

Upland Oak Ecology Symposium: History, Current Conditions, and Sustainability

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Editor

Martin A. Spetich

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PREFACE

The “Upland Oak Ecology Symposium: History, Current Conditions, and Sustainability” was held October 7–10, 2002, in Fayetteville, AR. Recent events such as drought and oak decline are hastening the loss of oaks in upland oak forests of the Interior Highlands. This and the lack of oak regeneration in many areas of the Highlands raise questions of future viability and sustainability. In response, a group of natural resource organizations cosponsored a symposium on upland oak ecology. Their objective was to convene a diverse group of resource specialists and scientists to examine upland oak ecosystems in the light of historical influences, problems and trends, how they function, and ideas about their long-term restoration.

Sponsors of the symposium included the Arkansas Wildlife Federation; Arkansas Forest Resource Center; Arkansas Game and Fish Commission; Arkansas Forestry Commission; U.S. Department of Agriculture (USDA), Forest Service, Southern Research Station; and the University of Arkansas Cooperative Extension Service. Each sponsor provided at least one representative to the steering committee. The committee worked long hours to prepare and implement the symposium. Its members included:

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Introduction and Synthesis

UPLAND OAK ECOLOGY SYMPOSIUM: A SYNTHESIS

Martin A. Spetich¹

Abstract—Recent changes in upland forests of the Interior Highlands have raised the interest of and questions from professional resource specialists and the public. This renewed interest in Interior Highland forests provided researchers an opportunity to update resource specialists on new knowledge regarding upland oak ecology. Symposium presentations and the papers presented in this volume offer up-to-date knowledge that can be applied to the management of upland oak forests and can help resource specialists keep the public better informed.

INTRODUCTION

This manuscript is a synthesis of major ideas presented at the Upland Oak Ecology Symposium held October 7–10, 2002, in Fayetteville, AR. More than 350 managers, scientists, landowners, and others gathered to discuss problems and opportunities common to upland oak (*Quercus* spp.) forests, focusing mainly on forests of the Interior Highlands. However, much of the information contained is applicable to upland oak forests in general. This paper highlights common threads among symposium papers and incorporates additional supporting information to help link the full range of ideas presented.

As the proceedings papers illustrate, upland oak forests are complex systems that have evolved over millennia. Both human and natural disturbances have played an important role in their development. In his keynote paper, Paul Johnson explains that the response of upland oak forests to disturbance can be anticipated by understanding the stages of stand development, and by recognizing that such forests are in a constant state of change. Dr. Johnson's presentation set the stage for a valuable, informative conference.

HISTORICAL PERSPECTIVES INFLUENCING THE ESTABLISHMENT AND SUSTAINABILITY OF UPLAND OAK FORESTS

Oak- and hickory- (*Carya* spp.) dominated forest communities of what is now known as the Central Hardwood Region (Merritt 1980) became established at least 5,000 years ago (Fralish, in press). The use of fire by Native Americans influenced development of this forest complex. Without modern fire breaks such as roads or fire lines, once set, fire would likely transform large landscapes on a regular basis.

Native Americans also intimately interacted with these forests in many other ways. For instance, hardwoods were the most important wood for native dwellings in northern Arkansas, and oak was the most important species for fuelwood. Thus, between 500 and 5,000 years ago, communities of at least 250 people were an important component of the forest ecosystem in the Boston Mountains of Arkansas, especially where wood, water, and productive soils existed (George Sabo III, in press).

The overall impact of Native Americans on the landscape varied with their historic population levels. DeVivo (1990) presents a convincing argument that presettlement Native American populations were much greater than previous estimates. He suggests that by the time Europeans began settling the interior, noncoastal areas of North America (nearly 200 years after Columbus landed on the continent), the diseases transmitted over the previous 200 years had depopulated the areas significantly. He and others have based their estimates on historical information about disease-caused depopulation of Latin American regions. He further quotes Williams (1989): "There is the strong possibility that in the late 15th century the Western Hemisphere may have had a greater total population than Western Europe."

By the early 1800s, European settlement of northern Arkansas had begun. Tree measurements taken then have allowed scientists to estimate relative forest species composition and structure of the period. During that time, General Land Office surveys were conducted in the Arkansas Ozarks. Based on those records, the Boston Mountains and the Springfield Plateau Subsection had more trees per acre than areas to the north. Today, the Boston Mountains have even more trees per acre than they did then, probably a result of fire suppression (Foti, in press). In fact, a fire-history study in the Lower Boston Mountains by Guyette and Spetich (2003) found major changes in the mean fire interval (MFI) since 1680. They divided the time since 1680 into four periods: the Native American period (1680 to 1820), Euro-American settlement period (1821 to 1880), regional development period (1881 to 1910), and fire suppression period (1911 to 2000), in which they found the MFI to be 11.2 years, 2.7 years, 2.9 years, and > 80 years, respectively. This provides quantitative evidence of how effective the past 80+ years of fire suppression has been in this region.

Over the past 80+ years, fire suppression likely has altered species dynamics of these upland hardwood forests. On medium- to high-quality sites, one impact has been a lack of successful regeneration and recruitment of oak into forest overstories while shade-tolerant species such as red maple (*Acer rubrum* L.) have become more dominant. For instance, in a study of four mature oak stands in north-central Arkansas, Soucy and others (in press) found that oak establishment has declined while establishment of

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shade-tolerant species has continued successfully over the past 50 to 60 years. This likely is due to lack of disturbance. Based on the ecology and physiology of oaks, and the fire history of these forests, reduced fire disturbance and the resultant increase in competing species over the last 100 years appears to be a major factor in the loss of successful oak regeneration on these medium- and high-quality sites.

However, on low-quality sites, oaks can regenerate and successfully compete, even in the absence of fire. For instance, a study in the Ouachita Mountains comparing early records and recent data for a xeric site where fire had long been absent indicated a trend toward successful oak regeneration (Bragg, in press; Murphy and Nowacki 1997).

The 5,000-year history of these oak-hickory forests provides many lessons for the modern forest manager. New information is being used to better understand upland oak forest ecology and dynamics and, where appropriate, to mimic past disturbances.

UPLAND OAK FOREST ECOLOGY AND WILDLIFE ECOLOGY

The Central Hardwood Forest region (Merritt 1980) has been dominated by oak and hickory trees for thousands of years, with oaks being a keystone species (Fralish, in press; Spetich and others 2002). Disturbance and oak forest dynamics relative to disturbance are overriding themes in this section of the proceedings, and many papers focus primarily on disturbance by fire. Historically, these forests were regularly subjected to fire. Fire frequency and intensity were greatly influenced by humans (Dey and others, in press) and by topography (Guyette and Dey, in press).

Of all the disturbance factors that have shaped upland oak forests, fire probably is among the most important. Van Lear (in press) proposes that, because oaks adapt to low-intensity surface fires, it is possible to use prescribed fire to reach a variety of management goals in oak-dominated forests. Brose and Van Lear (in press) point out several reasons why oak is better at surviving surface fires than other species. For example, due to the hypogeal germination strategy of oaks and hickories, their root collars are closer to ground level than many other hardwood species. This helps protect their dormant buds from fire.

