure 3.1. Relationship between stand age and density in 53 fully stocked stands in Pennsylvania.

Figure 3.2. Relationship between stand age and average stand diameter in 53 fully stocked stands in Pennsylvania.
reaches 9.4 cm at a stand age of 23.5 yrs. These results indicate that, on average, actual stand structure is consistent with the model stand during the third decade of development.

Regeneration Modeling

A plot-level regeneration model was developed to predict the probability that an individual 13.3 m² plot will be occupied by oak in the third decade after harvest. A "top down" modeling approach was used, modeling regeneration success first at the stand level and then at the plot level. This approach contrasts with the "bottom up" approach of modeling individual tree success and then scaling to the stand level (e.g. Sander et al. 1984, Loftis 1993, Beli and others 1999). The approach was designed to capitalize on a long-term dataset describing the third-decade success of seed-origin oak regeneration in 41 mixed-oak stands. These data were used to model third-decade stocking based on the distribution of advance oak regeneration. Because of limitations of the dataset, the initial "base model" relates only a single stand-level attribute of advance oak regeneration, distribution, to third-decade stocking.

Inverse modeling was used with a second, short-term dataset to fit the plot-level model. Inverse modeling has previously been applied to ecological problems such as modeling plant population dynamics (Cropper and Anderson 2004) and modeling canopy structure from image spectrometry (Asner et al. 1998). Under inverse modeling, prior knowledge of a system is used to formulate a model to account for an observable output (e.g., third-decade stocking). Model parameters are then fit using an algorithm to identify parameter values that minimize the difference between observed and modeled outputs (Asner et al. 1998). The goal was to identify a plot-level model that reproduced the base model relationship between advance oak regeneration distribution and third-decade seed-origin oak stocking, while allowing for greater variability in predicted values due to the effects of oak seedling size and density. This modeling approach was successful due to underlying relationships, described below, between advance oak regeneration distribution, and oak seedling size and density.
Data Collection and Summary

The locations of the stands included in the long-term and short-term datasets are shown in Figure 3.3. The stands fall within the Appalachian Plateaus and Ridge and Valley physiographic provinces (Cuff et al. 1989). The two physiographic provinces stretch parallel to one another from northern Alabama to New York. The Allegheny Plateau province is an uplifted region of rolling hills dissected by river valleys. The Ridge and Valley province is a folded and faulted region characterized by steep, nearly parallel ridges oriented northeast to southwest. Ridges are covered by forest and valleys are typically in agricultural production. The soils where the study sites are located in both provinces are derived from sandstone, siltstone, and shale and are generally well drained. Stand elevations range from approximately 300 ft above MSL in the Ridge and Valley to 730 m on the Allegheny Plateau. Precipitation and frost-free periods vary with elevation and topography. Mean annual precipitation ranges from 96 to 115 cm and frost-free periods range from 140 to 160 days (Cuff et al. 1989). Oak forests are the dominant natural vegetation in the Ridge and Valley. Common oaks species are northern red oak (Quercus rubra L.), chestnut oak (Quercus prinus L.), white oak (Quercus alba L), black oak (Quercus velutina Lam.), and scarlet oak (Quercus coccinea Muenchh.). Oaks transition into Allegheny hardwoods moving from south to north on the Allegheny Plateau, though oaks continue to be locally dominant (Stout 1991; Bailey et al. 1994). Site index was not consistently measured in the study stands, but productivity is typically low to moderate with oak site index from 18 - 23 m (60 - 75 ft) at 50 yrs (Bowersox and Ward 1972).

The long-term dataset was developed from operational data collected in 41 stands located on Pennsylvania State Forest land. All stands were oak dominated (>50 percent basal area in oak) before harvest, and all were harvested by clearcutting at least 20 yrs prior to the initiation of this study. Advance regeneration data were collected in the stands approximately one year before harvest. Data were collected in each stand on sixty milacre plots (13.3 m²). The presence or absence of advance oak regeneration (< 5 cm dbh) was recorded by species on each plot. An acceptable stem was defined as a
vigorouse stem, at least two years old, which was a competitor for dominance on the plot. Data describing the size and density of advance oak regeneration were not collected.

The stands in the long-term dataset were re-measured at least twenty years after harvest (mean = 27.3 yrs; range = 21 – 32yrs). Approximately 30 variable-radius plots were measured with a 2.3 m² ha⁻¹ basal area factor prism in stands of 30 acres or more and one plot was measured for each acre in stands of less than 30 acres. A minimum of 10 plots was measured per stand. The diameters of “in” trees were measured to the nearest 2.5 cm and crown classes were recorded (Smith et al. 1997). Each tree was determined to be seed-origin (a single stem arising from a seedling or seedling sprout) or stump-origin (one or more stems arising from a cut stump). The origin of stems occurring singly was determined by examining root collars for evidence of a previous stump.

The distribution of advance regeneration was calculated for each stand in the long-term data as the percentage of milacre plots where any oak seedling was recorded. Chestnut oak was the most common oak regeneration recorded (30.9 percent of
observations), followed by northern red oak (27.9 percent), black oak (21.3 percent),
white oak (14.4 percent), and scarlet oak (5.4 percent).

Third-decade densities of dominant, codominant, and intermediate seed-origin oaks were calculated by diameter class using the procedures described by Avery and Burhardt (1994, p. 221). Gingrich’s (1967) stocking equation for upland oak stands was applied to the density data to calculate third-decade stocking values for upper canopy (dominant, codominant, and intermediate crown classes) seed-origin oaks. Gingrich's stocking equation is based on the tree-area ratio method (Chisman and Shumacher 1940). Stocking values for species (e.g., oaks) are equivalent to the percentage of stand area occupied by a species when stands are near maximum stocking (Gingrich 1968).

Short-term data were collected as part of a continuing study of the oak regeneration process in Pennsylvania. Data were collected in 46 stands on State Forest land as “pre-treatment” data (i.e., before treatments were applied to regenerate the stands). All stands were mixed-oak stands before treatment. In stands of 30 acres or more, approximately 30 plots were established and permanently located. In stands of less than 30 acres, one plot was established per acre with a minimum of 15 plots per stand. Within each plot, four 13.3 m² subplots were established 5 m from the plot center along the cardinal directions. Within each subplot, the density, height, and origin (seedling or stump sprout) of advance regeneration were recorded by species. Heights were recorded in eight classes (> 5 cm, 0.17 - 15 cm, 16 - 30 cm, 31 - 60 cm, 61 - 90 cm, 91 - 120 cm, 121 - 150 cm, and > 150 cm). Northern red oak was the most common oak regeneration recorded (42.1 percent of seedlings), followed by chestnut oak (28.3 percent), black oak (13.9 percent), white oak (11.8 percent), and scarlet oak (4.2 percent).

To help illustrate relationships between advance oak regeneration distribution and oak seedling size and density, the distribution of advance oak regeneration in the short-term stands was calculated as the percentage of subplots containing at least one stem of advance oak regeneration. This measure of advance regeneration is identical to the measure of regeneration in the long-term stands. Oak seedling densities were then calculated for each short-term stand as the mean density of oak stems on subplots that contain at least one oak stem. This calculation was used in place of a simple average to
remove the explicit correlation between distribution and density. Percentages of subplots containing stems in each of three size classes (< 30 cm, 31 - 90 cm, > 90 cm) were calculated for subplots that contained at least one oak stem. This calculation removed the explicit correlation between the distribution of stems in a given size class and the distribution of stems in all size classes.

Model Fitting

A nonlinear logistic model (Sit and Poulin-Costello 1994) was fit to the long-term data to produce a base model describing the relationship between the distribution of advance oak regeneration and third-decade seed-origin oak stocking. Model fitting was done using the nonlinear least-squares regression procedure (Proc NLIN) in the SAS statistical software (SAS Institute Inc. 1999). Several nonlinear models were examined and the logistic model was selected based on its explanatory power ($r^2$), interpretability, and a visual judgment of goodness-of-fit.

Long-term data are plotted with the base model fit in Figure 3.4. The logistic function captures a quasi-threshold effect in the relationship between the variables. In stands where the distribution of advance regeneration was < 60 percent, third-decade stocking was almost uniformly poor. In stands where the distribution ranged between 60 and 80 percent, a range of outcomes was observed, though third-decade stocking remained poor in some stands. Third-decade stocking was more consistently favorable in stands with > 80 percent distribution. In all, the distribution of advance regeneration explained 61.2 percent of the variation in third-decade seed-origin oak stocking. The unexplained variation is largely due to the wide range of outcomes observed in stands with distributions of > 60 percent. Although the base model captures a potentially useful relationship, the high level of variation indicates that it alone may not provide very precise estimates of third-decade stocking.

Relationships observed in the short-term data between the distribution and density and size of advance oak regeneration suggest that some of the unexplained variation in the base model was due to variations in regeneration size and density (Figure 3.5). A
Figure 3.4. Logistic model fit of the relationship between the distribution of advance oak regeneration and third-decade oak stocking in 41 mixed-oak stands. A statistically significant relationship was found between regeneration distribution and mean subplot density (Figure 3.5A). Stands with well-distributed oak regeneration had greater subplot mean stem densities. However, as with the base model, stands with > 60 percent distribution had a range of mean subplot densities, while stands with < 60 percent distribution had uniformly lower densities. In most stands, stems < 30 cm tall were found on nearly all subplots that had advance oak regeneration, regardless of overall regeneration distribution (Figure 3.5B). However, larger stems tended to be common only in stands with > 60 percent regeneration distribution. Statistically significant relationships were found between the distribution of advance oak regeneration and the
Figure 3.5. Plots of short-term data showing relationships between advance regeneration distribution (x-axes) and mean plot density (A), percentage of plots with regeneration > 30 cm (B), 31 - 90 cm (C), and > 90 cm (D). Percentage of subplots with stems 31 - 90 cm tall (Figure 3.5C) and stems > 90 cm (Figure 3.5D). In both cases, stands with > 60 percent distribution exhibited a range of large stem distributions, while larger stems were uniformly uncommon in stands with <60 percent distribution. In other words, the larger size classes of advance oak regeneration occurred only when regeneration was abundant (> 60 percent of plots with oak seedlings). However, a high frequency of oak seedling occurrence was not a guarantee that large seedlings were present.
The first step of inverse modeling was to develop a plot-level model that reflects our current understanding of the oak regeneration process. The contribution of each seedling to plot-level success was modeled as a function of seedling height. Basal diameter (diameter at ground line) is sometimes considered to be a better predictor of post-harvest growth than stem height (Sander 1971; Loftis 1990b). In Pennsylvania, the relationship between basal diameter and stem height is fairly deterministic ($r^2 = 83.0\%$; authors’ unpublished data), probably because oak seedlings seldom survive long enough to become stout, but short, seedling sprouts (Steiner et al. 1993). The relationship suggests that these measures of stem size are generally interchangeable in the region. Environmental variables (e.g., site index, slope position, aspect) were not included in the plot-level model and all species of oak regeneration were modeled together. As a result the plot-level model represents the average probability of success across a range of site conditions and regeneration compositions.

A negative exponential function ($1 - e^{-\alpha x}$) was selected for the plot-level model. Like the logistic function, response values are bound between 0 and 1. Similar exponential functions have been widely used to model seedling growth and survival (Leak 1969, Belli and Ek 1988, Payandeh 1996), and the negative exponential function has a desirable mathematical property that greatly simplifies the calculation of plot-level success probabilities. Substituting the negative exponential function into eq. 2 yields:

$$\prod = \frac{1}{\prod (1 - e^{-\alpha j})}$$

This simplifies to:

$$P(success)_{plot} = 1 - e^{-n \sum x_j}$$  \hspace{1cm} eq. 4

\begin{align*}
\alpha & = \text{Constant fit with short-term data} \\
x_j & = \text{Height (cm) of stem j} \\
n & = \text{Number of stems on the plot}
\end{align*}
The form of eq. 3 allows the plot-level probability of success to be calculated as a function of the sum of the heights of all stems of advance oak regeneration within the plot. The stand-level model is the average of the plot-level probabilities:

\[
\text{Third-decade stocking (percent)} = \frac{\sum_{i=1}^{N} \left[ 1 - e^{\alpha \sum_{j=1}^{N_i}} \right]}{N} \quad \text{eq. 5}
\]

Where:

\[N = \text{Number of plots sampled}\]

Equation 5 has a single coefficient, \(\alpha\), which specifies the relationship between aggregate oak seedling height and probability of plot-level success.

Predicted third-decade stocking values were calculated for each short-term stand using the base model. These values were then treated as "observed" values for inverse modeling. Because the model is relatively simple, an incremental search procedure was used to find the optimal \(\alpha\)-value for eq. 5. The value of \(\alpha\) was initially set to zero, corresponding to a condition where the probability of success for all stems is nil. The value was then incrementally decreased by a step size of \(3.3 \times 10^{-6}\). After each step, eq. 5 was solved for each short-term stand to produce an expected third-decade stocking level. Mean-squared error (MSE) was then calculated as the squared difference between this expected stocking and the expected stocking under the base model. The final value of \(\alpha\) was selected when MSE was minimized. The incremental search procedure was executed in the R programming environment (Ihaka and Gentleman 1996).

The incremental search procedure minimized the MSE between base model predictions and eq. 5 at \(\alpha = -0.0032\). The resulting plot-level model, when stems are measured in cm, is given by:
\[ P(\text{success}) = 1 - e^{-0.0032x} \quad \text{eq. 6} \]

If stems are measured in feet, then \( \alpha = -0.0973 \).

The respective stand-level model is:

\[
\text{Third-decade stocking (percent)} = \frac{\sum_{i=1}^{N} \left[ 1 - e^{-0.0032 \sum_{j=1}^{x_i}} \right]}{N} \quad \text{eq. 7}
\]

Results of the incremental search procedure suggest that MSE is moderately sensitive to variation around the optimal \( \alpha \)-value (Figure 3.6). Rather than reaching a minimum MSE at a single well-defined point, which would indicate high sensitivity, minimum MSE was reached within a small trough. For example, the minimum MSE was 89.5 percent stocking\(^2\), but MSE did not exceed 100.0 percent stocking\(^2\) for \( \alpha \)-values ranging from \( < -0.0025 \) to \( > -0.0040 \). Although error in the estimate of \( \alpha \) cannot be calculated conventionally, the stand-level model appears tolerant of moderate error in the parameter estimate.

Predicted third-decade stocking levels for the short-term stands (eq. 7) are compared with third-decade stocking levels observed in the long-term stands in Figure 3.7. The two sets of data points indicate that the stand-level model reproduced the general trend observed in the long-term stands. As expected, predicted values from eq. 7 also include a great deal of variation around the trend, since they are now a function of the distribution, density, and size of advance oak regeneration. For example, stands with
Figure 3.6. Results of search procedure to minimize MSE by incrementally decreasing $\alpha$. The line depicts the result of 5000 iterations.

approximately 80 percent regeneration distribution are predicted to have between 12 and 42 percent third-decade stocking. The base model alone predicts 30 percent third-decade stocking with 80 percent distribution. Both predicted and observed third-decade stocking levels are generally $< 10$ percent with regeneration distributions of $< 60$ percent.