Acorns must survive predation if they are to become seedlings. Differences between red oak (*Q. rubra* L.) and white oak (*Q. alba* L.) acorns—such as the energy contained within them, palatability to wildlife, and masting time—help these species survive predation (Steel and others, in press). Acorns that survive and germinate have additional challenges. In forests of many Northern and Eastern States where white-tailed deer (*Odocoileus virginianus*) populations are high, browsing of oak seedlings has a significant impact on oak regeneration. However, in the large contiguous forest matrix of Arkansas's Boston Mountains, we have rarely observed oak-specific browsing damage to seedlings from deer. This likely is due in part to the preponderance of other species preferred by deer, such as poison ivy (*Toxicodendron radicans* L.), greenbrier (*Smilax Bona-nox* L., *S. glauca* Walt., *S. rotundifolia* L.), huckleberry (*Vaccinium vacillans* var. *crinitum* Fern.), red maple (*A. rubrum* L.), and

Virginia creeper (*Parthenocissus quinquefolia* L. Planch.). When making management decisions, it is important to determine the existing mix of impacts on acorn and oak seedling survival.

Survival and successful competition of oak seedlings can lead to changes in forest composition and structure, which are important to bird communities. For instance, Patterson and James (in press) found that birds in this region used oaks more often than other tree species. Further, bird habitat can be improved through management activities such as prescribed fire, various harvesting techniques, and natural disturbances (Dickson, in press).

Management activities also can be used to provide a wide range of habitats. For instance, maintaining a wider range of successional stages in oak forests of the Interior Highlands likely would have reduced the impact of oak decline and enhanced habitat for a wide range of wildlife species, some of which need both mature forest and early successional habitat. For example, both oak mast found in mature forests and soft mast found in early successional habitats are needed by black bears (*Ursus americanus*) (Clark, in press). Natural disturbances such as wind, fire, and oak decline also can create early successional habitats, but unlike well-planned management activities, not necessarily at the time, place, or scale that would most benefit wildlife populations and the public.

Forest managers know the importance of predicting how mature oak trees respond to natural disturbances such as oak decline and associated factors like increased red oak borer (*Enaphalodes rufulus* Haldeman) populations. For instance, Muzika and Guyette (in press) present an innovative study that invites exploration of past oak borer events relative to tree age, ring width, and temperature. Such studies will help identify conditions that influence oak borer populations and lead to models that help managers predict future population levels and activity.

To accurately model upland oak forest systems, scientists need data that have been collected over a long time. In addition, standard, comparable, precise, quantitative data among species are necessary when modeling oak life-history characteristics (Guyette and others, in press). It is often difficult to discern significant changes over the short term in these forests; e.g., Demchik and Sharp (in press). Even in small, gap-size disturbances, seedling dynamics are highly variable during the first several years after a disturbance event; e.g., Berg (in press). At the stand scale, the stand-initiation stage is chaotic, making predictions of species and stand structure problematic (Johnson, in press). Even more broadly, when modeling large landscapes, ecologically discrete areas need to be well defined and evaluated (Kabrick and others, in press; McNab and others, in press).

To increase the predictive power of forest models, it will be necessary to make greater commitments to long-term studies. Mechanisms should be developed to continue orphaned studies; i.e., studies where the responsible researcher has retired or otherwise moved on. Such mechanisms will allow future generations of scientists

and managers to examine stand dynamics throughout the life of a forest, rather than the life of an individual researcher. Such commitment will make future restoration and management of these forests possible and help maximize benefits to the public.

UPLAND OAK ECOSYSTEM RESTORATION AND MANAGEMENT

There was general agreement at the symposium that oak regeneration and appropriate disturbance factors, which allow successful survival and growth of oak regeneration, are critical to restoration of the upland oak forest. In fact, successful oak regeneration has been acknowledged as problematic in eastern forests for at least 25 years (Lorimer 1989). The potential for even larger losses of keystone oak species helped focus authors in this section on the success of oak regeneration and disturbance factors that could facilitate successful oak restoration. Without oaks, there would be no oak ecosystem. Effective management methods will be necessary to help guide oaks into a successful position relative to their interspecific competitors, so they may survive to become part of the future forest (Spetich and others, in press).

The outcome of interspecific competition between oak regeneration and other natural vegetation is a function of site factors, associated differences in growth rates of co-occurring species, the genetics of plant populations, and the state of the vegetation complex when silviculturally prescribed or naturally imposed disturbances occur. The competitive capacity of a species, therefore, may vary as those factors vary in time and space (Spetich and others 2002). This in turn influences the composition and structure of the next stand.

Understory and midstory structure and composition are important factors in species composition and dynamics of the next stand (Miller and others, in press; Ruffner and Groniger, in press). Managing these components properly is necessary for successful restoration of oak-hickory forests. This leads us to the two key requirements for successful oak regeneration: "(1) to ensure that competitive regeneration sources are present, and (2) to provide timely, sufficient release of these regeneration sources" (Loftis, in press).

In order to restore and maintain oak forests, we need a well-developed understanding of how they function and respond under various environmental conditions and disturbances. For example, we know there are major differences in relative competitive capacity of oaks across the spectrum from low-quality xeric sites to high-quality mesic sites (Loftis, in press; Spetich and others 2002). As site index increases, the competitive capacity of oak decreases because more and more species can survive and compete. Without disturbance, oaks are competitively excluded from the higher quality, more mesic sites.

Fire is probably the most widely recognized disturbance element missing from these upland forests today. This has led to increased research activity in prescribed fire with the intent of finding the best method(s) of restoring this disturbance agent. For instance, a study by Dey and Hartman (in press) examined the effects of repeated burning of oak

forest vegetation, providing valuable insight into relative fire response among species in the Missouri Ozarks. They found that although repeated burns reduced survival of all species one growing season following the last fire, the overall effect resulted in favoring oak and hickory reproduction. Iverson and others (in press) demonstrated how a combination of sensors, data recorders, and landscape-level analysis helped them gain significant insight into fire behavior in an oak forest.

Once a stand has been successfully regenerated through natural or anthropogenic disturbance, an appropriate management regime will be necessary to keep the stand growing vigorously. Increased stand vigor can help reduce losses to oak decline, insects, and disease, as well as maximize yield. Shifley (in press) explains that an understanding of forest development stages will help practitioners administer appropriate thinning regimes to achieve vigorously growing forest stands. Practitioners can achieve the most successful thinning regime by starting early in the stem-exclusion stage and working with the stand's natural dynamic as presented by Shifley (in press). Stages of stand development can be illustrated pictorially, which gives resource specialists an important visual reference of forest development. Such visual references can also provide deeper insight into structural changes caused by disturbance events, such as the current oak decline event.

OAK DECLINE

From 1856 to 1986 there have been 57 oak-mortality events recorded in the Eastern United States (Millers and others 1989). This included one in 1959 in the Ozark Mountains of Arkansas (Tool 1960), one in 1980-81 in Northwestern Arkansas (Bassett and others 1982, Mistretta and others 1984), and another in Missouri from 1980 to 1986 (Law and Gott 1987). The current oak-decline event in Arkansas and Missouri has been recognized as unique among other known oak-decline events due to the proliferation of oak borers, one of the contributing factors. Because of this extraordinary proliferation, the development has received widespread attention from experts around the country (Starkey and others, in press). However, many factors, such as drought, also influence oak decline.

Starkey and others (in press) have defined drought as an "inciting factor" of oak decline. Crook and others (in press) examine three drought events over the past 50 years. Even though the last drought (1998 to 2000) was not as severe as the previous two major droughts (one in the early 1950s and one in the mid-1960s), the authors suggest that it likely led to the current unprecedented outbreak of red oak borer. One of the major changes that occurred in upland forests over the last few decades is an increase in tree density and tree age, both conditions that make forests more vulnerable to oak decline (Oak and others, in press). Crook and others (in press) also did an extensive survey of 21 trees on a plot in the Ozarks and concluded that oak borers were responsible for tree death. Their conclusion that red oak borers are a main cause of tree death differs from the conclusion of others who view oak borers as one of several contributing factors (Law personal communication; Oak and others, in press; Starkey and others, in press). With or without oak borers, oak species across large landscapes

die during an oak-decline event. There is little doubt that the additional stress of this large population of borers is helping to contribute to the demise of many trees, as are advanced stand age, high stand density, and drought. However, the latter three stresses predispose a stand to oak decline whereas oak borers are opportunistic organisms that take advantage of already stressed trees. For trees on the verge of death, additional stress from any one of these stress mechanisms could result in earlier mortality.

A regional oak-decline study covering 12 Southeastern States examined data from 26,907 forest inventory plots (Oak and others, in press). The authors found a total area of 104.7 million acres dominated by oaks. Of that total, 43.5 million acres constituted sites with trees large enough and with enough oak basal area to be considered susceptible to oak decline. Those results are based on the most recent Forest Inventory and Analysis inventory cycle (from 1991 to 1997). In Arkansas, they found that the area affected by oak decline more than doubled from 1988 to 1995 and that this was concurrent with increases in stand age and stand density.

An oak-decline event such as the current one has the potential to significantly alter forest structure and species composition, which in turn will affect wildlife. Both Smith and others (in press) and James (in press) addressed potential effects of oak decline on bird populations. Smith predicted that 10 to 20 species would decline, while 11 or more species would increase. However, James predicted that 21 bird species would decrease while 38 would increase. The difference between the two studies may be due in part to their interpretation of how extensively oak decline will impact tree species composition. For instance, Smith and others suggest elimination of red oaks while James appears to view this as a thinning of the forest with some areas of high oak mortality.

Based on previous oak-decline events (Oak and others 1988, Starkey and others 1989, Tainter and others 1984), it is likely that oaks will remain an important component of these forests at the regional scale, but that the species no longer will be the dominant tree in many stands without active management to encourage competitive oak regeneration. On sites where oak reproduction is present but competing species have the advantage, active management will be necessary to successfully guide a new cohort of oak into the tree canopy.

MANAGEMENT

We now recognize that there are often multiple management options in a given stand (Loftis, in press). Generally, more management options are available on low-productivity, xeric to xero-mesic sites where oak regeneration tends to be more successful than on more productive sites. Loewenstein and Guldin (in press) define such low-productivity sites as successional stable oak stands. On more productive, mesic sites where fire or other disturbance mechanisms have been absent, long-term oak regeneration is seldom very successful. On those sites, competitive woody species (including shade-tolerant species that easily out compete oaks in the absence of disturbance) often are more abundant. If the management objective is to maintain

oak as a major component of the stand, then management options typically are more limited and problematic on the more productive sites.

We often separate high-quality (mesic) and low-quality (xeric) sites when referring to a specific management technique. For instance, Loewenstein and Guldin (in press) describe a technique to convert even-aged oak stands to uneven-aged stands on sites where oaks are successional stable (low- to medium-quality sites). Schweitzer and others (in press) modeled forest stands that fall into the low- and high-quality categories. They concluded that significantly different management regimes would be necessary on each site due to differences in the relative competitiveness of oaks. Prescribed fire is often suggested as a possible management option on high-quality sites. However, fire alone may not be sufficient because these forests have been without fire for so long that competing species can be large in diameter and therefore resistant to fire. In such cases additional work, perhaps through mechanical or chemical control, will be needed initially to control competing species, helping to restore the desired understory and midstory forest structure and species composition.

Brose (in press) describes optimal times and methods to apply prescribed fire. One method combines a shelterwood system with prescribed fire. This is supported by a recent study by Rebbeck and others (in press), who found that the number of fire top-killed seedlings was highest when overstory removal and fire were combined. Fire top-killed oak seedlings resprout under those conditions while accumulating energy in their root system, but shade-tolerant competitors do not. Additionally, results from a study by Dolan and Parker (in press) show that fire and silvicultural treatments can be combined to improve growing conditions for oak seedlings.

However, Brose (in press) also suggests that mechanical site scarification may be a better management strategy than fire for initial establishment of new seedlings. Lhotka and others (in press) review four studies on how scarification affects oak seedling establishment. For seedlings to survive, scarification would need to be combined with other management practices. On areas where scarification is operationally feasible, it likely would be most useful in small, defined areas. Studies suggest that future research also should consider time of scarification relative to time and amount of seed fall. For instance, Miller and Schlarbaum (in press) found that weevil predation on early-fall acorns differed from predation on acorns that fell later.

Fertilization is another seldom-used tool in management of upland oak forests, and it can be a useful option where the desire for increased growth rate outweighs costs. Happel and Sharp (in press) examined the use of fertilizer, lime, and herbicide, and found an increase in radial growth of oak on extremely acidic soils. DeWalle and others (in press) found that nitrogen fertilization can cause short-term soil acidification. A study by Graney (1986), in which a one-time fertilizer application of a nitrogen and phosphorus combination was applied to oaks, found significant increases in diameter growth over a 10-year period.

CONCLUSIONS

Upland oak-dominated forests are complex ecosystems that became established at least 5,000 years ago. Both human and natural disturbances have played a role in their development. Native American activities probably had a major impact on upland oak forest development, especially through the use of fire as a management tool. By the mid-1800s, European settlers began to substantially alter the landscape through forest clearing and increased fire frequency. Over much of the 20th century, massive and effective fire suppression efforts resulted in changes in forest structure and composition. Oak regeneration has changed the most on medium- to high-productivity sites.

Today's land managers face many challenges and difficult decisions in caring for upland oak forests. Competitive oak regeneration often is absent on productive sites; oak decline is changing forest structure and composition throughout the Interior Highlands; disturbance mechanisms are not yet thoroughly understood; and new problems such as gypsy moth and sudden oak death pose additional threats.

Nonetheless, a renewed commitment to research, as well as active management on a large scale over the next 15 years, could make the restoration of upland oak forests possible across the region. Development of models for predicting the competitive capacity of oak, relative to disturbance in specific plant communities and site-quality combinations, will greatly improve the chances for success in restoring and managing oak-dominated plant communities.