Although the stand-level model reproduces the relationship found in the long-term dataset between advance oak regeneration distribution and third-decade stocking, the question remains: does the model accurately describe the relationship between oak regeneration height and third-decade success? Data from the Central Appalachians are not available to directly answer this question, but a long-term dataset from the Missouri
Figure 3.7. The distribution of advance oak regeneration and actual third-decade oak stocking for 41 mixed-oak stands (long-term data), and the distribution of advance oak regeneration and expected third-decade oak stocking for 46 mixed-oak stands (short-term data).

Ozarks, a somewhat similar oak-dominated region, can address it. The Ozark dataset (study OH-466; Sander 1973) includes 405 oak seedlings (49 percent black oak, 36 percent white oak, 10 percent scarlet oak, and 5 percent northern red oak) that were measured in advance of harvest and periodically remeasured through the onset of the third decade of stand development. Crown classes were assigned to surviving trees 20 or 21 yrs after overstory removal.

The Ozark data were used to examine 20-yr success percentages by pre-harvest height class. The Ozark data are summarized and compared with the plot-level model in
Figure 3.8. The plot-level model (line) and mean 20-yr success by pre-harvest height class for Missouri Ozark data (points). Success is defined as 1) reaching a dominant or codominant crown position (open points) and 2) reaching a dominant, codominant or intermediate crown position (filled points) 20 - 21 yrs after harvest.

Figure 3.8. Because the plot-level model aggregates the regeneration potential of one or more seedlings, it can be applied as an ITS model to individual seedlings. Success percentages for the Ozark data were calculated as 1) success = stem is in dominant or codominant crown class in the third-decade after harvest (open points in Figure 3.8) and 2) success = stem is in the dominant, codominant, or intermediate crown class (closed points). The Ozark results closely match the plot-level model. The plot-level model (which includes intermediate trees in its definition of success) generally underpredicts success relative to the Ozark data when intermediate trees are included in the success definition, but appears essentially unbiased when intermediate trees are excluded. Importantly, the Ozark data follow the same trend as the plot-level model, supporting the use of the negative exponential function for modeling success.
Discussion

Silvicultural systems that rely on natural regeneration are often faulted for producing inconsistent and unpredictable results (Kolowski 2002). The model presented here provides a method to improve the predictability of regeneration treatment, which is essential for the development of regional oak regeneration guidelines. The model estimates third-decade seed-origin oak stocking based on the size, density, and distribution of advance oak regeneration. An important characteristic of the model is its ease of use. In practice, advance oak regeneration is measured on 13.3 m² plots. Stem heights are summed to yield an aggregate height. Aggregate height is entered into eq. 6 to yield the probability that an oak will occupy the plot in the third decade after harvest. Values from eq. 6 can be presented as a table of total heights and probabilities, eliminating the need to for difficult calculations. Plot probabilities are averaged (eq. 7) to yield the expected proportion of the stand occupied by oak. When expressed as a percentage, rather than a proportion, eq. 7 yields expected third-decade seed-origin oak stocking.

Several elements from other models were incorporated into the present model. The influence of regeneration distribution is accounted for through the model stand template (Sander et al. 1984). Oak seedlings that occupy the same sample plot contribute to the success probability of that plot only. As a result, the contribution of dense, but poorly distributed regeneration is limited. The influence of density is accounted for by evaluating the probability that at least one stem will succeed on the sample plot (Belli et al. 1999). Individual stem success probabilities are calculated as a function of height (Sander et al. 1984, Loftis 1990b). Calculating multiple probabilities for a single plot is prohibitively difficult for non-computerized models. The negative exponential model was used to simplify these calculations using aggregate height. In this sense, the model predicts plot-level success as a function of the success probabilities of individual oaks within the plot. Long-term data from the Missouri Ozarks strongly support the final model fit and the selection of the negative exponential function to express the relationship between seedling size and probability of success.
Inverse modeling was employed to make use of the best available data to fit the plot-level model. Though limited in detail, the long-term dataset provided an important link between pre-harvest advance oak regeneration and third-decade seed-origin oak stocking. Long-term regeneration data are not likely to be available for regeneration modeling in many forest types where natural regeneration is employed. Researchers have used several strategies for dealing with limited data, including extrapolating short-term results to the end of the regeneration period (Sander et al. 1984, Loftis 1990b) and assembling multiple datasets to produce complete chronologies (Dey 1991). Inverse modeling provides a useful method for drawing upon available data to fit a single regeneration model. The model fitting strategy was to propose a simple model (eq. 5) that represents our current understanding of the oak regeneration process, and then select a value for the single parameter that produces predictions that are consistent with long-term measurements. The goal was not to identify a plot-level model that perfectly matched predicted values from the base model, but instead to reintroduce some of the variation around the base model fit that was evident in the long-term data. This approach can be generalized readily and may be used to model regeneration in other forest types where consistent long-term data are not available. Like all models that project long-term stand development, there is a need to validate and refine this model as more data become available. Future measurements of stands in the short-term dataset will be used for this purpose.

In the present study, the link between the long-term and short-term data relied heavily on the assumption that advance oak regeneration populations were similar in the long-term and short-term stands. Specifically, it was assumed that advance oak regeneration size and density increased with increasing distribution in the long-term stands, leading to the observed variation in third-decade seed-origin oak stocking. These trends were then modeled with the short-term data. It was hypothesized that these relationships reflect underlying factors that control the overall "favorability" of the growing environment for advance oak regeneration.

The favorability of the growing environment may be viewed through a simple model of oak seedling germination, growth, and senescence. In stands with oak-
dominated overstories, periodic large seed crops temporarily produce dense, well-distributed cohorts of small seedlings. If stand conditions are unfavorable for growth and survival, seedlings remain small and the distribution and density of seedlings decline rapidly. The process may be repeated after each large seed crop. When growth and survival are more favorable, the density and distribution of regeneration decline less rapidly and surviving seedlings accumulate height, thereby increasing the stand's overall regeneration potential. Additional cohorts may establish, further improving regeneration potential.

Under this model, a high distribution of advance regeneration may be a temporary condition that is soon lost due to poor growth and survival, or it may reflect stand conditions that are generally favorable for the regeneration of oaks. Both cases are apparent in the short-term data. Larger stems are found only in stands where advance regeneration is well distributed, but not all stands with well-distributed advance regeneration contain large stems. Stem density follows a similar pattern. This variation contributed to the final plot-level model, which reflects the range of stand conditions in the short-term data.

Factors not included in the stand-level model may limit the regeneration potential of oaks in some stands. Browsing by white-tailed deer contributes to regeneration problems throughout the central Appalachians (Jordan 1967; Marquis and Brenneman 1981). Competing vegetation and well-established advance regeneration of less desirable tree species may also limit the success of oaks (Lyons and Sharpe 1996; Steiner and Joyce 1999; Lorimer et al. 1994). These factors likely contributed to the poor third-decade oak stocking found in some long-term stands with well-distributed advance regeneration. Site index and topographic position have been used as an indirect measure of post-harvest competition (Loftis 1990b, Dey 1991), but were not included in this model. In stands where browsing or competition limits the regeneration of oaks, additional treatments may be required before stands will reach their oak regeneration potential. These factors can be addressed in the comprehensive regeneration guidelines as part of an expert system.
Literature Cited


Chapter 4
Modeling Sprout-Origin Oak Regeneration in the Central Appalachians

Abstract

Models were developed for common Appalachian oak species (northern red oak (*Quercus rubra* L.), black oak (*Quercus velutina* Lam.), chestnut oak (*Quercus prinus* L.), and white oak (*Quercus alba* L.) to estimate, in advance of complete overstory removal, the contribution of sprout-origin oak regeneration to stand stocking in the third decade (20 - 30 yrs) after harvest. Models are based on the probability that cut "parent" trees will sprout and the sprouts will reach a competitive position four years after harvest. These success probabilities are then factored with the amount of growing space occupied by an average sprout group in the third-decade after harvest to yield estimates of third-decade sprout stocking. The amount of growing space occupied by sprout groups was estimated from direct measurements of 429 sprout groups that originated after clearcutting 24 to 27 years prior to measurement. Parent tree diameter and species were found to be important predictors of third-decade stocking. Environmental factors (slope position, slope percentage, and aspect class) were statistically significant predictors, but provided relatively little explanatory power and were not included in the models. Predicted sprout-origin stocking values calculated for fully stocked mature stands compared favorably with stocking values observed in third-decade stands that had regenerated following the harvest of similar overstories. The models provide forest managers with essential information on stand development following planned regeneration treatments.
Introduction

Stump sprouting is a near-universal trait of woody angiosperms (del Tredici 1992), and is a particularly valuable source of oak regeneration following timber harvests in the central Appalachians (McIntyre 1936). Sprout-origin oaks grow rapidly (McQuilkin 1975) and have the potential to produce quality sawtimber (Roth and Hepting 1969, Lamson 1976). In most oak stands managed under even-aged silvicultural systems, forest managers can expect some contribution of stump sprouts to future oak stocking. However, the amount of sprouting varies according to the composition and diameter distribution of the parent stand (Weigel and Peng 2002) and other factors. Quantitative models that accurately predict sprout-origin oak stocking at the end of the regeneration period (at least 20 yrs after harvest) are needed so that treatments to reach overall regeneration goals can be judiciously prescribed.

An understanding of sprout development provides a basis for modeling sprout-origin regeneration. The development of oak stump sprouts can be divided into two phases – the initial emergence of sprouts and the subsequent development of the sprout group through the regeneration period (Johnson 1975, Cline 1997). Sprouts originate from previously dormant buds concentrated near the tree root collar. Buds that create stump sprouts in oaks were initially formed during primary growth (Liming 1940). Shortly after bud formation, further development of some buds is inhibited and a state of dormancy is induced. The precise mechanism by which dormancy is induced and maintained in some buds but not others is not entirely understood and may vary between species, but hormones produced by more terminal buds have been demonstrated to play a role (Romberger 1963, Vogt and Cox 1970, Cline 1997). Viable dormant buds elongate annually to remain at the stem surface, just below the bark, producing a characteristic bud trace between the pith and outer surface of the stem (Church and Godman 1966). Buds are released from dormancy by cutting or injury to the tree, apparently due to the interruption of hormone flow from terminal buds (Romberger 1963, Vogt and Cox 1970).

Several parent tree attributes have proven useful for predicting whether or not Appalachian oaks will sprout following cutting. The probability of sprouting decreases
with increasing parent tree diameter (Roth and Hepting 1943, Johnson 1975, Weigel and Johnson 1998). A similar trend has been found with age and older oaks are less likely to sprout (Roth and Hepting 1943, Johnson 1977, Weigel and Johnson 1998). The form of these relationships varies by species. The sprouting potential of white oak (*Qercus alba* L.), in particular, declines sharply with increasing diameter (Weigel and Johnson 1998).

Mixed results have been reported regarding the relationship between initial sprouting and site conditions. Greater sprouting frequencies have been reported for more productive sites, as measured by site index (Johnson 1977, Weigel and Johnson 1998). However, other studies have failed to find statistically significant relationships (Wendel 1975, Dey 1991) or meaningful trends (Lynch and Bassett 1987) between sprout probabilities and site index.

The post-sprout development of oak sprout groups can be characterized from several studies. After the initial flush of sprouts, the number of stems within a sprout group declines rapidly. Mean group density declines from approximately ten stems to four or five stems during the first decade (McIntyre 1936, Roth and Hepting 1969, Johnson 1975). The rate of within-group thinning then appears to slow considerably. Reported mean group densities range from 4 stems at age 23 (Johnson 1975) to approximately 1.5 stems during the fourth decade after cutting (McIntyre 1936, Roth and Hepting 1969).

Sprout group mortality (i.e., the loss of all stems within a sprout group) appears to be low during the first several decades after cutting. Wendel (1975) reported almost no group mortality among northern red oak (*Quercus rubra* L.), white oak, and chestnut oak (*Quercus prinus* L.) sprout groups over a 10 yr period in West Virginia. Johnson (1975), examining a chronosequence of stands ranging from 4- to 23-yr-old, did not detect any loss of sprout groups over the age range, suggesting minimal sprout group mortality. Roth and Hepting (1969) found that approximately 80 percent of stumps that sprouted 1 yr after cutting retained at least one stem over a 32 yr period. Sander and others (1984), in developing regeneration guidelines for the Missouri Ozarks, estimated sprout group survival at 89 percent over the first two decades of stand development.
During sprout development, parent tree characteristics appear to have a decreasing influence on sprout group characteristics. Johnson (1977) reported a weak negative relationship between parent tree diameter and dominant sprout height in 5-yr-old oak sprouts in the Missouri Ozarks. Dey and others (1996) reported a similar relationship for 5-yr-old oak sprouts in the same region. Johnson (1975) found larger northern red oak stumps in the Midwest initially produced more sprouts, but differences in sprout numbers were no longer statistically significant after 12 yrs. In a study in West Virginia, Wendel (1975) found that the height of the tallest sprout in oak sprout groups was uncorrelated with parent tree diameter and vigor 10 yrs after cutting. Lowell and others (1987) failed to find a statistically significant relationship in unthinned stands between parent tree diameter measured at the time of harvest and sprout dbh measured both 12 yrs and 30 yrs after cutting.

In summary, the studies cited above suggest parent tree characteristics, and possibly site conditions, influence the probability of initial sprouting among oaks. After sprouting, the relationship with parent tree characteristics weakens, suggesting they may have little value in predicting this stage of development. Within-group thinning is rapid, but whole-group mortality is typically low. Several decades after cutting, many sprout groups retain more than one stem.

This general description of sprout development was used to construct a quantitative model to predict, in advance of overstory removal, sprout-origin oak stocking in the third decade following harvest. The probability of sprouting was first modeled considering parent tree characteristics and site attributes, then group survival into the third decade of stand development was estimated, and finally the growing space occupied by individual sprout groups was estimated. The resulting models are designed to be incorporated into comprehensive oak regeneration guidelines for the central Appalachians. Simplicity and ease-of-use were important in the model design to ensure that the guidelines will be readily accessible to a wide range of users.
Methods

Data Collection

Three data sets were used for modeling. All data were collected in oak-dominated stands on Pennsylvania State Forest land. Stands were even-aged and generally ranged between 80 and 110 yrs old, reflecting the narrow age range typical to the region. Soils are derived from sandstone, siltstone, or shale and are typically well drained (Cuff et al. 1989). Regional mean annual precipitation ranges from 38 to 45 in and frost-free periods range from 140 to 160 days (Cuff et al. 1989).

Data to determine initial sprouting success were collected in 30 stands (Data Set I). Permanent plots were established in each stand in advance of harvest. Harvests ranged from near-complete overstory removals to first-stage shelterwood treatments. After harvest, plots were revisited and the cut stump closest to each plot center was identified. The species, stump diameter, stump age (field ring counts), number of sprouts, and height of the tallest sprout were recorded. Diameters at breast height were reconstructed from stump diameters using highly deterministic, species-specific equations developed by Weigel and Johnson (1997). Species were identified based on bark characteristics and ring morphology. About two percent of oak stumps could not be identified to the species level. These stumps were divided among species proportional to sample sizes. Data describing the plot-level (slope, aspect) and stand-level (site index, slope position) environment were also recorded. Distances and directions from plot centers to stumps were recorded to facilitate their relocation. In total, 1173 stumps were sampled. Data Set I is summarized in Table 4.1.