But a commitment to long-term and orphaned studies also will be necessary. For example, in the Boston Mountains of Arkansas the author has found (Spetich, unpublished observations) that tagged oak rootstocks that have been top-killed sometimes will lie dormant for 1 year or more before resprouting, a fact that short-term studies would not have captured. Monitoring rootstocks over time will allow better determination of their true survival and competitive success. In addition, long-term studies will improve the land manager's working knowledge of forest dynamics and benefit other components of the upland oak ecosystem.

As forests evolve, so does our knowledge of them. The papers in this volume represent views of various authors' knowledge at one point in time. But a caring, responsible stewardship will require a continuous monitoring of change—both in forest dynamics and in our knowledge of them. In carrying out such stewardship, the scientist and land manager both must be willing to use new information in ways that ensure the evolution of responsible decision-making.

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The Oak Forest Ecosystem

THINKING ABOUT OAK FORESTS AS RESPONSIVE ECOSYSTEMS

Paul S. Johnson¹

Abstract—Like all forests, oak forests are continually responding to disturbances originating from both within and outside the forest. Oaks (*Quercus* spp.) owe their very existence to disturbance. In this context, silvicultural and other management practices can be thought of as planned disturbances designed to direct forest change in specific ways. The internally (endogenously) controlled stages of stand development provide a useful framework for anticipating such changes together with an understanding of how external (exogenous) forces can further modify such changes.

INTRODUCTION

Because forests are “open systems,” they are continually responding to forces originating from both within and outside the forest itself. Unlike a tree seedling in a growth chamber with precisely fixed growth conditions, trees and other organisms in a forest must continually adjust to changing conditions, many of which are unknown or only occur probabilistically. The list of factors that can change are indeterminate, i.e., they are so numerous and often unknown that we are unable to list all of them even for a single acre of forest. They include both physical and biological factors. Some factors produce effects that are sudden and result in major changes, while others operate more slowly and subtly. The only constant is the forest’s continual response to relentless change.

TYPES OF RESPONSES

All forests respond to external (exogenous) and internal (endogenous) forces. Exogenous forces include, but are not limited to, wind, fire, insects, tree diseases, and human activity. Endogenous forces include crown closure, tree growth, tree mortality and associated self-thinning, and changes in species composition. In all cases, the forest “responds” to internally or externally induced changes. Because these changes are endless, an oak forest or savanna is therefore never “finished”—whether it is the product of human endeavor or of exclusively “natural” processes. Human activity, from an ecological and historical perspective, represents only one of the many forces that influence forests. Moreover, silvicultural and ecological restoration projects may not always produce their intended results. Forests are in effect “equal opportunity” responders to whatever forces and events come their way. We nevertheless need not be working blindly in achieving management goals. On the contrary, the manager can capitalize on a wealth of information on how oak forests respond to endogenously and exogenously caused changes.

Endogenous Change in Even-aged Oak Stands

Even-aged stands usually originate from sudden large-scale disturbances, natural or human-caused, that destroy all or most of the overstory of the previous stand. An even-aged stand thus consists of a group of trees comprising a single age class. This usually means that tree ages differ by no more than about 20 years.

Even-aged stands progress through a relatively predictable series of developmental stages until the next stand-initiating disturbance or some other severe disturbance occurs. These stages result from the internal dynamic of the stand itself. Defining these stages is useful in understanding the development of oak forests even though the duration of each stage and the accompanying changes in stand structure, density, and species composition may differ from stand to stand.

Although various terms have been used to define the stages of stand development, it is convenient here to follow the terminology of Oliver and Larson (1996) as modified by Oliver (1997). They defined four stages: (1) the stand initiation stage, (2) the stem exclusion stage, (3) the understory reinitiation stage, and (4) the complex stage (fig. 1). The complex stage of development also has been called the old-growth stage (Oliver 1981). These stages and their definitions provide a convenient conceptual framework for anticipating the inevitable changes in the ecological states that occur in oak forests.

The stand initiation stage—The development of an even-aged stand begins with the stand initiation stage (fig. 1). This stage typically lasts about 20 years in eastern oak forests. A brushy mass of woody vegetation comprised of thousands of trees and shrubs per acre, usually mixed with a luxuriant growth of vines and herbaceous plants characterizes this stage. It is a period of rapid change with intense competition among trees and other plants for growing space. Standing biomass is small relative to later stages of development, but the rate of biomass increase is high. During this stage, the quantity of dead biomass is often larger than during other stages of stand development. This results from the stand-initiating disturbance itself, which except when preceded by fire, usually leaves a large residue of tree boles and branches on the forest floor.

During the stand initiation stage, gaps in the new vegetative cover may persist for a decade or longer while new trees and other vegetation become established. New tree seedlings and herbaceous vegetation initially require little growing space. During this stage there are numerous microenvironments where seeds find the necessary conditions for germination and growth free from predators, competitors, and pathogens. Changes in the number, species, and size

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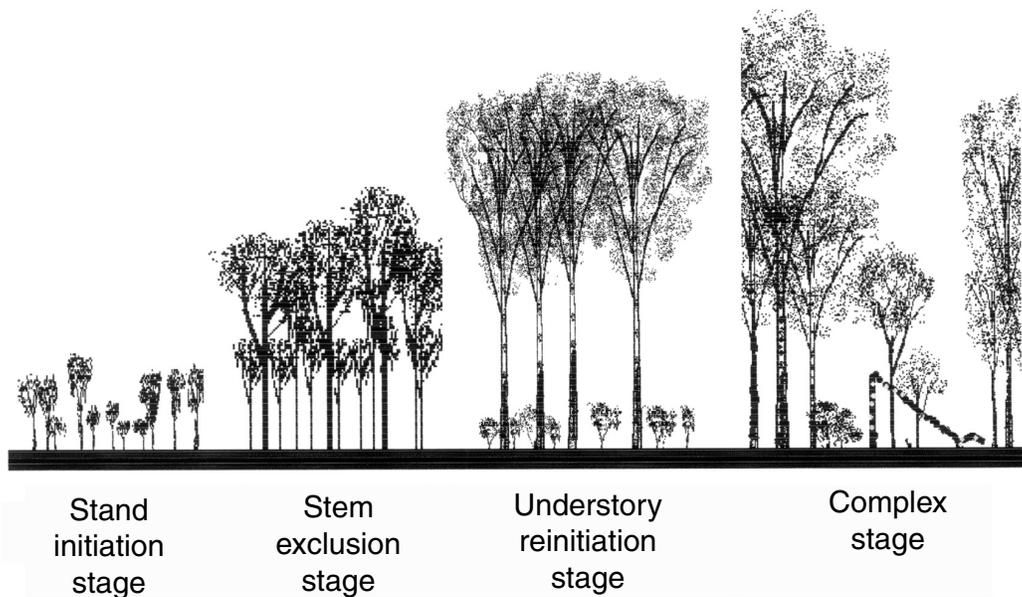


Figure 1—Stages of stand development occurring after a major disturbance that destroys all or most of the parent stand (from Johnson and others 2002).