Sprouts in 12 stands were remeasured four years after harvest to determine sprout survival beyond the first year (Data Set II). Stumps were relocated and the number of live sprouts and the height of the tallest sprout were recorded. In total, 321 stumps were remeasured.
Table 4.1. Data summary for initial sprouting model.

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>Sprouted (percent)</th>
<th>Reconstructed DBH (in)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Quercus alba</em></td>
<td>209</td>
<td>25.4</td>
<td>Mean 14.8, Min 2.2, Max 39.0</td>
</tr>
<tr>
<td><em>Q. prinus</em></td>
<td>519</td>
<td>73.2</td>
<td>Mean 11.9, Min 3.4, Max 27.1</td>
</tr>
<tr>
<td><em>Q. rubra</em></td>
<td>328</td>
<td>64.3</td>
<td>Mean 16.4, Min 1.9, Max 34.6</td>
</tr>
<tr>
<td><em>Q. velutina</em></td>
<td>117</td>
<td>46.2</td>
<td>Mean 15.6, Min 7.3, Max 29.0</td>
</tr>
</tbody>
</table>

Data to determine the average growing space occupied by individual sprout groups in the third decade after harvest were collected in 6 stands (Data Set III). Stands had been oak dominated before being regenerated with silvicultural clearcuts 24 to 27 years prior to measurement. Sprout groups were sampled along belt transects. All living oaks that fell within the transects were examined to determine their origin (stump sprout or seedling / seedling sprout). Oaks were considered sprout origin only when remnants of a cut stump were found immediately adjacent to the living stems. The species of the sprout group and the diameters of upper canopy stems (dominant, codominant, and intermediate crown classes) were recorded. Sprout group crowns were measured along two diameters, first in the longest direction and then perpendicular to the first diameter and passing approximately through the crown center. Field crews were trained to identify crown edges using a clinometer, but clinometers were not used after the training period. Approximately equal numbers of northern red oak, black oak (*Quercus velutina* Lam.), scarlet oak (*Quercus coccinea* Muenchh.), chestnut oak, and white oak sprout groups were measured. In total, 429 sprout groups were measured.

**Modeling**

A three-part model was used to estimate the contribution of a single overstory oak to third-decade sprout-origin stocking. The model form is:
Stocking_3 = P(S_1) \cdot P(S_4) \cdot \text{Stocking}_{3rd} \quad \text{eq. 1}

Where:

P(S_1) = \text{Probability of success in year 1}
P(S_4) = \text{Probability of success through year 4}

\text{Stocking}_{3rd} = \text{Average percentage stocking of oak sprout groups in the third decade.}

Logistic regression was used to develop models to predict the probability of success in year 1 (i.e., initial sprouting success) and success through year 4. Logistic regression is a statistical method for developing models with a dichotomous response variable (e.g., sprouting success or failure) (Cook and Weisberg 1999). The resulting models estimate the probability of one outcome conditional on a set of independent variables. In this application, our goal was not to identify all the independent variables that correlate with sprouting success, but to develop parsimonious models. Therefore, the model fitting process was started by assuming that success in year 1 and year 4 was dependent only on parent tree dbh. Additional independent variables (species, age, slope position, slope percentage, and aspect) and interactions were then added to the base model and tested for improvement in model fit and additional explanatory power.

Improvements in model fit were evaluated by comparing "full" and "reduced" models as measured by $X^2$-distributed differences in deviation between models fit using the maximum likelihood method (Collett 2003, pg 73). Differences in explanatory power between models were examined by comparing modified coefficients of determination (Collett 2003, pg 90) and rates of concordance ($c$). Concordance is calculated by pairing "successful" observations with "failed" observations and comparing modeled probabilities of success ($p$). Pairs are in concordance when $p_{\text{successful}} > p_{\text{failed}}$. The $c$ statistic is the proportion of pairs in concordance, plus one-half the proportion of ties ($p_{\text{successful}} \approx p_{\text{failed}}$). Once a final model was selected, lack-of-fit was assessed with the Hosmer and Lemeshow test, which compares predicted and observed proportions against
the chi-square distribution (Collett 2003, pg. 88). Analyses were completed using the LOGISTIC procedure in the SAS statistical software (SAS Institute 1999).

The dichotomous response variable for year 1 success was coded as "1" when a stump sprouted and at least one live sprout was retained through the first growing season after cutting. Otherwise it was coded as "0". The response variable for year 4 success was coded as "1" when a stump sprouted and produced at least one live stem ≥ 7ft by the end of the fourth growing season after harvest. This criterion insured that the sprout was beyond the typical browse height of white-tailed deer (*Odocolieus virginianus* Boddaert) and in a highly favorably competitive position (Gould et al. 2004). Because our definition of year 4 success is probably conservative (i.e., some "unsuccessful" sprouts likely contribute to third-decade stocking), 100 percent survival was assumed from year 4 to the third decade of stand development.

Crown areas of third-decade sprout groups were calculated from crown diameters assuming an elliptical crown shape ($CA = \pi \cdot (d_1 / 2) \cdot (d_2 / 2)$). Third-decade stocking was then calculated as a percentage on a per acre basis ($CA / 43,560 \cdot 100$). Although this measure provides a direct measure of stocking, stocking is more easily measured indirectly using Gingrich's (1967) stocking equation, which is based on stem diameter:

$$
Stocking = 10 \cdot \left( -0.0507 \cdot N + 0.1698 \cdot \sum_{i=1}^{N} D_i + 0.0317 \cdot \sum_{i=1}^{N} D_i^2 \right) \quad \text{eq. 2}
$$

- \text{N} = \text{number of stems in the sprout group}
- \text{D}_i = \text{diameter of stem } i

Hypothetically, stocking estimates using eq. 2 should agree with our direct measures of crown area. However, the equivalence of these measures of stocking has not been tested for sprout groups and it is unclear whether sprout groups occupy stand area as predicted using eq. 2. This question has important implications for regeneration modeling. If sprout groups occupy growing space differently than predicted by eq. 2, they need to be modeled and measured using different methods. Linear regression
analysis was used to determine whether stocking directly measured from crown area significantly departs from expected stocking using Gingrich's stocking equation. Analysis of variance with means separation using Duncan's Multiple Range Test (Neter et al. 1996) was used to determine whether third-decade stocking differed among species.

The final predictive models were tested by comparing predicted sprout-origin oak stocking in 34 mature oak-dominated stands with observed sprout-origin oak stocking in a second sample of 31 stands that originated after the harvest of oak overstories 20-33 yrs prior to measurement (see Gould et al. 2003). Both sets of stands are located on Pennsylvania State Forest Land in the Ridge and Valley physiographic province (Cuffs et al. 1989). Pre-harvest overstory compositions in the regenerated third-decade stands were similar to the current overstories in the mature stands, suggesting similar sprouting potentials. However, the two samples are independent and predicted and observed oak stocking were not expected to match exactly. Instead, a general agreement between the means and distributions of sprout-origin oak stocking values was expected.

**Results**

Logistic regression model fits for the initial sprouting model \( P(S_1) \) are summarized in Table 4.2. The model with dbh as the only independent variable was statistically significant, but explained relatively little variation \( (r^2 = 8.1 \text{ percent}) \) and had poor concordance \( (c = 0.647) \). Additional model terms were added individually to the dbh model. Among these other terms, the species and dbh x species terms improved the model most, increasing the \( r^2 \)-value to 24.3 percent and concordance to 0.737. Other individual independent variables, except for age, were statistically significant, but contributed relatively little to the model.

The species terms were incorporated into the model and other independent variables were again individually added with two-way interactions (Table 4.2). Although several variables remained statistically significant, they added relatively little to the explanatory power of the model. The addition of slope position had the greatest influence on the coefficient of determination \( (r^2 = 29.0 \text{ percent} \text{ vs. 24.3 percent with dbh}) \).
Table 4.2. Statistical comparisons of initial sprouting models.

<table>
<thead>
<tr>
<th>Full Model</th>
<th>$r^2$</th>
<th>$P_{\text{full} - \text{reduced}}$</th>
<th>$c$</th>
</tr>
</thead>
<tbody>
<tr>
<td>dbh</td>
<td>8.1</td>
<td>&lt;0.001</td>
<td>0.647</td>
</tr>
<tr>
<td>dbh + age + interaction</td>
<td>8.2</td>
<td>0.833\textsuperscript{a}</td>
<td>0.647</td>
</tr>
<tr>
<td>dbh + species + interactions</td>
<td>24.3</td>
<td>&lt;0.001\textsuperscript{a}</td>
<td>0.737</td>
</tr>
<tr>
<td>dbh + site class + interactions</td>
<td>10.7</td>
<td>&lt;0.001\textsuperscript{a}</td>
<td>0.658</td>
</tr>
<tr>
<td>dbh + aspect class + interactions</td>
<td>10.3</td>
<td>&lt;0.001\textsuperscript{a}</td>
<td>0.664</td>
</tr>
<tr>
<td>dbh + position class + interactions</td>
<td>12.5</td>
<td>&lt;0.001\textsuperscript{a}</td>
<td>0.674</td>
</tr>
<tr>
<td>dbh + slope class + interactions</td>
<td>12.9</td>
<td>&lt;0.001\textsuperscript{a}</td>
<td>0.683</td>
</tr>
<tr>
<td>dbh + species + site class + interactions</td>
<td>26.2</td>
<td>0.001\textsuperscript{b}</td>
<td>0.748</td>
</tr>
<tr>
<td>dbh + species + aspect class + interactions</td>
<td>25.7</td>
<td>0.010\textsuperscript{b}</td>
<td>0.747</td>
</tr>
<tr>
<td>dbh + species + position class + interactions</td>
<td>29.0</td>
<td>&lt;0.001\textsuperscript{b}</td>
<td>0.766</td>
</tr>
<tr>
<td>dbh + species + slope class + interactions</td>
<td>27.1</td>
<td>0.002\textsuperscript{b}</td>
<td>0.757</td>
</tr>
</tbody>
</table>

\textsuperscript{a.} reduced model = dbh.
\textsuperscript{b.} reduced model = dbh + species + dbh x species.

and species only) but had little effect on concordance ($c = 0.766$ vs. 0.737). This marginal gain from adding an additional model term was considered insufficient to offset the increase in model complexity. The final logistic regression model to predict the probability that a given oak will sprout contained three terms -- dbh, species, and dbh x species. The Hosmer and Lemeshow test failed to show evidence of lack-of-fit for the model ($p = 0.28$).

Among the stumps that initially sprouted, 76 percent had at least one stem $\geq 7$ ft tall, four growing seasons after cutting (Table 4.3). However, logistic regression failed to detect a statistically significant relationship between sprout group survival and dbh or species ($r^2 = 5.8$ percent, $p = 0.08$). There is some evidence that the rate of success for white oak is lower (53 percent) than for the other species (about 77 percent), but the small sample size for white oak (15 stumps) provides little statistical power.
Table 4.3. Summary of year four success rates

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>Yr 4 Success (percent)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Q. alba</td>
<td>15</td>
<td>53.3</td>
</tr>
<tr>
<td>Q. prinus</td>
<td>183</td>
<td>77.0</td>
</tr>
<tr>
<td>Q. rubra</td>
<td>88</td>
<td>78.4</td>
</tr>
<tr>
<td>Q. velutina</td>
<td>35</td>
<td>77.1</td>
</tr>
<tr>
<td>All species</td>
<td>321</td>
<td>76.3</td>
</tr>
</tbody>
</table>

Accordingly, $P(S_4)$ was not considered to differ by species or size, and was set at 76 percent.

Consequently, $P(S_4)$ differed little from expected stocking measured directly by crown area stocking for oak sprout groups (Figure 4.1). The linear regression coefficient, 0.959, is close to 1.0 and the intercept, 0.041, is fairly small. These results
Table 4.4. Summary of third-decade sprout group measurements. Stocking values with different superscripts differ at the $\alpha = 0.05$ level.

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>Stocking (percent)</th>
<th>Stems (N)</th>
<th>DBH (in)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Q. alba</td>
<td>84</td>
<td>0.41$^d$</td>
<td>1.7</td>
<td>6.1</td>
</tr>
<tr>
<td>Q. coccinea</td>
<td>77</td>
<td>0.60$^{ab}$</td>
<td>2.0</td>
<td>7.5</td>
</tr>
<tr>
<td>Q. prinus</td>
<td>87</td>
<td>0.66$^a$</td>
<td>2.3</td>
<td>7.2</td>
</tr>
<tr>
<td>Q. rubra</td>
<td>85</td>
<td>0.52$^{bc}$</td>
<td>2.2</td>
<td>6.4</td>
</tr>
<tr>
<td>Q. velutina</td>
<td>96</td>
<td>0.48$^{cd}$</td>
<td>1.8</td>
<td>6.8</td>
</tr>
</tbody>
</table>

suggested the two measures of stocking are approximately equivalent. For example, a sprout group with 0.5 percent stocking using the Gingrich equation had about 0.52 percent stocking based on direct measurements. Variation between the two measures of stocking appears to increase with increasing stocking, but there is little evidence for a systematic difference.

The average growing space occupied by sprout groups in the third-decade after harvest differed among species ($F = 13.9, p < 0.001$). Chestnut and scarlet oak sprout groups occupied the most growing space (0.66 and 0.60 percent stocking, respectively), while white oak occupied the least (0.41 percent stocking) (Table 4.4). Sprout groups of all species maintained more than one live stem, on average, into the third-decade. Mean sprout group dbh ranged from 6.1 – 7.5 in.

Figure 4.2 illustrates the final models (eq. 1) to predict third-decade stocking based on parent tree dbh for white oak, chestnut oak, northern red oak, and black oak. The shape of each curve is determined by the probability of sprouting. The white oak model shows a rapid loss in sprouting ability with increasing diameter. The northern red oak model, in contrast, shows little loss in sprouting ability with increasing diameter. The y-intercepts of the models reflect expected third-decade crown areas and year 4 success, in addition to sprouting potential. Chestnut oak, for example, has high sprouting potential among small trees and occupies more growing space than other species. Hence,
Figure 4.2. Third-decade stocking models for northern red oak (upper left), black oak (upper right), chestnut oak (lower left), and white oak (lower right). Model equations are given in each graph.
expected third-decade stocking for chestnut oaks is greater than for the other species across the range of diameter classes. White oak, in contrast, has relatively poor sprouting potential and occupies less area in the third decade after harvest. Expected third-decade white oak stocking, therefore, is generally low.

When the models were applied to mature oak-dominated stands in the Ridge and Valley province of Pennsylvania, predicted stocking values compared favorably to stocking values observed in third-decade stands that regenerated following the harvest of similar overstories (Figure 4.3). Observed sprout-origin oak stocking averaged 18.9 percent among third-decade stands. Predicted stocking calculated in advance of harvest in similar stands averaged 21.5 percent. The distributions of predicted and observed stocking values are comparable, even though they reflect two independent samples. Less than 10 percent stocking was observed in, and is predicted in, about one-quarter of
stands. Percentages of stands in most other stocking classes differ by about 6 percent. About 8 percent more stands are predicted to reach the higher stocking classes (> 40 percent stocking) than was observed in the third-decade stands. While this suggests that the model may overestimate third-decade stocking in some cases, it is also quite possible that the two samples differ in sprouting potential. Notably, the maximum predicted value (59.7 percent stocking) is close to the maximum observed value (55.2 percent stocking).