of trees during the stand initiation stage are difficult to accurately predict. This is due to numerous essentially random events that influence the timing and spatial distribution of seed dispersal, germination, and seedling survival. Stand development during this period is subject to great natural variation, and predictions of stand development during this stage are usually only specifiable probabilistically (Dey and others 1996a, Johnson and others 2002). Future stand composition is heavily dependent on the amount and size of tree reproduction that is pre-established (i.e., occurring in “advance” of) the time of disturbance. Whether oaks are successful in attaining dominance during this stage largely depends on the number and size of oak seedlings and seedling sprouts present at the time of disturbance. In turn, this largely depends on site quality, the occurrence of prior disturbances such as fire or windthrow, or the natural development of overstory canopy gaps. Site quality combined with natural or silviculturally reduced stand densities during the stand initiation stage are closely connected to conditions that favor the development and accumulation of oak reproduction under the parent stand. This accumulation is more persistent on the poorer sites and where canopy closure is incomplete (Johnson and others 2002). Under those conditions, some of the oak reproduction can grow to a large size (fig. 2). When large advance oak reproduction is released from the inhibiting effect of the parent stand overstory it responds by producing one or more long flushes of terminal shoot growth in a single growing season (Johnson 1979, Johnson and others 2002). In turn, this imparts an initial growth advantage to the relatively shade-intolerant oaks.

The species composition of trees during the initiation stage is continually responding to the growth and maturation of the stand. Early theories of forest succession proposed that each species modifies the site to make it more favorable for the establishment and growth of succeeding species.

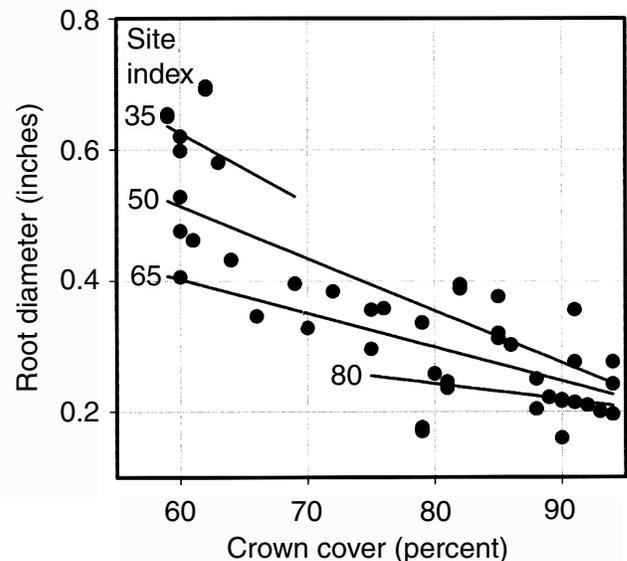


Figure 2—Diameters of roots of oak reproduction measured just below the root collar in relation to overstory crown cover and site index in West Virginia forests. The estimates represent the average of the scarlet, black, white, northern red and chestnut (*Quercus prinus* L.) oaks sampled. Estimates are based on a linear regression model that includes slope percent as a predictor; for this graph slope percent is held constant at 25. Each data point represents 7 to 10 trees (adapted from Matney 1974).

However, the actual processes can vary widely among the different types of oak forests. For example, in the Ozark Highlands of Missouri, the major tree species present at the time of disturbance become quickly stratified into crown classes through a process that could be described as competitive sorting. By the end of this stage, the initially abundant and ubiquitous sassafras (*Sassafras albidum*

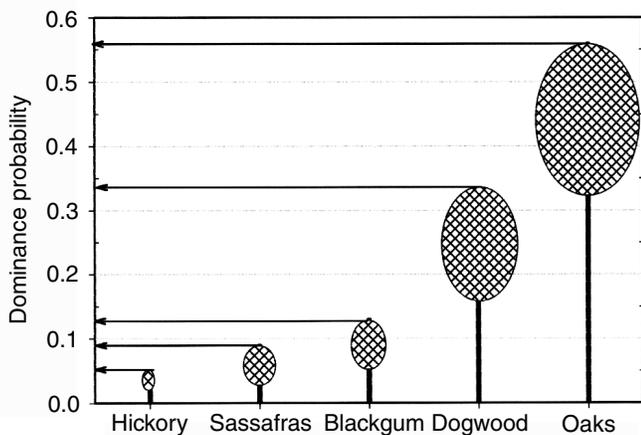


Figure 3—Dominance probabilities for advance reproduction (seedlings and seedling sprouts) of different species in the Ozark Highlands of Missouri. Dominance probability is defined here as the probability that advance reproduction of a given initial size will attain an intermediate-or-larger crown class 21 years after clearcutting. For each species, probabilities are for 6-foot-tall advance reproduction with 1-inch basal diameters growing on southeast- or northwest-facing mid-slopes. Probabilities differ by aspect and slope position. The five species groups shown are the predominant hardwoods occurring within this ecoregion. Probabilities were generated by the regeneration model *ACORn* (Dey and others 1996b).

(Nutt.) Nees), flowering dogwood (*Cornus florida* L.), blackgum (*Nyssa sylvatica* Marsh.), and hickories (*Carya* spp.) are largely relegated to the inferior crown classes. Black oak (*Quercus velutina* Lam.), white oak (*Q. alba* L.), scarlet oak (*Q. coccinea* Muenchh.) and other oaks by then usually predominate in the dominant and codominant crown classes. This competitive sorting process is reflected in each species' probability of attaining dominance. For a given species, this probability depends on a tree's size at the time of the stand initiating disturbance and site factors (fig. 3).

During the next two stages of stand development, few if any new trees are added to the overstory. Consequently, the composition of an even-aged stand at the end of the stand initiation stage is a good indicator of the species' richness of the future overstory. However, a species' relative abundance at this stage is often a poor indicator of its future importance. During the ensuing stem exclusion stage, species composition usually shifts toward the species that are best adapted to the site and able to attain and hold dominant or codominant crown positions. Dominance by oaks at the end of the stand initiation stage therefore does not always assure their continued dominance. The longer-term outcome varies among the many different types or classes of oak forests, and is often implicit in ecological classification systems (Johnson and others 2002).

The stem exclusion stage—In oak forests of the Eastern United States, crown closure is usually complete by the beginning of the second decade after a stand-initiating disturbance. By that time, trees have stratified into well-defined crown classes and natural mortality has changed the initially clumped spatial distribution of trees to a more random dis-

tribution (Rogers 1983). This stage of stand development is termed the stem exclusion stage because few, if any, new stems are added to the population of overstory trees (Oliver and Larson 1996). Mortality rates are high, especially among trees in intermediate and suppressed crown classes. The combined growth, competition, and mortality of trees during this stage produce spatial adjustments in the main canopy that maintain full utilization of growing space. It is usually not until after the stem exclusion stage begins that predictive growth and yield models are applicable. During this and subsequent stages, patterns of stand development and changes in species composition are more predictable than during the stand initiation stage.

If oaks are to maintain a position of dominance at this stage of development, they must outgrow their competitors. Oaks do this in three ways: (1) through inherently faster growth, (2) through an initially superior crown position, or (3) through greater persistence than their competitors. On some sites in the Ohio Valley, persistence may allow oaks to survive when other faster-growing species such as yellow-poplar (*Liriodendron tulipifera* L.) or red maple (*Acer rubrum* L.) succumb to drought (Hilt 1985). Persistence also may allow more oaks than other species to survive fires, or permit oaks to eventually grow taller than species of inherently small stature such as flowering dogwood, which may temporarily overtop the oaks.