Discussion

The models presented here provide a method for estimating, in advance of harvest, the contribution of stump sprouts to third-decade oak stocking. An estimate of oak densities (stems ≥ 2 in dbh) by species and size class is required for model input. Model output is the estimated growing space occupied by oak sprouts, expressed as third-decade stocking. Directly measured third-decade stocking closely agrees with stocking using Gingrich's (1967) stocking equation. As a result, the model output should match stocking calculated from third-decade inventories.

The model parameters generally agree with published studies of oak sprout group development. Initially sprouting probabilities decline with increasing diameter and vary by species, with white oak exhibiting the lowest sprouting potential for most sizes (Weigel and Johnson 1998). Statistically significant relationships were found between sprouting probabilities and several site attributes, but the improvement to the model was too small to warrant the increase in model complexity. Other models have been developed to predict sprout-origin oak regeneration (e.g., Sander et al. 1984, Weigel and Peng 2002), but I am not aware of other attempts to quantify the growing space occupied by individual sprout groups at the end of the regeneration period. This model element appears critical for accurately predicting third-decade stocking. On average, sprout groups occupy much more growing space in third-decade stands (about 0.4 to 0.7 percent stocking per group) than would be expected of individual seed-origin oaks (about 0.1 percent stocking per stem) (Gingrich 1971). The difference is due to the more rapid
growth of sprout-origin versus seed-origin stems and the tendency of sprout groups to retain more than one stem into the third decade of development.

The success rate of sprout groups between the first year after cutting and third decade (76 percent) is similar to, though somewhat lower than, estimates reported elsewhere (Roth and Hepting 1969, Sander et al. 1984). In this case, the estimate was based on the assumption that all sprout groups with at least one stem over 7ft in the fourth year after cutting will be successful into the third decade. Consistent with the trend of decreasing influence of parent tree attributes over time, parent tree species and diameter did not prove useful for predicting fourth-year success. As our sample is remeasured at more advanced stages of the development, statistically significant relationships may be found and can be incorporated into the model if they prove useful.

A model was not developed for scarlet oak, a fairly common species in the central Appalachians, due to an insufficiency of data on initial sprouting. The northern red oak model may be used as a reasonable substitute. Weigel and Johnson (1998) did not find a significant difference in the relationship between parent tree diameter and initial sprouting for these two species. The average growing space occupied by scarlet oak sprout groups did not differ significantly from northern red oaks in this study, suggesting similar development of the two species.
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Chapter 5

Developing Oak Regeneration Guidelines for the Central Appalachians

Abstract

The development of guidelines for the regeneration of oaks (*Quercus* spp.) in the central Appalachians is presented. The guidelines consist of 1) methods to evaluate oak regeneration potential in advance of harvest, and 2) decision charts to identify appropriate prescriptions based on existing regeneration potential and management goals. Oak regeneration potential is evaluated using predictive models that estimate future oak stocking. Predictive models include a seed-origin regeneration model that estimates "third-decade" stocking (e.g. oak stocking in the third-decade after harvest) that develops from oak seedlings and a sprout-origin oak regeneration model that estimates third-decade stocking from oak stump sprouts. An understory classification system is used to help identify potential barriers to regeneration success. Overstory removals are recommended when the current oak regeneration potential is adequate to meet management goals. Otherwise, prescriptions designed to enhance seed-origin oak regeneration potential are recommended.

Introduction

Oak-dominated forests occupy much of the forestland in the central Appalachian region. Oaks have a long history of dominance in the region (Abrams 2002) and are often considered the best species for many sites due to their high value for timber and wildlife (Krikpatrick and Pekins 2002). With this in mind, the goal of regeneration treatments in oak-dominated stands is usually to regenerate new stands with a large oak component. Even-aged silvicultural systems that rely on natural regeneration are generally the best option for achieving this goal (Sander 1977). However, the
regeneration of oaks is not assured after a final overstory removal unless a high potential for oak regeneration is already in place. A stand's oak regeneration potential refers to the capacity for advance oak regeneration (i.e., oak seedlings) and stump sprouts to capture and maintain growing space after an overstory removal.

Guidelines for assessing oak regeneration potential in advance of harvest have been developed for the Missouri Ozarks (Sander et al. 1984, Dey 1991), the southern Appalachians (Loftis 1990), New England (Hibbs and Bentley 1983), and southern bottomland stands (Belli et al. 1999). Some of these guidelines simply prescribe a fixed density of advance oak regeneration, while others employ more sophisticated research-based models (e.g., Sander et al. 1984). Similarly, some guidelines indicate only whether oak regeneration potential is "adequate" for an overstory removal (e.g., Hibbs and Bentley 1983), while others produce quantitative predictions of the importance of oak in the future stand (e.g., Dey 1991).

In this chapter, the development of new oak regeneration guidelines for the central Appalachians is described. The guidelines are designed to deliver emerging research results to forest managers to improve the predictability and success of oak regeneration treatments. Models to predict future oak stocking based on pre-harvest conditions and decision charts to identify appropriate prescriptions based on model results and management goals are the main components of the guidelines. The development of the models and decision charts are described in the following sections and the complete guidelines are found in Chapter 6.

A primary goal of this chapter is to explain the rationale and assumptions that went into creating the guidelines. The construction of the decision charts, in particular, relied heavily on expert interpretation of emerging information. A workshop was held in February 2004 to gather input from researchers with the USDA Forest Service's Northeast Forest Experiment Station and from forest managers with the Pennsylvania DCNR, Bureau of Forestry. Several important improvements were made to the guidelines based on suggestions from workshop participants.

The guidelines were developed, in large part, using data from two studies of oak regeneration development on Pennsylvania State Forest land. Stands included in the
studies were dominated by northern red oak (Quercus rubra L.), chestnut oak (Quercus prinus L.), white oak (Quercus alba L.), black oak (Quercus velutina Lam.), and scarlet oak (Quercus coccinea Muenchh.). The FM-T-24 study includes 42 oak-dominated stands that were measured before harvest, clearcut, and then remeasured during the third decade of stand development (about 20 - 30 yrs after harvest). Data from this study were used to develop a predictive model of third-decade seed-origin oak stocking based on measures of advance oak regeneration. The Pennsylvania Regeneration Assessment (PRA) study is a more detailed, on-going study of regeneration development in 52 oak-dominated stands. Data from this study were used to refine the seed-origin regeneration model, to develop a sprout-origin model, and to develop an understory vegetation classification system (Northrup 2003). Results from PRA study were also used to develop the decision charts used to assign prescriptions.

Models and Measurements

Field data are collected for use in two research-based oak regeneration models and an understory vegetation classification system. Basic descriptions of the regeneration models are provided here. Thorough descriptions of model development will be published elsewhere (see Chapters 3 and 4). The seed-origin oak regeneration model is used to estimate third-decade oak stocking (i.e., the percentage of stand area occupied by oaks in the third-decade after harvest) originating from oak seedlings (< 2 in dbh). Third-decade stocking estimates are based on the distribution, density, and size of advance oak regeneration. The sprout-origin oak regeneration model is similarly used to estimate third-decade oak stocking originating from stump sprouts. Estimates are based on the species, size, and density of oaks > 2 in. dbh in the parent stand. The understory vegetation classification system is used to identify potential obstacles to regeneration success based on the density and composition of understory vegetation.

The seed-origin oak regeneration model was developed using data from the FM-T-24 and PRA studies. Long-term data from the FM-T-24 study were used to develop a "base" model linking third-decade seed-origin oak stocking to the distribution of advance
Figure 5.1. Base model relationship between the distribution of advance oak regeneration and third-decade seed-origin oak stocking in the FM-T-24 stands.

Advance oak regeneration was measured on 60 milacre plots (3.7 ft radius) per stand. The distribution of advance oak regeneration is the percentage of plots with at least one oak seedling. The base model fit is shown in Figure 5.1. Although there is a clear relationship between the distribution of advance oak regeneration and third-decade seed-origin oak stocking, there is a great deal of variation in stands where the distribution exceeded 65 percent. The density and size of advance oak regeneration likely contributed to the variation in seed-origin oak stocking, but these attributes were not measured in the FM-T-24 study.

More detailed data from the PRA study were used to fit a second model that used the size, density, and distribution of advance oak regeneration to reproduce the relationship found in the base model. The second model estimates the probability that an
Figure 5.2. Seed-origin regeneration model illustrating the relationship between plot aggregate height and the probability that an oak will successfully occupy the plot in the third decade after harvest.

The relationship between aggregate height and the probability of plot-level success is shown in Figure 5.2. About 9 out of 100 milacre plots that contain a single 1 ft oak seedling are expected to be occupied by an oak in the third decade after harvest. If the plot contains two 1 ft seedlings (or one 2 ft seedling) the probability of success
increase to about 17 out of 100 plots. Clearly, seed-origin oak regeneration potential can be improved through treatments that increase seedling size and/or seedling density.

The sprout-origin regeneration model was developed, in part, from measurements of 1173 oak stumps in the PRA study. Stumps were randomly selected about 1 yr after cutting. Stump diameter, species, and the density and size of sprouts, if present, were recorded for each stump. Statistical models were developed to predict sprouting probabilities based on dbh (reconstructed from stump diameter) and species. For all species, sprouting frequencies decrease with increasing dbh. Remeasurements on 321 stumps, 4 yrs after cutting, indicated that about 76 percent of sprout groups survived and grew fast enough to be successful in the regenerated stand. Sprout group size in the third decade after harvest was estimated from measurements on 429 sprout groups that were between 24- and 27-yrs-old. Mean sprout group sizes differed by species. For a given oak species, the mean sprout-group size was multiplied by its sprouting probability to yield an estimate of third-decade sprout-origin oak stocking.

Understory vegetation can strongly influence oak regeneration success. An understory classification system was developed using data from the PRA study to identify understory conditions that are problematic, or potentially favorable, for oak regeneration development (Table 5.1). The classification system is based largely on the classes described by Northrup (2003). Comparisons of advance oak regeneration densities between classes demonstrated that larger oak seedlings (> 1 ft) are associated with understories predominantly composed of blueberry (Vaccinium spp.) and black huckleberry (Gaylussacia baccata (Wangenh.) K.Kock) (Northrup 2003). The occurrences of these understory species may reflect underlying topographic and edaphic conditions that are relatively favorable for oak regeneration development (Fike 2002). Most other understory classes include species, such as hayscented fern (Dennstaedtia punctilobula (Michx.) Moore) and mountain-laurel (Kalmia latifolia L.), that have been found to inhibit oak regeneration development. Inhibiting vegetation cover of 30 percent or more is commonly considered problematic for regeneration development (Marquis et al. 1992). This threshold generally agrees with the mean cover values found in Northrup's (2003) cover classes.
Table 5.1. Understory vegetation classes.

<table>
<thead>
<tr>
<th>Class</th>
<th>Description</th>
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<tbody>
<tr>
<td>F</td>
<td>( \geq 30% ) cover by rhizomalous ferns (hayscented, New York, and bracken fern).</td>
</tr>
<tr>
<td>ML</td>
<td>( \geq 15% ) cover by mountain-laurel.</td>
</tr>
<tr>
<td>BB</td>
<td>( \geq 30% ) cover, primarily huckleberry or blueberry.</td>
</tr>
<tr>
<td>LS</td>
<td>( \geq 30% ) low shade: non-oak tree or shrub cover from 5 – 20ft.</td>
</tr>
<tr>
<td>OT</td>
<td>( \geq 30% ) cover by non-oaks, but not in any other category.</td>
</tr>
<tr>
<td>NO</td>
<td>&lt; 30% total cover (i.e., mostly bare).</td>
</tr>
</tbody>
</table>

**Identifying Prescriptions**

The guidelines include worksheets to record stand data, calculate expected seed-origin and sprout-origin third-decade oak stocking, and classify and summarize understory vegetation. After stand data are collected and summarized, decision charts are used to identify prescriptions. The first question addressed in the decision charts is whether expected total oak stocking (seed + sprout) is sufficient to meet the user's goal. Prescriptions are provided for regenerating the stand when expected total oak stocking is considered sufficient. Prescriptions for improving seed-origin oak regeneration are provided when total oak stocking is considered low.

**Overstory Removal**

When expected third-decade oak stocking meets the user's goal, a final overstory removal is typically prescribed. The exception is when inhibiting vegetation is very high (> 60 percent) and cannot be controlled by selective herbicide application. Very high levels of inhibiting vegetation may threaten regeneration success, even when oak regeneration appears otherwise adequate. Treating very high inhibiting vegetation before proceeding with an overstory removal is recommended. If the treatment, such as a broadcast herbicide application, reduces the stand's oak regeneration potential, the stand should be re-evaluated after the treatment.
Figure 5.3. Oak regeneration development in 10 stands from the PRA study that were regenerated by clearcutting without a post-harvest fence. For each stand, bars show oak seedling densities about 1 year before harvest, 1 yr after harvest, and 4 yrs after harvest (left to right). Stands to the left of the dotted line had ≥10 ft aggregate oak seedling height on <30 percent of sample plots. Stands to the right of the line had ≥10 ft aggregate oak seedling height on ≥30 percent of sample plots.

White-tailed deer browsing has major impacts on regeneration in the central Appalachians. Fencing to exclude deer is often needed to reach regeneration goals and fencing is recommended in most cases. However, fencing is costly, and it is valuable to recognize cases where fencing does not appear to be necessary. Fencing is not recommend in conjunction with an overstory removal when high levels of advance oak regeneration have developed without a fence, suggesting relatively low browsing.
pressure. Figure 5.3 illustrates oak regeneration development in 10 stands from the PRA study that were clearcut with reserves and not fenced after harvest. For each stand in Figure 5.3, the left-most bar shows oak seedling densities shortly before harvest, the middle bar shows seedling densities 1 yr after harvest, and the right bar shows seedling densities 4 yrs after harvest. Bars are divided into three parts representing different size classes -- < 1 ft, 1 - 4 ft, and > 4 ft.

Stands are divided into two groups in Figure 5.3, those with at least 10 ft of aggregate oak regeneration height on at least 30 percent of sample plots (right), and those that did not meet this criterion (left). Most of the stands that exceeded the criterion appear to be developing satisfactorily without a fence. They generally did not experience significant losses of oak seedlings after harvest and oak seedling growth was also generally favorable. On average, these stands had 2400 oak seedlings / acre > 4 ft, four years after clearcutting. A clear exception is stand 9803, which experienced a sizable loss of oak seedlings and had only about 450 seedlings / acre > 4 ft, four years after harvest. Stand 9803 just reached the criterion, with 10 ft of aggregate oak seedling height on 32 percent of sample plots. However, other stands that just reached the criterion (9717 and 9715) developed much more favorably, suggesting the threshold is not too low. Most stands that did not meet the criterion experienced marked declines in oak seedling densities. These stands had, on average, 450 oak seedling / acre > 4 ft, four years after clearcutting.