As an even-aged stand matures, its diameter frequency distribution continually changes. For example, in 10-year-old upland oak stands of the eastern United States, diameter distributions form reverse J-shaped curves comprised of thousands of trees per acre. However, in the absence of exogenous disturbance, this diameter distribution may progressively transform itself into a bell-shaped diameter distribution comprised of few hundred trees per acre by the time the stand reaches a mean diameter of 8 inches in diameter at breast height (d.b.h.) (Schnur 1937). On sites of average quality, this occurs at approximately stand age 85, which is well into the understory reinitiation stage of development. In the absence of exogenous disturbance, numbers of trees decline with time through the process of self-thinning (Johnson and others 2002). During the stem exclusion stage, about 80 percent of trees die from crowding during self-thinning on average sites (Schnur 1937). Where markets for small trees exist, thinning stands during the stem exclusion stage thus can utilize many trees that would otherwise die from self-thinning. Moreover, the retained trees accelerate their growth in response to crown expansion, which in turn is facilitated by the increase in growing space available to them. Thinning during this stage also can be used to control species composition and the quality of future final crop trees.

When oak forests are subject to recurrent low-intensity disturbances (as in oak savannas maintained by periodic burning) they may not pass through the stem exclusion stage. In oak savannas, periodic burning maintains a relatively open overstory, which in turn maintains relatively high light intensities in the understory. Although the reproduction of oaks and other species is usually abundant under these conditions, its recruitment into the overstory is inhibited by recurrent topkill of reproduction unless there is a

fire-free period of sufficient duration. Under these conditions, growth of oak reproduction into the overstory is limited more by the disturbance regime than by insufficient light. The fire-tolerant oak reproduction nevertheless responds to this disturbance regime by slowly accumulating beneath the savanna understory.

The understory reinitiation stage—During the understory reinitiation stage, tree reproduction becomes reestablished beneath the parent stand (fig. 1). In oak forests, this reproduction often becomes a major component of the new stand that develops after the next stand-initiating disturbance. Many factors influence which species become established in the understory and consequently which species are likely to dominate after a stand-initiating disturbance. In oak forests, light and soil moisture rank among the most important of these factors. This is also the stage of stand development when oak forests usually attain economic maturity. Consequently, it is a critical period in the development of an oak stand silviculturally. The reproduction that becomes established (naturally or by human design) largely determines future stand composition.

Compared to the stem exclusion stage, trees in the main canopy are larger and fewer in number during the understory reinitiation stage. At this stage of stand development, some main canopy trees periodically produce large quantities of seed. Large crowns are important determinants of acorn production and thus the establishment of oak seedlings and the availability of acorns to wildlife. Moreover, when large trees die they create larger canopy openings than those created during earlier stages of stand development. The crowns of large main canopy trees also expand more slowly than they did during earlier stages of stand development. Consequently, canopy gaps remain open for longer periods, and this often results in light intensities near the forest floor sufficient for seedling establishment and growth. The resultant spatial heterogeneity of the main canopy creates spatial variation in the amount of light that reaches the forest floor. This produces microenvironments favorable for the establishment of oak reproduction that can develop large root systems, which in turn are correlated with rapid height growth. Established trees in subordinate crown positions also benefit from the increased growing space when an overstory tree dies and creates a canopy opening.

The successional replacement of oaks by more-shade tolerant species is one of the most pervasive problems associated with oak silviculture on highly productive sites. The understory reinitiation stage is therefore a critical time for intervening silviculturally if the objective is to maintain or increase the proportion of oak in the future stand. However, not all oak forests are successional to non-oaks. In the Ozark Highlands of Missouri and similar dry oak forests in the Eastern United States, the successional displacement of oaks is limited by the inability of other hardwoods to persist in the superior crown classes. Although non-oaks may aggressively fill canopy gaps immediately after disturbance, their occurrence as canopy dominants is usually ephemeral. This limitation to persist as a canopy dominant is determined by each species' life-history, stature, and physiological responses to site conditions. Regardless of the spatial scale of disturbance, the non-oak hardwoods

rapidly drop out of the stand or assume a subordinate canopy position as competition intensifies with crown closure (Dey and others 1996a).

Differential dropout rates among species are reflected in their probabilities of attaining an intermediate-or-better crown class after clearcutting. For a given initial (pre-harvest) basal diameter, these probabilities are higher for oaks than for other hardwoods 15 years after cutting. By that time, oaks dominate stands and species are stratified into well-defined crown classes. This outcome is the result of the collective influence of initial floristics, overstory inhibition, and competitive sorting processes that control secondary succession in oak-dominated ecosystems such as the Ozark Highlands and elsewhere where oak reproduction naturally (intrinsicly) accumulates.

Reverse J-shaped diameter distributions are most often associated with uneven-aged forests, but they also occur in certain even-aged forests—including those beyond the stem exclusion stage of development. These stands often originate following the disturbance of stands comprised of both shade-tolerant and shade-intolerant species. In subsequent stages of stand development, reverse J-shaped diameter distributions may evolve through the recruitment of shade tolerant reproduction into the overstory. Meanwhile, the less tolerant oaks may develop a bell-shaped diameter distribution (Johnson and others 2002).

The complex stage—In the absence of timber harvesting or other exogenous disturbances that eliminate the overstory, even-aged stands progress toward the complex stage (Oliver 1997). During this stage, the natural mortality of large overstory trees creates canopy gaps, which occur irregularly in time and space. Gap size is typically equal to the crown area of one tree or a small cluster of trees. Because these gaps are relatively large, crown expansion of trees adjacent to a gap is insufficient to fill the gap. This lag in crown closure allows subcanopy trees and established reproduction to increase height growth and crown expansion to fill the canopy gap. As new canopy gaps occur, they are filled by new age classes of trees. If this gap-filling process continues in the absence of a stand-initiating event, an uneven-aged stand eventually evolves.

The complex stage of stand development includes old-growth forests, and Oliver and Larson (1996) originally termed this stage the old-growth stage. However, there is a basis for distinguishing between the two. All old-growth forests are complex, but not all complex forests are old-growth. Definitions of old-growth oak forests are usually based on overstory age, stand disturbance history, and structural characteristics such as the presence of old trees, snags, and down wood. The various definitions of old-growth all assume that human impact on forest development has been minimal. However, older second-growth forests (managed and unmanaged) may have complex structures that do not meet the strict definition of old-growth.

The Development of Uneven-aged Oak Stands

As even-aged stands advance toward the complex stage of development, trees initially comprising a single age class gradually evolve into a multi-aged population as a result of

the successional processes accompanying stand maturation and gap formation and filling. As stands mature, canopy gaps become more numerous until the forest forms a mosaic of old trees and gaps filled with younger trees of various ages. As reproduction within gaps captures growing space, stand-wide diameter distributions gradually change. In the absence of a stand-initiating disturbance, the diameter distribution may change from bell-shaped to reverse J-shaped. Regardless of the shape of the diameter distribution, the normal evolution of stand structure from even- to uneven-aged eventually produces an uneven-aged collection of highly dispersed, even-aged groups of trees, each occupying a relatively small area. Eventually, the various tree age classes become visually indiscernible.

Although the overall diameter frequency distributions of old-growth forests containing oaks often form a reverse-J shape, the diameters of the oaks themselves may not conform to that distribution. The way a stand evolves structurally and compositionally largely depends on differences in the rates at which co-occurring species of tree reproduction are recruited into the overstory. Where non-oaks fill most of the canopy gaps created during the complex stage, those species will predominate among the smaller trees (e.g., the left tail of a reverse-J diameter distribution). Depending on the interaction of site factors with the biological characteristics of the non-oaks, the oaks may or may not ascend to dominance. The competitive capacity of the oaks largely depends on site quality and correlatively the tree species they are competing with. In the more productive oak forests, a bell-shaped diameter distribution of oaks embedded within an overall reverse J-shaped distribution reveals an oak population doomed to displacement by other species. A bell-shaped distribution for any given species reflects its failure to grow into the overstory. Oaks often lose this successional race to other long-lived species that are better adapted to establishment and survival under shade (e.g., sugar maple (*Acer saccharum* Marsh.)). Bell-shaped oak diameter distributions thus are harbingers of the oak's replacement unless there are disturbances that specifically favor oak regeneration.

In the Ozark Highlands of Missouri, crown stratification among the oaks persists into the complex stage (Shifley and others 1995). There, oaks are usually not successional displaced by other tree species and the relative permanence of oaks is reflected by their relatively high abundance in the smaller diameter classes, even in old-growth stands. In mature, relatively undisturbed second-growth forests, the diameter frequency distributions of the oaks tend to peak in the smaller diameter classes. In these stands the diameter distributions of oaks approach the reverse-J shape characteristic of all-aged stands. Diameter distributions of all species combined (including non-oaks) clearly have a reverse J-shaped form because the smaller diameter classes are comprised of relatively large numbers of shade-tolerant species such as flowering dogwood and blackgum. However in that region, the predominant subcanopy species are largely relegated to the subcanopy (Dey and others 1996a). The relative permanence of the oaks is indicated by the persistence of diameter distributions that, under natural conditions, often approach a reverse-J shape. However, specific characteristics of diameter distributions in this

ecosystem, and their natural occurrence and silvicultural maintenance, depend on species composition and stand density (Larsen and others 1999, Loewenstein and others 2000).

Exogenous Forces and Disturbance-Recovery Cycles

When forest disturbance is limited to gap-scale events, stand development follows the normal sequence (fig. 1). However, stand-initiating events that eliminate all or most of the overstory can occur during any stage of stand development. These events return stands to the stand initiation stage of development. In contrast, smaller-scale (incomplete stand-scale disturbances) may eliminate only a portion of the overstory and leave significant numbers of trees standing. Although incomplete stand-scale disturbances change the stage of stand development, they do not return the stand to the stand initiation stage. Rather, they create a mixed stage of stand development. Mixed-stage stands resulting from natural events often form mosaics of younger trees developing in large canopy openings interspersed with patches of older trees. They often form irregularly spaced tree populations of variable size and age structure. Mixed-stage stands also can result from various types of timber harvesting.

Stands in the mixed stage of development are distinguishable from stands in other stages by: (1) the spatial scale of disturbance, which is greater than gap-scale, and (2) stand density, which is often below average maximum density. Relatively young trees also may dominate mixed stage stands. Low density, highly disturbed stands of all descriptions therefore fall into the mixed stage of development. Examples of stands in the mixed stage include oak savannas, stands resulting from indiscriminate timber harvests, and some silvicultural practices. The latter include heavily thinned stands, shelterwoods, and some stands managed by group selection or single-tree selection cut to low or moderate densities. Oak forests in the mixed stage of development are ubiquitous because the exogenous forces that create them are so common.

The complete spectrum of forest developmental stages thus includes the mixed stage plus the four stages previously defined. Collectively they represent points in a potentially endless series of disturbance-recovery cycles initiated by stand-scale and gap-scale disturbances. These cycles follow specific sequences determined by the developmental stage of the stand at the time of disturbance and the type and spatial scale of disturbance. Disturbance and recovery cycles provide a conceptual framework for ecological process and silvicultural practice. However, control of stand composition and structure is often complicated by unpredictable natural disturbance events that often lie beyond the direct control of the forest manager. Even when forests are intensively managed, unplanned and unwelcome disturbances are a part of management reality.

Frequent stand-initiating disturbances can maintain a forest in the stand initiation stage indefinitely. Such disturbance regimes were common and extensive in many regions of North America before European settlement. For example, in the prairie-forest border region of southwestern Wisconsin,

plant communities described as “oak scrub” failed to develop beyond the sapling stage because of frequent wildfires that persisted for centuries (Grimm 1984). As long as frequent fires occurred, the stands of oak scrub persisted. The fires arrested succession, and thus maintained stands in the stand initiation stage of development. But by the early twentieth century, wildfires were largely controlled and region-wide the oak scrubs quickly responded by developing into closed canopy forests so common in that region today (Curtis 1959).

SUMMARY AND CONCLUSIONS

A panoply of events and processes, predictable and unpredictable, represent the reality of managing oak forests. Our current management models are based largely on the sequence of changes occurring during the initiation stage through the reinitiation stage of stand development—with and without timber harvesting or other management practices. Superimposed on those changes are a myriad of possible unplanned exogenous disturbances that can abruptly redirect forest development at any time. Moreover, rapidly emerging interests include managing for old growth, wildlife and acorn production, biodiversity, various aesthetic values, and restoring savannas and the other historical plant communities associated with the oaks. A common denominator to all of these issues is the regeneration of oak forests, which ultimately determines the sustainability of the oaks for whatever end. However, the controlling ecological processes for all of these problems differ greatly among the various kinds of plant communities dominated by oaks. Understanding the likely responses of such communities to both endogenous and exogenous forces is central to formulating effective management practices and thus to minimizing unintended consequences.

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**Historical Perspectives Influencing the
Establishment and Sustainability
of Upland Oak Forests**

UPLAND HARDWOOD FORESTS AND RELATED COMMUNITIES OF THE ARKANSAS OZARKS IN THE EARLY 19TH CENTURY

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Abstract—Historic accounts of the 19th Century Arkansas Ozarks mention such communities as oak forests, pine forests, barrens and prairies. I document the region-wide distribution of these types based on data from the first land survey conducted by the General Land Office (GLO). Structural classes used here include closed forest, open forest, woodland, savanna, open savanna and prairie or herbaceous-dominated. The analysis is based on subsections of the Ozark Mountains within Arkansas. These provide areas small enough to represent the landscape level diversity of the Ozark ecoregion, but large enough to encompass a relatively large number of GLO corners, the basic unit of analysis. As of the 1820s and 1830s, there were differences in the proportion of structural classes within these subsections: the Boston Mountains had more closed forest than the Ozark Highlands to the north, but communities were more open than today, probably as a result of recent fire suppression.