Fencing is recommended following overstory removal except when aggregate oak seedling height is ≥ 10 ft on at least 30 percent of sample plots. This criterion provides some guidance to forest managers, but is clearly not infallible. Past experience in a particular area should also factor strongly into the decision of whether to fence after overstory removal.
Figure 5.4. Oak regeneration development in 6 stands in the PRA study that were treated with a shelterwood cut.

**Shelterwood**

The shelterwood regeneration method is widely recommended for stands lacking sufficient oak regeneration potential. Oak regeneration potential may be improved by increasing the size of existing oak seedlings in the more favorable growing environment created by the shelterwood cut and by increasing oak seedling density. While the growth of established oak seedlings can be expected to accelerate after a shelterwood cut (when combined with fencing), it is less clear whether managers can depend on periodic acorn crops to increase oak seedling densities. Without a fortuitous acorn crop, less desirable species may benefit most from the improved growing conditions. A risk of the shelterwood method is that it will encourage the establishment and growth of less desirable plant species that can later inhibit oak regeneration establishment.
Figure 5.4 illustrates patterns of oak seedling development in six stands from the PRA study that were treated with shelterwood cuts after their first measurement. Cutting intensities ranged from about 34 percent of basal area removed (stand 9907) to about 80 percent removal (stand 9716). All stands other than stand 9602 and 9716 were treated with a broadcast herbicide application after the first measurement to reduce inhibiting vegetation. All stands were fenced before or shortly after the shelterwood treatment. Stands 9602, 9611, and 9716 had advance oak regeneration on less than 65 percent of sampled plots. Stands 9908, 9606, and 9907 exceeded this threshold. The 65 percent distribution threshold was identified from the results for the FM-T-24 study (see Figure 5.1). Stands below this threshold uniformly failed to regenerate with much seed-origin oak, but a wide range of outcomes was observed for stands above the threshold. Although seedling growth is evident for all stands, increases in seedling density were fairly modest for stand 9602 and there was little increase in stand 9611. The large increase in oak seedling density in stand 9716 resulted from a large acorn crop after the stand was fenced, but before the shelterwood cut had started. Stands with well-established advance oak regeneration experienced declines in seedling densities after herbicide applications, but densities later rebounded.

The mixed results found for oak seedlings contrast with developmental patterns in red maple, which are illustrated in Figure 5.5 for the same set of stands. Red maple is a common competitor to oaks in the central Appalachians and may inhibit oak regeneration success. In stands 9602 and 9611, where shelterwood treatments led to modest or no improvement in oak regeneration densities, red maple densities increased dramatically. Red maple seedlings were already very numerous in stands 9716 and 9907 and remained so after the shelterwood cut. Other stands experienced less dramatic, though marked, increases in red maple density.

To balance the potential benefits of shelterwood cuts with the risk of increased competition, the shelterwood regeneration method is recommended in stands where 1) expected third-decade oak stocking is too low to meet management goals, 2) oak regeneration is already established and 3) inhibiting vegetation levels are low (> 30 percent). The distribution of advance oak regeneration is used as a criterion for
Figure 5.5. Red maple regeneration development in 6 stands in the PRA study that were treated with a shelterwood cut.

An exception is when inhibiting vegetation exceeds 30 percent, but the forest manager does not consider it problematic or expects to reduce it without comprising the stand's oak regeneration potential. Examples of the latter include a selective herbicide application and possibly prescribed fire. A second exception originated from forest managers who have found a light shelterwood cut is appropriate in stands without well-established advance oak regeneration. This, of course, is at the manager's discretion.
Consider a shelterwood treatment in such cases if the potential benefits appear to outweigh possible risks.

Inhibiting Vegetation Treatment

Non-tree understory vegetation and small undesirable trees can inhibit oak seedling establishment and growth. Inhibiting vegetation may need to be reduced through herbicide application or other means before oaks can be successfully regenerated. Treating understory vegetation is recommended when 1) expected third-decade oak stocking is too low to meet management goals and 2) 30 percent or more of sample plots are occupied by inhibiting vegetation. The 30 percent threshold was adopted from regeneration guidelines for Allegheny hardwood stands (Marquis et al. 1992) and reflects expert opinion. Herbicide treatments are not recommended when 50 percent or more of sample plots are classified in the BB understory vegetation class. This understory class reflects generally favorable conditions for oak regeneration development.

Conclusions

The regeneration guidelines are based on the best available information on oak regeneration development in the central Appalachian region. Continuing research will lead to refinements, and possibly major revisions, to the guidelines. The guidelines are meant to be a vehicle for adaptive management, and the models and recommendations will be periodically re-evaluated to incorporate emerging information. Forest managers will hopefully use the guidelines when considering regenerating oak-dominated stands. User feedback is also valuable and users are invited to contact us with suggestions for improvements.
Literature Cited


Chapter 6

Oak Regeneration Guidelines for the Central Appalachians

Introduction

These guidelines are designed to aid forest managers in securing adequate oak regeneration before harvesting oak-dominated stands. What comprises “adequate” oak regeneration may vary from stand to stand. The guidelines provide a method for measuring a stand’s oak regeneration potential in advance of harvest. The user must decide whether a stand’s regeneration potential, measured in oak stocking in the third-decade after harvest, meets his or her regeneration goal.

The guidelines contain three parts. The first part describes procedures for collecting the data to 1) estimate a stand’s oak regeneration potential from seed-origin regeneration and stump sprouts, and 2) identify barriers to regeneration success. Work forms are included for collecting and summarizing seed-origin and sprout-origin data. The second part consists of two decision charts designed to determine an appropriate prescription based on stand conditions and the user’s regeneration goal. Prescriptions are described in detail in the third part of the guidelines.

The guidelines augment professional judgment; they do not replace it. Although the guidelines are based on current research, it is not possible to identify every situation encountered in practice. Prescriptions should be adapted based on specific conditions and professional experience. As new research results become available, the guidelines will be revised to reflect our expanded understanding of the regeneration process.
Data Collection

Collect regeneration data using the Seed-Origin Oak Regeneration Work Form (pg 119) and the Sprout-Origin Oak Regeneration Work Form (pg 120). Measure 15 plots in stands of 15 acres or less. Add one additional plot per acre for stands over 15 acres, up to a maximum of 30 plots. Advanced oak regeneration is measured on milacre (3.7 ft radius) plots. Competing vegetation and sprout-origin regeneration data are collected on 1/20th acre (26.3 ft radius) plots. Use the same plot center for both plots.

A. Seed-Origin Regeneration Work Form

A1. Measure advance oak regeneration on milacre plots. On each plot, measure heights to the nearest foot of all oaks at least 1-yr-old and < 2” dbh (include larger stems if they will not be cut). Use dot tallies to record the number of stems in each height class. Tally stems <1 ft tall in the 0.5 ft height class. Print the heights of stems > 4.5 ft tall in the "5+" box. Add the heights together and record in Table 1 under “Total Height.” For example: 3 oak seedlings are tallied in the 1 ft height class and 2 seedlings in the 2 ft class. Total Height = 1 + 1 + 1 + 2 + 2 = 7 ft.

A2. Determine the “Stocking Value” from Table 2 that corresponds to the plot’s total height. Record the stocking value under “Plot Stocking” in Table 1.

A3. Assign the 20th acre (26.3 ft radius) around each plot to a vegetation cover class using the Vegetation Classification Guide (Table 3). Reading the guide from top to bottom, find the first class that describes the plot. For example, a plot that meets the criteria for both the "F" class and the "ML" class is assigned to the "F" class. Circle the appropriate code under "Vegetation Cover Class" in Table 1. Once a code is circled, underline any other classes that apply. Except where stated otherwise, estimate cover looking downward from 5ft above the plot. Use the Cover Guide (Figure 1) to aid in determining percentage cover.
A4. Record sprout-origin data (see instructions below) before moving to the next plot.

A5. Data summary. Count the number of plots where total height was > 0 (i.e., at least one stem of advance oak regeneration was present) record the sum in the "Totals" row, beside ">0". Do the same for plots where total height was ≥ 10 ft.

A6. Sum the values in the “Plot Stocking” column. Record the sum in the “Totals” row.

A7. Count the number of plots assigned to each vegetation cover class (circled codes). Record these sums in the "Totals" row. Each plot should be counted once. Do not count codes that are underlined.

A8. Calculate the percentage of plots where total height was > 0 by dividing the count by the number of plots measured and multiplying the product by 100. For example: 25 of 30 plots had a total height > 0, so the percentage of plots is 25 / 30 x 100 = 83%. Use the same procedure to calculate the percentage of plots where total height was ≥ 10 ft and the percentage of plots assigned to each vegetation cover class. Record these percentages in the "Percentages" row.

A9. Calculate seed-origin oak stocking by dividing the “Plot Stocking” total by the number of plots measured. Record under “Seed-Origin Oak Stocking.” This value represents expected seed-origin oak stocking in the third-decade after harvest.

B. Sprout-Origin Regeneration Work Form

B1. Collect data on 1/20th acre plots (26.3 ft radius). On each plot, measure the dbh (by diameter class in Table 4) for all oaks ≥ 2 in. Use dot tallies to tally oaks under the appropriate species names and diameter classes in Table 4. For example, a 16” black
oak would be tallied in the “Black Oak” row and the “15-18 (inch)” column. Tally oaks from all plots together.

B2. Data summary. After measuring the last plot, calculate the average plot density of each species and diameter class. First, sum the dot tallies by species and diameter class. Second, record the total number of overstory plots measured in the “N” rows. Next, divide each tally total by N. Round to one decimal place and record this number in the “Average Density” row. For example: 11 black oaks were tallied in the 15-18” diameter class on 30 plots, the average density is $11 / 30 = 0.37 = 0.4$.

B3. Multiply the average densities by the “Stocking Factors” and enter the products, with one decimal place, in the “Sprout Stocking” rows. For example: an average of 0.4 black oak were tallied in the 15-18” diameter class, stocking = $0.4 \times 3.3 = 1.3$.

B4. Sum the sprout stocking values for each species and record the sum at the far right of the row, under “Species Total.”

B5. Sum species totals and record under “Sprout-Origin Stocking.” This value represents expected sprout-origin stocking in the third-decade after harvest.

Determining a Prescription

1. Fill out the Regeneration Data Summary (Table 5) on page 120. Record the seed-origin oak stocking value calculated on the Seed-Origin Oak Regeneration Work Form. Likewise, record the sprout-origin oak stocking value calculated on the Sprout-Origin Oak Regeneration Work Form. Sum the two stocking values and record under "Total Oak Stocking". This represents expected oak stocking in the dominant, codominant, and intermediate crown classes during the third-decade after harvest. Record the percentage of plots in each vegetation class from the Seed-Origin Oak Regeneration Work Form. Sum the percentage of plots in the “F”, “ML”, “LS”, and
“OT” vegetation cover classes and record the sum under “Inhibiting Vegetation.”
Record the percentage of plots with total heights > 0 ft and the percentage with total heights ≥ 10 ft.

2. Use Charts I and II to determine a prescription to meet your regeneration goal. Begin at the top of Chart I. First consider whether “Total Oak Stocking” is consistent with the desired future stand condition. As a guide, oak stocking > 50 percent represents an oak-dominated stand during the third-decade after harvest. Oak stocking of 30-50 percent represents a strong oak component during the third-decade after harvest, with other species occupying the majority of the stand. Oak stocking of 15 to 30 percent represents a minor oak component and <15 percent represents little or no oak. Use this information to answer the first question on Chart I.

3. Follow Chart I and, if needed, Chart II until a prescription is found. Questions include reference numbers to find necessary information in Table 5. Prescriptions are described in detail below.

**Prescriptions**

*Prescription I: Overstory Removal*

The oak regeneration potential is adequate to regenerate the stand with an overstory removal. If expected total oak stocking is < 50 percent, the stand may not fully regenerate unless sources of non-oak regeneration are also present. Other resources should be used to determine the adequacy of non-oak regeneration. All, or most, stems > 2” dbh should be felled. Basal spraying of non-oak seedlings and saplings is recommended if inhibiting vegetation, primarily of class T, occurs on ≥ 60 percent of plots. The presence of abundant advanced oak regeneration indicates that deer browsing is not likely to inhibit regeneration success; therefore a fence is not recommended unless prior experience in the area suggests otherwise.
**Prescription II: Overstory Removal with Post-Harvest Fence**

The stand is ready to regenerate with an overstory removal. If expected total oak stocking is < 50 percent, the stand may not regenerate adequately unless sources of non-oak regeneration are also present. Other resources should be used to determine the adequacy of non-oak regeneration. All, or most, stems > 2” dbh should be felled. Basal spraying of non-oak seedlings and saplings is recommended if inhibiting vegetation, primarily of class T, occurs on ≥ 60 percent of plots. The lack of abundant advanced oak regeneration may indicate that deer browsing will inhibit regeneration success; therefore a post-harvest fence is recommended to maintain the current potential for oak regeneration. The fence should be constructed as soon as possible after the overstory removal is complete.

**Prescription III: Shelterwood and Fence**

A shelterwood treatment is recommended to improve the growth of existing advanced oak regeneration. Up to one-half of the initial basal area should be removed, but the residual stand should have more or less continuous canopy cover. Non-oaks should be the first trees marked for removal. Research results indicate overstory black birch and red maple strongly impact future stand composition. Consequently, all stems of these species should be removed where possible. Fencing is recommended after treatment. Understory vegetation does not appear to inhibit the establishment and growth of regeneration at this time and no understory treatments are recommended. The stand should be reevaluated two years following treatment.

**Prescription IV: Understory Treatment and Fence**

An understory treatment to reduce inhibiting vegetation is recommended. Review the Vegetation Cover Class data recorded in Table 1 to formulate a prescription. Broadcast herbicide treatments are effective for controlling rhizomous ferns, but may be less
effective for mountain-laurel and tree vegetation. A basal herbicide application may be most effective for controlling tree vegetation. Prescribed fire, if it can be used, is another option for controlling inhibiting vegetation. Mechanical treatments, such as mowing, may be effective for treating mountain-laurel. Fencing is recommended after treatment to protect newly established seedlings. An overstory treatment is not recommended, as the understory treatment will likely negate its benefit to oak regeneration. The stand should be reevaluated two years after treatment.

Prescription V: Understory Treatment, Shelterwood, and Fence

An understory treatment to reduce inhibiting vegetation is recommended (see Prescription IV). In addition, the current level of advanced oak regeneration suggests that a shelterwood treatment may be appropriate (see Prescription III). However, the understory treatment (especially broadcast herbicide) may reduce the level of advanced oak regeneration. Understory treatments that are not expected to reduce advanced oak regeneration (i.e., prescribed burning, mowing, basal herbicide applications) may be done in conjunction with a shelterwood. Alternately, a shelterwood without an understory treatment may be appropriate if the level of inhibiting vegetation is only marginally high (30 – 40 percent of plots). Fencing is recommended to protect existing seedlings and allow new seedling to establish.

Prescription VI: Fence in Advance. Consider Shelterwood. Or wait

Fencing is recommended to allow oak regeneration to establish without high levels of deer browsing. Understory vegetation does not appear to be a factor inhibiting the establishment and growth of oak regeneration. The current level of advanced oak regeneration appears too low to benefit from an overstory treatment. However, a light shelterwood treatment (< 25 percent removal, mainly in smaller trees) may stimulate the establishment of new oak regeneration in some cases. The benefit of a shelterwood treatment must be weighed against the possibility that it will stimulate the establishment
and growth of undesirable non-oak regeneration. Professional judgment and past experience should be used to determine whether this treatment is appropriate. Alternately, no treatments may be appropriate at this time and the stand should be reevaluated in 2 yrs.
Table 1. Understory Data Collection

<table>
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<tr>
<th>Oak Seedling Height Class (ft)</th>
<th>Total Height</th>
<th>Plot Stocking</th>
<th>Vegetation Cover Class</th>
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</table>

Figure 1. Cover Guide

15 percent cover
30 percent cover

Table 3. Vegetation Classification Guide (20th plots plots)

<table>
<thead>
<tr>
<th>Code</th>
<th>Description</th>
</tr>
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<tbody>
<tr>
<td>F</td>
<td>≥ 30% cover by rhizomalous ferns (hay-scented, New York, and bracken fern).</td>
</tr>
<tr>
<td>ML</td>
<td>≥ 15% cover by mountain-laurel.</td>
</tr>
<tr>
<td>BB</td>
<td>≥ 30% cover, primarily huckleberry or blueberry.</td>
</tr>
<tr>
<td>LS</td>
<td>≥ 30% low shade non-oak tree or shrub cover from 5 – 20 ft.</td>
</tr>
<tr>
<td>OT</td>
<td>≥ 30% cover by non-oaks, but not in any other category.</td>
</tr>
<tr>
<td>NO</td>
<td>&lt; 30% total cover (i.e., mostly bare).</td>
</tr>
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</table>
### Sprout-Origin Oak Regeneration Work Form (Version 1.2)

#### Table 4. Overstory Data Collection

<table>
<thead>
<tr>
<th>Diameter Class (in)</th>
<th>N (plots)</th>
<th>Average Density</th>
<th>Species Total</th>
<th>Stocking Factor</th>
<th>Species Total</th>
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<td>2-6</td>
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<td>7-10</td>
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<td>11-14</td>
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<td>15-18</td>
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</tr>
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<td>19-22</td>
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<td>31-34</td>
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<tr>
<td>&gt;34</td>
<td></td>
<td></td>
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<td></td>
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</tr>
</tbody>
</table>

- **Chestnut Oak**

- **N. Red Oak**

- **Scarlet Oak**

- **Black Oak**

- **White Oak**

**Sprout Stocking** =

Total Sprout-Origin Stocking

---

**Note:** The table entries are placeholder values for demonstration purposes.
Chart 1 – Regeneration Treatment Evaluation (Version 1.2)

Table 5. Regeneration Data Summary

<table>
<thead>
<tr>
<th>Seed-Origin Oak Stocking</th>
<th>Vegetation Class Percentages</th>
<th>Height &gt; 0</th>
<th>Height ≥ 10ft</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sprout-Origin Oak Stocking</td>
<td>F</td>
<td>ML</td>
<td>LS</td>
</tr>
<tr>
<td>Total Oak Stocking (Seed + Sprout)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1. Start

Is expected total oak stocking adequate to meet desired future stand condition?

1. YES

Is expected total oak stocking > 50%?

1. YES

Is inhibiting vegetation < 60%?

2. NO

Is most inhibiting vegetation class LS and controllable with basal spraying?

2. NO

Include basal spray in final prescription.

2. YES

Was Total Height ≥ 10ft on at least 30% of plots?

5. NO

Prescription II: Overstory removal with post-harvest fence.

5. YES

Prescription I: Overstory removal

Consider managing for other species (use other guidelines such as SILVAH).

NO

Go to Chart II
Chart II – Regeneration Problem Diagnostics (Version 1.2)

Start

Is inhibiting vegetation >30% and BB <50%?

Yes

Was Total Height > 0 on at least 65% of plots?

Yes

Prescription V: Understory treatment, shelterwood, and fence.

No

Can inhibiting veg. be controlled without reducing oak regeneration?

No

Was Total Height > 0 on at least 65% of plots?

Yes

Prescription III: Shelterwood and fence.

No


2 3

4

4
Chapter 7

Modeling Oak Regeneration Development: Effects of Competition

Abstract

Data from a 20-yr study of oak regeneration development in the Missouri Ozarks, USA, were used to evaluate the effects of competition on individual oak seedling success (defined as reaching a dominant or codominant crown position 20 yrs after overstory removal). Individual oak seedlings (Quercus alba L., Q. coccinea Muenchh., Q. rubra L., and Q. velutina Lam.) and all regeneration on 16.2 m² subplots were measured before harvest and remeasured periodically after clearcutting. Logistic regression models were fit to predict individual oak seedling success based on pre-harvest size (size model) and size plus measures of local competition (competition model). Competition indices were calculated as functions of the size, density, and composition of regeneration measured on subplots. Step-wise logistic regression selected oak AH₄ (sum of heights of four largest oaks on the subplot) as the best competition index to add to the size model. There was little evidence suggesting competition with other species groups influenced oak regeneration success. The size and competition models were compared by applying them to the pre-harvest subplot data and comparing expected 20-yr densities with observed densities. The competition model performed better, on average, than the size model. More importantly, the competition model better predicted 20-yr oak densities across a range of competition levels. The size model underestimated 20-yr densities somewhat under low competition and systematically overestimated densities with increasing competition. In addition, the competition model mitigated sample bias effects that caused the size model to systematically overestimate 20-yr densities. Our results indicate that simple measures of competition can appreciably improve individual tree regeneration models.
Introduction

Understanding expected outcomes to stand treatments is essential to successful silviculture. The ability to predict outcomes is particularly valuable to even-aged silvicultural systems that rely on natural regeneration. Management options are often limited after overstory removals and forest managers typically need to ensure conditions are met for adequate regeneration in advance of final harvest. Determining regeneration adequacy is not a trivial task. Overstory removal marks the beginning of what is arguably the most complex and least understood period of stand development (Rogers and Johnson 1998, Raucher et al. 2000). Research-based models that link pre-harvest conditions with conditions at the end of the regeneration period (usually several decades after harvest) can provide forest managers with valuable insight when making management decisions.

Understanding and modeling regeneration development in oak-dominated stands in the eastern United States is particularly important. Regenerating oaks in even-aged silvicultural systems depends on securing, in advance of harvest, well-distributed advance oak regeneration with the ability to successfully compete in the post-harvest environment. Securing adequate advance oak regeneration is often difficult and potentially costly, underscoring the need for methods to determine regeneration adequacy. Research-based models that predict oak regeneration success approximately 20 yrs after overstory removal have been developed for the Missouri Ozarks (Sander et al. 1984, Dey et al. 1996), the southern Appalachians (Loftis 1990), and the central Appalachians (Gould et al. in review). The models assign success probabilities (i.e., the probability of reaching a free-to-grown or dominant / codominant crown position in the future stand) to individual oak seedlings based on pre-harvest size (height and/or ground diameter) and environmental variables. The ecological process reflected by the models is superficially simple -- larger oak seedlings grow faster, which reduces their likelihood of being excluded from the upper canopy during early stand development (Sander 1971). The rate at which seedlings can accumulate height, however, is only one aspect of their competitive capacity (Spetich et al. 2002). The competitive capacity of neighboring
vegetation also influences individual seedling growth and success. Competition is a central concept in the study of forest development, but its significance for modeling natural regeneration on an individual tree basis has been largely unexplored.

Competitive interactions between desirable tree seedlings and neighboring vegetation are better understood for artificial regeneration. Site preparation treatments are routinely applied to reduce competition, thereby improving the growth and eventual success of planted seedlings (Smith et al. 1997). Retrospective and experimental studies have demonstrated the importance of local competition on seedling growth in conifer plantations, and provide some insight into the underlying ecological processes (Wagner and Radosevich 1991, White and Elliot 1992, Perry et al. 1993). Wagner and Radosevich (1991), in a study of 4- to 9-yr-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands that were planted following experimental site preparation treatments, found that seedling height and diameter were correlated with percentage cover of woody vegetation within a 2.1 m radius neighborhood. The best correlations were achieved when only woody vegetation equal to, or taller than, the focal tree was considered. In a second example, planted loblolly pine (*Pinus taeda* L.) seedling densities, sweetgum (*Liquidambar styraciflua* L.) sprouts densities, and broomsedge (*Andropogon virginicus* L.) plant densities were experimentally controlled in replicated blocks (Perry et al. 1993). Pine seedling height and diameter were repeatedly measured over a single growing season. Pine seedling growth was negatively affected both by inter- and intra-specific competition, with the magnitude of competitive effects varying between species. These examples demonstrate that competition is a function of the density (or percentage cover), size, and identity (i.e., species) of competitors. The spatial distribution of competitors is also potentially important, but requires more detailed measurements, such as distance and direction to the focal tree (Miina and Pukkala 2002). Competition does not appear to fundamentally change as trees grow larger. Similar measurements have been used to model competitive effects on tree growth beyond the seedling and sapling stages (Tome and Burkhart 1989, Uriarte et al. 2004).

Neighborhood competition has important implications for modeling the post-harvest development of oak regeneration. Probabilistic regeneration models, in effect,
assign "value" to oak seedlings, reflecting their expected contribution to the next-generation stand (Sander et al. 1984, Loftis 1990). Predictive models that lack competition terms can reasonably be expected to accurately value oak seedlings that experience about the same level of competition as those seedlings that were observed to generate the model data. However, oak seedlings that experience less competition are expected to be undervalued and, concurrently, seedlings that experience more competition are expected to be overvalued. Competition, expressed as a function of the size, density, distribution, and species of understory vegetation, can vary greatly from stand to stand due to differences in productivity, disturbance history, and cultural treatments (Johnson et al. 1989, Fredericksen et al. 1999, York et al. 2000). Intra-specific competition merits particular consideration, since it reduces the value of individual seedlings without a proportional effect on future stand composition.

The importance of competition has been alluded to in past studies (Sander 1972, Johnson et al. 1989) and demonstrated for oak seedlings planted in shelterwoods (Spetich et al. 2002), but it has not been previously addressed for individual stem modeling of natural oak regeneration. Existing research-based models (Sander et al. 1984, Loftis 1990, Dey 1991) do not account for local competition in predicting individual stem success. Competition may vary systematically with site index and topographic position, which are included in the models. However, the size, density, and composition of neighboring competitors should provide more precise information on the competitive environment. The purpose of this chapter is to evaluate the influence of local competition on individual tree model performance using a long-term data set from oak-dominated stands in the Missouri Ozarks, USA. The data are unusually valuable since measurements span the first two decades of seedling development following clearcutting, which is often considered the length of the regeneration period (Sander et al. 1984, Loftis 1990). Individual tree data were used to fit a "size" model (no competition term) and a "competition" model (competition terms included). The models were then compared by applying them to long-term subplot-level data to estimate 20-yr oak densities. I expected 1) measures of local competition would significantly influence individual tree success, and 2) the size model would adequately estimate plot-level densities on average, but
undervalue seedlings that experienced low competition and overvalue seedlings that experienced high competition. The competition model was expected to be more flexible and better estimate success across a range of competition levels.

**Methods**

*Data Collection*

Data were collected in six mixed-oak stands on the Mark Twain National Forest in the Missouri Ozarks as part of a long-term study of regeneration development after clearcutting (study OH-466). Plots were established and first measured in advance of overstory removal. Pre-harvest stands were fully stocked and dominated by white oak (*Quercus alba* L.) and black oak (*Quercus velutina* Lam.) (Dey 1991). Pre-harvest overstories were measured on 0.08 ha plots. Advance regeneration (stems < 5 cm dbh) was measured within each plot on three 16.2 m$^2$ subplots. Subplot slope positions and aspects were recorded.

All advance regeneration within the subplots was tallied by species and 0.3 m height class (up to 2.4 m). A subset of these stems was selected for detailed individual tree measurements, including species, height, and basal diameter (2.5 cm above ground). Distances and azimuths from subplot centers to these stems were recorded to facilitate relocation. Stands were harvested by silvicultural clearcutting (all stems > 5 cm cut) after the initial measurements. Subplots and individual trees were remeasured 2, 5, 10, 15, and 20 (or 21) yrs after overstory removal. Crown classes (Smith et al. 1997, pg. 30) were recorded for the 5-yr and subsequent remeasurements. Regeneration originating from cut stumps was included in the subplot remeasurements. Stems were recorded as occurring singly or as part of a sprout group. Subplot and individual tree data collected before overstory removal and 20 yrs after were used in the data analysis.
Data Analysis

Pre-harvest and 20-yr stand compositions were summarized to evaluate general compositional changes. Because this chapter is focused on the development of upper canopy trees, comparisons of composition were limited to pre-harvest trees > 12.5 cm dbh (crown classes were not measured) and 20-yr trees in the dominant and codominant crown classes. Relative basal areas and densities of common species are reported. The densities and average heights of common advance regeneration species were also summarized and are reported.

Individual tree data from 405 oak stems measured on 185 subplots were used to develop probabilistic models of individual tree success. Success was defined as reaching a dominant or codominant crown class 20 yrs after harvest. The dataset includes 148 white oaks, 198 black oaks, 39 scarlet oaks (Quercus coccinea Muenchh.), and 20 northern red oaks. Logistic regression was used for model development. Logistic regression is a statistical method for developing models with a dichotomous response variable (e.g., 20-yr success or failure) (Cook and Weisberg 1999). The resulting models estimate the probability of one outcome conditional on a set of independent variables.

Model fitting and testing occurred in two phases. In the first phase, a size model (similar to existing individual tree models) and a competition model were developed. The size model estimates an individual stem success probability based on its size and possibly topographic variables (slope position and aspect). Independent variables included stem height, basal diameter, transformations of these variables (x^2, x^{0.5}, log_e(x)), and classification variables for slope position (upper, middle, lower) and aspect (NE, SE or NW, SW). Topographic classes were selected based on past results reported by Sander et al. (1984) and Dey (1991).

Step-wise logistic regression was used to identify a best model from the set of independent variables. Independent variable selection was based on comparisons between "full" and "reduced" models, as measured by X^2-distributed differences in deviation between models fit using the maximum likelihood method (Collett 2003, pg 73). At each step, independent variables were evaluated for addition to, or removal from,
the models. Variables with larger differences in deviation were added first and removed last. The threshold for variable additions was set at P ≤ 0.05; the threshold for removal was set at P ≥ 0.10. The final model fit was evaluated using a modified coefficient of determination (r²) (Collett 2003, pg 90) and rate of concordance (c). Concordance is calculated by pairing "successful" observations with "failed" observations and comparing modeled probabilities of success (p). Pairs are in concordance when p_{successful} > p_{failed}. The c statistic is the proportion of pairs in concordance, plus one-half the proportion of ties (p_{successful} ≈ p_{failed}). Lack-of-fit was assessed with the Hosmer and Lemeshow test, which compares predicted and observed success probabilities against the chi-square distribution (Collett 2003, pg. 88). Analyses were completed using the LOGISTIC procedure in the SAS statistical software (SAS Institute 1999).

After the size model was fit, stepwise logistic regression was used to identify competition indices that significantly improved the size model and to select a best competition model. Competition indices were calculated from the pre-harvest subplot data to evaluate the influence of competing trees on individual tree success. Focal trees were removed from the subplot tree list for index calculations. Five competition indices were evaluated for three species groups (15 indices total). Competition indices for each species group were:

D: Density

D_s: Density superiority. Density of stems equal to or taller than the focal tree

AH: Aggregate height - the sum of heights of all stems. This measure efficiently summarizes seedling population size and density during early stand development (Fei in review).

AH_4: Sum of heights of the four largest stems (or fewer stems if < 4 are present) within the species group. On average, four 20-yr-old trees are expected to occupy a fully-
stocked 16.2 m$^2$ subplot (Gingrich 1967). This index focuses on the stems considered most likely to hold these positions.

$AH_4$: Aggregate height superiority. Sum of height differences (other stem - focal tree) for stems taller than the focal tree.

$D$, $AH$, and $AH_4$ are independent of the focal tree height. $D_s$ and $AH_s$ depend on focal tree height and are expected to better reflect one-sided (size asymmetric) competition (Lorimer 1983, Thomas and Weiner 1989, Schwinning and Weiner 1998).

Species groups were selected based on their abundance and competitive ability. Oaks comprised one group. Initial analysis indicated that oak advance regeneration was abundant and oaks generally dominated the post-harvest stands. Hickory ($Carya$ spp.) and shortleaf pine ($Pinus echinata$ Mill.) comprised a second group. Advance regeneration of these species was also abundant and some of these stems reached the upper canopy in the regenerated stands. Several generally small trees in the Ozarks region, flowering dogwood ($Cornus florida$ L.), blackgum ($Nyssa sylvatica$ Marsh.), and sassafras ($Sassafras albidum$ (Nutt.) Nees), had abundant advance regeneration, but largely failed to reach a dominant or codominant crown position. They were grouped into a small trees class.

After the size and competition models were developed, they were evaluated in the second phase of the analysis by comparing predicting 20-yr seed-origin oak densities with observed densities. Predicted densities were calculated by applying the models to the pre-harvest subplot data. Recorded observed 20-yr densities were modified to reduce, to the extent possible, densities of oaks originating from cut stumps. Oaks that occurred in sprout groups were not included as part of the observed 20-yr densities, since they likely originated from cut stumps (Johnson 1977). It is also possible that some single 20-yr oaks also originated from cut stumps. To lessen the influence of these trees, 20-yr densities of a given oak species were reduced if they exceeded advance regeneration densities for the same species on the same subplot. Densities were reduced on 15 percent of subplots using this method. Even with these adjustments, 20-yr observed densities
Table 7.1. Summary of pre-harvest and 20-yr relative basal area (left) and relative density (right) in sampled stands.

<table>
<thead>
<tr>
<th>Species</th>
<th>Relative Basal Area (percent)</th>
<th>Relative Density (percent)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pre-Harvest</td>
<td>20-yr</td>
</tr>
<tr>
<td>Quercus alba</td>
<td>25.3</td>
<td>37.4</td>
</tr>
<tr>
<td>Quercus velutina</td>
<td>37.0</td>
<td>20.1</td>
</tr>
<tr>
<td>Quercus coccinea</td>
<td>12.2</td>
<td>11.6</td>
</tr>
<tr>
<td>Pinus echinata</td>
<td>10.4</td>
<td>7.6</td>
</tr>
<tr>
<td>Carya spp.</td>
<td>5.7</td>
<td>6.7</td>
</tr>
<tr>
<td>Nyssa sylvatica</td>
<td>0.6</td>
<td>2.8</td>
</tr>
<tr>
<td>Quercus rubra</td>
<td>2.5</td>
<td>2.7</td>
</tr>
<tr>
<td>Quercus stellata</td>
<td>4.9</td>
<td>2.6</td>
</tr>
<tr>
<td>Others¹</td>
<td>1.4</td>
<td>8.6</td>
</tr>
</tbody>
</table>

¹Includes Acer rubrum, Cornus florida, Fraxinus spp., Juglans nigra, Prunus serotina, Sassafras albidum, and Ulmus spp.

may be somewhat overestimated since all sprout-origin oaks may not have been identified.

Results

Overstory and Regeneration Compositions

Pre-harvest and 20-yr upper canopy compositions are summarized in Table 7.1. The pre-harvest composition reflects trees > 12.5 cm dbh only and the 20-yr composition reflects dominant and codominant trees only. Pre-harvest basal area averaged 14.4 m²/ha and density averaged 247 stems / ha. Regenerated basal area averaged 11.6 m²/ha and density averaged 1533 stems / ha. The average composition of the 20-yr-old regenerated stands is highly similar to the pre-harvest composition. As a group, oaks were clearly dominant before harvest (82 percent of basal area) and the 20 yrs later (74 percent). In
terms of relative basal area, white oak became notably more important in the regenerated stands, while black oak became less important. Non-oak species were not well represented in the pre-harvest stands and did not increase appreciably in the regenerated stands. The increased importance of minor species (Others) in the regenerated stands is probably seral and these small trees are not likely to continue to occupy upper canopy positions as stand development continues.

The advance regeneration composition is summarized in Table 7.2. Several species which are typical understory obligates in the Missouri Ozarks (sassafras,

**Table 7.2. Advance regeneration densities and mean heights.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Density (stems / ha)</th>
<th>Mean Height (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Sassafras albidum</em></td>
<td>3361.2</td>
<td>0.5</td>
</tr>
<tr>
<td><em>Quercus velutina</em></td>
<td>1488.7</td>
<td>0.7</td>
</tr>
<tr>
<td><em>Quercus alba</em></td>
<td>1455.3</td>
<td>0.8</td>
</tr>
<tr>
<td><em>Carya spp.</em></td>
<td>1448.6</td>
<td>1.1</td>
</tr>
<tr>
<td><em>Cornus florida</em></td>
<td>1114.8</td>
<td>1.1</td>
</tr>
<tr>
<td><em>Nyssa sylvatica</em></td>
<td>784.4</td>
<td>1.2</td>
</tr>
<tr>
<td><em>Acer rubrum</em></td>
<td>694.3</td>
<td>0.4</td>
</tr>
<tr>
<td><em>Pinus echinata</em></td>
<td>460.6</td>
<td>0.7</td>
</tr>
<tr>
<td><em>Corylus spp.</em></td>
<td>383.9</td>
<td>0.8</td>
</tr>
<tr>
<td><em>Quercus coccinea</em></td>
<td>290.4</td>
<td>0.6</td>
</tr>
<tr>
<td><em>Quercus stellata</em></td>
<td>270.4</td>
<td>0.9</td>
</tr>
<tr>
<td>Misc. shrubs</td>
<td>186.9</td>
<td>1.2</td>
</tr>
<tr>
<td><em>Prunus serotina</em></td>
<td>173.6</td>
<td>0.2</td>
</tr>
<tr>
<td><em>Quercus rubra</em></td>
<td>113.5</td>
<td>0.4</td>
</tr>
<tr>
<td>Others</td>
<td>383.9</td>
<td>0.9</td>
</tr>
</tbody>
</table>

1Includes *Amelanchier arborea, Craetagus spp., Fraxinus spp., Juglans nigra, Juniperus virginiana, Quercus marilandica, Rhus spp., Ulmus spp.*
flowering dogwood, and blackgum) were well represented as advance regeneration. However, these species were poorly represented among upper canopy trees in the 20-yr-old stands. Hickories, which can reach and maintain upper canopy positions in the Missouri Ozarks, were also abundant as advance regeneration. After sassafras, black oak and white oak were the most abundant advance regeneration species (about 1500 stems / ha for each species). Other oak species were far less abundant as advance regeneration. Scarlet oak, post oak (*Quercus stellata* Wangenh.), and northern red oak each averaged less than 300 stems / ha. Shortleaf pine was also relatively poorly represented, with about 460 stems / ha.

*Model Fitting*

Step-wise logistic regression results for the size model are summarized in Table 7.3. Potential predictor variables included transformations of ground diameter and height, and slope position and aspect classes. The best model included the square root of basal diameter (*GD*<sup>0.5</sup>) as the sole predictor variable. None of the other variables significantly improved the model after *GD*<sup>0.5</sup> was added. Because this variable was not recorded for all stems measured on the subplots, a second model was fit without ground diameter, or transformations, as potential predictors. Step-wise logistic regression selected the natural log of height (*H*<sub>ln</sub>) as the sole predictor variable. The difference between the two models is minimal. The r<sup>2</sup> value for the *H*<sub>ln</sub> model (27.9 percent) was only slightly smaller than that for the *GD*<sup>0.5</sup> model (28.7 percent). Concordance was about equal for both models (78 percent). Both models were highly significant compared to the constant-only model (P < 0.001). There was no evidence of lack-of-fit for either model using the Hosmer and Lemeshow test. The final model is:

\[
P(\text{success}) = \frac{1}{1 + \exp(0.968 - 1.122 \cdot \text{H}_{\ln})}
\]
Table 7.3. Summary statistics for the size model fits.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter</th>
<th>P_{model}</th>
<th>r^2</th>
<th>Concordance</th>
</tr>
</thead>
<tbody>
<tr>
<td>All parameters</td>
<td>GD^{0.5}</td>
<td>&lt; 0.001</td>
<td>28.7</td>
<td>77.2</td>
</tr>
<tr>
<td>GD excluded</td>
<td>H_{ln}</td>
<td>&lt; 0.001</td>
<td>27.9</td>
<td>78.0</td>
</tr>
</tbody>
</table>

Statistical tests of the competition indices are summarized in Table 7.4. The size model was used as a base model and each competition index was added individually. P-values compare the base model to the expanded full model and reflect the probability that the full model is a significant improvement over the base model. Odds ratios < 1 indicate negative relationships, while odds ratios > 1 indicate positive relationships. All of the oak competition indices that incorporate height significantly improved the base model. The oak AH₄ index had the greatest X² value, indicating it provided the greatest improvement to the base model. All statistically significant oak competition indices had odds ratios < 1, indicating a negative relationship between individual tree success and the level of competition. Hickory and shortleaf pine D also significantly improved the base model, but it had an unexpectedly positive relationship with success and a relatively small X²-value. None of the small tree indices significantly improved the base model.

Step-wise logistic regression added only oak AH₄ to the base model. The final competition model is:

\[ P(\text{success}) = \frac{1}{1 + \exp(0.262 - 1.341 \cdot H_{ln} + 0.0196 \cdot \text{oak AH}_4)} \]

The r-squared value for the competition model was 32.3 percent and concordance was 80.1 percent, indicating some improvement over the size model. There was no evidence of lack-of-fit using the Hosmer and Lemeshow test ( p = 0.50).

The size and competition models are compared graphically in Figure 7.1. The figure illustrates the probability of individual tree success with increasing stem height. The competition model is fit for low competition (oak AH₄ = 0.25 m, upper heavy line).
Table 7.4. Results of statistical tests of competition indices.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Odds Ratio</th>
<th>$X^2$</th>
<th>$P_{\text{full} - \text{reduced}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Quercus spp.</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>0.98</td>
<td>2.38</td>
<td>0.123</td>
</tr>
<tr>
<td>AH</td>
<td>0.91</td>
<td>10.36</td>
<td>0.001</td>
</tr>
<tr>
<td>AH$_4$</td>
<td>0.53</td>
<td>12.41</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>D$_s$</td>
<td>1.01</td>
<td>0.01</td>
<td>0.933</td>
</tr>
<tr>
<td>AH$_s$</td>
<td>0.78</td>
<td>6.16</td>
<td>0.013</td>
</tr>
<tr>
<td><strong>Carya spp. + P. echinata</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>1.12</td>
<td>4.83</td>
<td>0.028</td>
</tr>
<tr>
<td>AH</td>
<td>1.01</td>
<td>0.36</td>
<td>0.551</td>
</tr>
<tr>
<td>AH$_4$</td>
<td>1.05</td>
<td>0.01</td>
<td>0.930</td>
</tr>
<tr>
<td>D$_s$</td>
<td>1.04</td>
<td>0.10</td>
<td>0.747</td>
</tr>
<tr>
<td>AH$_s$</td>
<td>1.01</td>
<td>0.00</td>
<td>0.991</td>
</tr>
<tr>
<td><strong>Small Trees</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>1.02</td>
<td>0.20</td>
<td>0.655</td>
</tr>
<tr>
<td>AH</td>
<td>1.03</td>
<td>0.65</td>
<td>0.422</td>
</tr>
<tr>
<td>AH$_4$</td>
<td>1.23</td>
<td>0.60</td>
<td>0.439</td>
</tr>
<tr>
<td>D$_s$</td>
<td>0.97</td>
<td>0.64</td>
<td>0.424</td>
</tr>
<tr>
<td>AH$_s$</td>
<td>0.96</td>
<td>0.74</td>
<td>0.391</td>
</tr>
</tbody>
</table>
Figure 7.1. Size and competition model comparisons. Competition model is fitted for oak AH$_4 = 0.25$ m (upper line) and oak AH$_4 = 1.5$ m (lower line).

and high competition (oak AH$_4 = 1.5$ m, lower heavy line). Predicted success probabilities under the competition model are higher compared to the size model when competition is low and lower when competition is high.

*Model Testing*

The size and competition models were applied to the pre-harvest subplot data to predict 20-yr oak densities. Mean predicted and observed densities across all subplots are summarized in Table 7.5. Subplots had an average of 0.97 seed-origin dominant or codominant oaks per subplot, 20 yrs after harvest. The average 20-yr density of main canopy trees of all species was 4.00 stems / plot. This density matches exactly the density expected using Gingrich's (1967) stocking equation and lends supports to the AH$_4$ competition index. Predicted densities of seed-origin oaks using the size model averaged 1.21 stems / subplot. The competition model predictions more closely matched average observed density, with 1.07 stems / subplot.
Table 7.5. Mean predicted 20-yr densities using the size and competition models and observed mean 20-yr density.

<table>
<thead>
<tr>
<th>Method</th>
<th>Mean 20-yr Density (stems / plot)</th>
<th>Std. Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Size Model Predictions</td>
<td>1.21</td>
<td>0.08</td>
</tr>
<tr>
<td>Competition Model Predictions</td>
<td>1.07</td>
<td>0.05</td>
</tr>
<tr>
<td>Observed</td>
<td>0.97</td>
<td>0.08</td>
</tr>
</tbody>
</table>

Observed and predicted values were summarized to evaluate trends across a competition gradient. Subplots were ranked and sorted by their level of competition, represented by oak AH4. The sorted subplots were placed into groups of 10 subplots. Mean values for oak AH4, observed densities, and predicted densities using the two models were calculated for each group. Figure 7.2 illustrates predicted values using the size model (A), predicted values using the competition model (B), and observed values (C) across the competition gradient. All but the left-most point on the figure represent the average of 10 subplots (the other represents 5 subplots). Predicted values for the size model increase linearly with oak AH4. Note that oak AH4 reflects both the main source of competition (large oak seedlings) and the main source of successful regeneration (large oak seedlings). In contrast, predicted values for the competition model reach an asymptote when oak AH4 reaches approximately 0.75 m. Above this competition level, predicted 20-yr densities remain approximately constant at about 1.7 stems / plot. A very similar pattern is apparent among observed oak densities.

Group residual values (observed - predicted densities) are shown in Figure 7.2 for the size model (D) and competition model (E). Underestimates, shown by positive residuals, are somewhat larger and more common for the size model versus the competition model when oak AH4 is small. Among subplots where oak AH4 ≤ 0.3 m, the mean size model residual was 0.07 stems / subplot, while the mean competition residual was 0.01 stems / subplot. The size model clearly overestimates densities as AH4 increase, evident by increasingly large negative residuals. The inclusion of AH4 into the
Figure 7.2. Expected 20-yr densities using the size (A) and competition models (B), and observed 20-yr densities (C) across a competition gradient (oak AH4). Size model error (observed - predicted 20-yr densities) (D) and competition model error (E) are shown at right.
competition model removed this trend and there is not a clear relationship between competition model residuals and AH4.

**Individual Tree Sample Bias**

The large overestimate in mean 20-yr density (about 25 percent) produced by the size model was unexpected and merited further investigation. The results suggest that, after accounting for variation in stem size, those stems selected for individual tree measurements were more successful than the larger population of stems found on the subplots. Sample bias is a likely source of error. Bias in the individual tree sample was examined by comparing the average level of competition encountered by all oak seedlings within each size class against the level of competition encountered by the seedlings selected for individual tree measurements. An oak AH4 value was calculated for each oak seedling in the individual tree sample and for each oak seedling in the subplot sample. Seedlings were grouped into 0.3 m height classes and mean oak AH4 values were calculated. Individual tree mean oak AH4 values were expected to equal subplot mean oak AH4 values under random sampling.

Results are shown in Figure 7.3. Across all height classes, the seedlings selected for individual tree measurement typically encountered lower than average competition (smaller mean oak AH4) than the larger population of seedlings in the same height class. For example, oak seedlings in the 0.15 m height class occurred on subplots where, on average, oak AH4 = 0.8 m. By contrast, the subsample of seedlings selected for individual tree measurements occurred on subplots where, on average, oak AH4 = 0.2 m.

**Discussion**

Incorporating a simple measure of local competition into a size-based individual tree model led to important improvements in model performance. Logistic regression results using individual tree data indicate that the competition model is a significant improvement over the size model. However, the summary statistics suggested the
Figure 7.3. Comparison of oak AH₄ for all oak seedlings in each height class (Subplot Sample; filled point) and for oak seedlings selected for individual tree measurements (Individual Tree Sample; open points). Oak AH₄ is a measure of the competitive environment around both sets of seedlings.
magnitude of improvement was modest. Model r-squared values increased from about 28 percent to 32 percent and concordance increased only slightly. However, the improvement to the individual tree model became much more apparent when the models were used to predict 20-yr densities. In this respect, the competition model showed marked improvements over the size model.

As expected, the competition model performed better than the size model across a range of competition levels. The key improvement of the competition model was to reduce predicted 20-yr densities on subplots with larger oak seedlings. Under high levels of competition, the probability of individual tree success was reduced. There was some evidence that the competition model also better predicted 20-yr densities on subplots with relatively low competition by increasing the probability of success for smaller oak seedlings. However, these subplots had relatively few and smaller oak seedlings and their regeneration potential remained low. In total, the capacity of the competition model to adapt to varying levels of competition indicates that it is a more flexible for predicting 20-yr densities across a greater range of stand conditions.

A second unexpected improvement in the competition model was to reduce the effects of bias in the individual tree sample. Bias in the individual tree sample became apparent when the size model was used to predict 20-yr densities. Expected 20-yr densities exceed observed densities by about 25 percent. This indicates that the population of seedlings selected for individual tree measurements (which was used to fit the size model) was, on average, more successful than the larger seedling population measured on the subplots. The greater level of success was linked to the competitive environment; seedlings selected for individual tree measurements experienced less competition than average compared with other seedlings in the same size class.

I hypothesize that the sample bias resulted from a tendency to select for individual measurements the larger seedlings within any given subplot. For example, seedlings in the 0.3 m size class were likely selected more often on subplots with few larger seedlings, and selected less often on subplots where larger, more competitive seedlings were abundant. Without considering competition, this sampling bias appears innocuous. However, the sampled trees failed to adequately reflect the range of competitive
environments within the stands. This underscores an important limitation to models lacking competition terms, even those based on truly random samples. Under the best circumstances, such models can only be expected to produce accurate estimates in stands with competition levels similar to those found in the stands where the model data were collected. The competition model largely removed the effect of the sample bias, and it produced a more accurate estimate, with a mean overestimate of about 10 percent. In addition, the competition model is more flexible than the size model and can potentially be applied successfully in stands with a greater range of competitive environments.

All but one competition index that improved the size model was a function of oak seedling height. Height is an indicator not only of seedling vigor, but also the capacity of seedlings to suppress neighbors. Oak AH₄ appeared to better summarize the subplot-level competitive environment compared with oak AH or oak AH₅. Oak AH₄, which is a function of the heights of the four largest oaks only, is more narrowly defined than oak AH, which is a function of all oak heights. Smaller seedlings contributed to oak AH, but were probably not as important as competitors. Oak AH₅ is also more narrowly defined, focusing only on stems taller than the focal stem. In this case, density may have played a role in limiting the utility of oak AH₅. For example, oak AH₃ = 2.5 m may indicate a single large competitor or many smaller competitors, each of only marginally superior in height. In contrast, oak AH₄ better distinguishes these clearly different competitive circumstances.

There is little evidence that the size and density of non-oak advance regeneration are useful for modeling oak seedling success. Small trees, including sassafras, flowering dogwood, and blackgum, were well represented as advance regeneration, but very few of these stems reached a dominant and codominant crown position 20 yrs after harvest. Correspondingly, their ability to compete with established oak seedlings appears limited. A similar situation was evident for hickories and shortleaf pine, although these species more frequently reach and maintain upper crown positions in the Missouri Ozarks. There was some evidence for a positive relationship between hickories and shortleaf pine density and individual oak success. This may reflect subplots where better competitors (oaks) were relatively sparse.
Topographic variables were not statistically significant predictors of individual stem success in the present study. Previous studies found similar variables to be significant predictors of oak regeneration height growth (Dey 1991) or "success" based on reaching a minimum height (Sander et al. 1984). Height growth clearly depends on site productivity, which typically varies with topographic position (McNab 1993). In the present study, success was based on crown class, which in even-aged stands is a function of height growth relative to neighbors (Oliver and Larson 1990, pg 148). Stems growing on less productive topographic positions were surrounded by neighbors growing under similar conditions. Relatively slow growing trees were likely more successful on less productive sites, thus reducing the potential for topographic variables to predict success.

Early canopy development in the study stands was largely a sorting process among oaks. Stand compositions 20 yrs after clearcutting were very similar to pre-harvest compositions. Oaks were dominant before harvest and quickly regained dominance in the decades after harvest. Other species occupied relatively little growing space in the 20-yr stands, accounting for less than one-quarter of dominant and codominant trees. Typically, xeric upland stands in the Missouri Ozarks do not support species that readily replace oaks (Rogers et al. 1993). Large oak seedlings appear to have been important in excluding smaller, less competitive seedlings from upper canopy positions. Oak sprouts from cut stumps may have also been important in limiting the success of oak seedlings, but competition from sprouts were not included in this study due to insufficient data.

The present results have implications for scaling regeneration success from individual seedlings to the plot and stand levels. Intra-specific competition influenced individual seedling success, but the stands regenerated with few non-oaks in dominant and codominant crown positions. Sander et al. (1984) and Gould et al. (in review) proposed plot-level oak regeneration models scaled so that each plot is expected to be occupied by a single tree at the end of the regeneration period. Intra-specific competition is irrelevant in these cases in that it does not influence plot-level success. However, inter-specific competition that results in non-oaks ultimately occupying some plots is
important. Distinguishing between these sources of competition is critical to developing more accurate regeneration models.

Early canopy development in more mesic oak forests includes competition from fast growing non-oak species. Although the present results cannot be used directly to model oak success in these forests, similar concepts may prove useful. Nearby competitors that establish as advance regeneration, whether they are oaks or other species, undoubtedly influence the success of individual oak seedlings. Such stems are readily measured, although the competitive abilities of many common species, such as red maple and black birch, remain poorly understood. Larger stems that typically are not measured as advance regeneration can produce highly competitive stump sprouts. Probabilistic sprouting models (Weigel and Peng 2002) may be helpful for characterizing sprout-origin competition. Predicting competition from species, such as yellow-poplar, that germinate after overstory disturbance may be especially challenging. Indirect measurements, such as proximity to seed sources, suitability of substrate, and site quality, may provide insights. Additional work is needed to identify the optimal plot size and configuration for measuring competition. In the present study, the competitive environment of individual oaks near the subplot edges was likely not summarized as precisely as it was for oaks closer to the subplot center. More purposeful measures of the competitive environment, possibly using nested concentric plots, may improve future models.
Literature Cited


White, A.S. and K.J. Elliot 1992. Predicting the effects of hardwood competition on red

Chapter 8

Conclusions

Central Appalachian hardwood forests are comprised of species that have a range of silvical characteristics and regeneration strategies. As a result, development following a major stand-replacing disturbance can appear unpredictable and does not follow a single, well-defined pattern. Most hardwood species throughout the globe sprout after a stem is injured or killed. Likewise, sprouting is an important source of regeneration in the central Appalachians. Seedlings of many central Appalachian species, such as northern red oak (Quercus rubra L.) and red maple (Acer rubrum L.), establish as advance regeneration. The size, density, and composition of advance regeneration at the time a disturbance occurs have a critical impact on post-disturbance stand development. Still other species, such as yellow-poplar (Liriodendron tulipifera L.) and black birch (Betula lenta L.), invade or germinate from the soil seed bank after a disturbance. Such pioneer species often grow rapidly and can dominate early stand development. Herbivory, inter-tree competition, and competition with non-tree vegetation can alter the composition and growth of young stands. Taken together, these factors produce a wide range of developmental patterns.

The developmental pathways described in Chapter 2 efficiently summarized the complex patterns of stand development found in some central Appalachian forests. The results underscore the importance of stand conditions around the time of harvest to future development. To some degree, the future stand is a product of the previous stand. This developmental pattern reflects the regeneration strategies of many hardwood species, specifically stump sprouting and advance regeneration. Ecological models of forest succession have described similar patterns, but the developmental pathways provide a more serviceable model of post-disturbance stand development. Future development is a product of stand condition immediately around the time of disturbance, rather than an inherent property of a forest community. This perspective better emphasized the role
forest managers can play in shaping future stands. Hypothetically, pre-harvest silvicultural treatments can alter a stand's developmental pathway, even if it amounts to "fighting" natural succession.

The regeneration models presented here provide methods for estimating the oak regeneration potential of stands managed under even-aged silvicultural systems. The models provide forester managers with important information for making management decisions. The ability to estimate oak regeneration potential in advance of harvest can reduce both undesirable outcomes and unnecessary treatments. Stands that have adequate oak regeneration potential and lack excessive competing vegetation can be harvested in a single entry and may not require any other treatments. Other regeneration treatments may be needed when the initial oak regeneration potential is inadequate.

The models and guidelines presented here are the first regional research-based methods for measuring oak regeneration potential and assigning prescriptions. The regeneration guidelines are designed to be used by forest managers and will, hopefully, lead to better forest management. However, professional judgment will continue to be at least as important as the models for formulating prescriptions. The models describe typical outcomes. Model results should be weighed against past experience and an understanding of local conditions when making a management decision for a particular stand.

The regeneration models are specific to central Appalachian oaks, but similar models can be developed for other species. Seed-origin regeneration potential can be modeled as a function of the size and density of advance regeneration of other species. The relationship between parent tree size and sprouting potential likely has a physiological basis that is common to other tree species. Oaks are generally considered unable to successfully regenerate from post-harvest germinants, leaving advance regeneration and sprouts as the only viable sources of regeneration. Pioneer species, such as black birch, successfully regenerate by this means. Modeling the regeneration potential of pioneer species is potentially difficult. The distance to seed sources and measures of environmental conditions may prove to be useful predictors. There is undoubtedly a need for such models for other forested regions of the world. Natural
regeneration is often purposefully or fortuitously used to restock harvested stands. In cases where the regeneration of desirable species is uncertain, regeneration models should prove useful for guiding management decisions.

As regeneration models become more complex, and presumably more accurate, the issue of competition must be better addressed. The results presented in Chapter 7 demonstrate that individual tree models are more accurate when neighboring competitors are considered. Competition is a central theme in the study of forest development and, not surprisingly, it is important to regeneration models. Competition varies between stands due to differences in productivity, disturbance histories, and cultural treatments. More sophisticated regeneration models should be able to better recognize the particular competitive environments found in specific stands. Several competition indices were tested and the best index was the aggregate height of the four largest oak seedlings on the subplot. The results suggest that a small number of the most competitive seedlings best describes the competitive environment as it relates to individual oak seedling success. However, the ecological significance of the results should be interpreted carefully. The competition indices do not describe competition, *per se*, but are approximations of the competitive environment. This distinction is particularly important for interpreting the competition indices that did not significantly improve the competition model. For example, small trees undoubtedly contribute to overall competition, even though the small tree indices were not good predictors of individual oak seedling success.

The plot-level and individual tree models describe the development of existing oak seedlings, but they do not address factors controlling initial seedling establishment. The issue of initial establishment is particularly important in stands with little advance oak regeneration. Prescriptions that can improve seedling establishment, such as fencing and herbicide treatments, are suggested in the regeneration guidelines. However, the effects of these treatments are not modeled. Competition may have important effects on seedling establishment that are different from its effects on seedling development. For example, small tree competition was not found to significantly improve the competition model, but it may have influenced the number of oak seedlings that had established within subplots. Experimental studies should be conducted to better understand factors
influencing seedling establishment. The present studies are observational and cannot adequately address this question.

Better conceptual models of early stand development can help in formulating the next generation of predictive models. Predictive plot-level and individual tree models were developed and evaluated in the present work. The models are based on a very simple view of stand development. For the plot-level model, development is viewed as a set of independent plots, each of which will be occupied by a single tree at the end of the regeneration period. For the individual tree model, individual stems are modeled essentially independently. The assumption that small plots or individual stems develop independently from one another is convenient, but ultimately untenable. Understanding interactions between tree seedlings, stump sprouts, and other vegetation at appropriate spatial scales is necessary. These interactions are complex, and can presumably have a large impact of early stand development. Competition is generally used to describe these interactions, but there is a need for more detailed conceptual models to bridge the gap between the concept of competition and useable predictive models. As more forest managers adopt field and office computers for regeneration analyses, the need for simplicity in predictive models will be greatly reduced. Future predictive models will be limited only by the demands of data collection and the imagination of the modelers.
Vita: Peter Jay Gould

Peter Jay Gould was born July 28, 1974 in Phoenix, Arizona. He attended public school in Santa Cruz and Pima counties in southern Arizona. He received a B.S. degree in Forestry from Northern Arizona University in 2000. He attended Pennsylvania State University from 2000 to 2005 and received a Ph.D. degree in Forest Resources. He married the former Jessica Frankel of Arivaca, Arizona in 2000. They are the proud parents of two children, Henry and Sylvia.