INTRODUCTION

Understanding the composition, structure and processes of natural communities of the past may provide valuable perspectives for developing appropriate forest management approaches and understanding of current issues such as oak decline and red oak borer. This does not mean that the goal of management today must be the restoration of past conditions; accomplishing that goal may be impossible given current social, economic or ecological constraints. Knowledge of past conditions may simply inform managers and decision makers about how much change has occurred in the landscape and what some of the implications of that change may be.

The presettlement character of the Ozark Mountain region has been the subject of considerable and sometimes acrimonious debate. A central issue has been the structure of the wooded areas, specifically whether they were open woodlands with herbaceous ground cover or whether they were closed-canopy forest. A further question involves the processes that may have led to a previously more open condition, especially fire frequency. These issues have substantial implications today for deciding on “appropriate” management for public lands, for achieving silvicultural objectives such as oak regeneration, and for understanding current forest health problems.

The typical view of the vegetation of the Ozark region that dominated the scientific literature of the first half of the 20th Century was that most of the non-prairie areas were dense forest (e.g., Braun 1950). This view was challenged by Beilmann and Brenner (1951), who presented historic descriptions and notes of the first land surveyors from the early 19th Century that provided evidence that much of the non-prairie area of the Missouri Ozarks was not closed forest but rather was open woodland often termed “barrens.” Such areas had trees spread widely enough to allow sunlight to reach the ground, dramatically increasing the density and diversity of vegetation in that stratum. In many cases, particularly in the most open woodlands, the ground-layer

flora was comprised of species typically found in prairies. Steyermark (1959) issued a spirited and devastating rebuttal, also quoting from historic sources and surveyor’s notes to argue his position that the patterns of vegetation structure in Missouri had changed little from the early historic time to the present. Many later researchers (Ladd 1991, Nigh and Pallardy 1983, Schroeder 1981) have provided more support for the Beilmann and Brenner view than that of Steyermark, and have provided considerable insight into the role of fire in maintaining the open condition.

Most of the debate over historic condition of oak woodlands of the Ozarks has been limited to the Missouri portion of the region. The conclusions reached there may apply to the Arkansas Ozarks as well, but there may be differences. While the physiography of part of the Arkansas Ozarks is the same as that of adjacent areas of Missouri, the Boston Mountains Subdivision (Foti 1974) does not extend into Missouri. The Boston Mountains and the Ozark Highlands have been recognized as separate sections (Foti and Bukenhofer 1998, Foti and Bukenhofer 1999, Keys and others 1995) as a result of the significant differences between them. In turn each of these sections has been subdivided into subsections, each of which varies somewhat from the others, in terms of both physical and biological features (fig. 1). Therefore the descriptions and analyses presented here will be stated in terms of these finer geographic regions. Subsections are still large enough to contain many of the GLO survey section corners, but are small enough to reduce the landscape and plant community variation within each.

HISTORIC DESCRIPTIONS OF THE ARKANSAS OZARKS

The most comprehensive map of the vegetation of Arkansas including the Ozarks in the 19th Century was provided by Sargent (1884) who mapped pine forest, hardwood forest and prairie. However, he did not map structural differences of the forest types.

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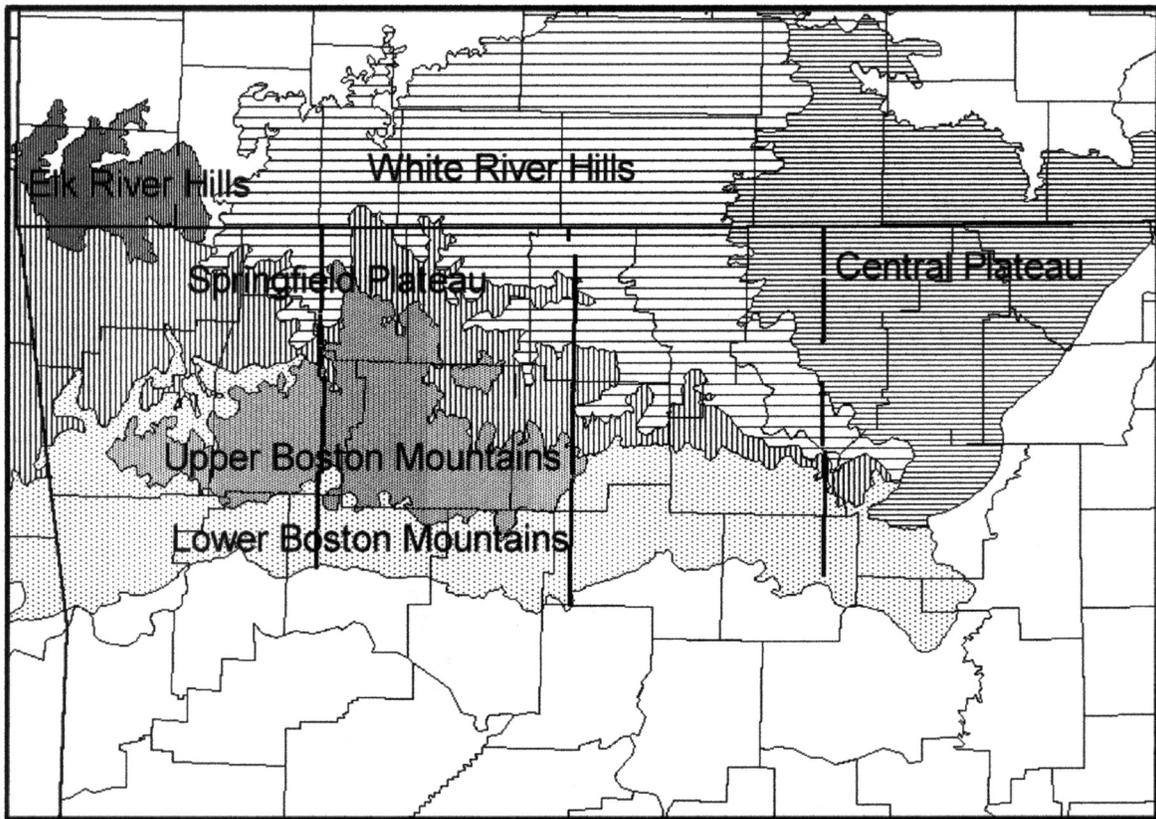


Figure 1—Subsections of the Arkansas Ozarks referred to in this study, along with the locations of GLO corners analyzed.

In the White River Hills Subsection of the Ozark Highlands Section Schoolcraft in 1818 found cane thickets and forests of oak, ash, maple, walnut, mulberry, sycamore, hickory, and elm on alluvial soils. He found prairies of coarse grass and “scanty” timber on the limestone hills and “bald mountains” (Rafferty 1996).

Owen (1858) described traveling north from Huntsville, Madison County, through the Boston Mountains and Springfield Plateau, saying one travels first through barrens and then prairie (p. 103). He described the land between the White River and Bentonville (Benton County) in the Springfield Plateau as being mainly barrens interspersed with prairies. He expressed the opinion that the prairies there had been of much greater extent and had been reduced by human activity.

Near the White River in the Upper Boston Mountains Subsection, Gerstacker (1881) described forest rather than barrens: “There was no trace of fir [cedar]; the mountains were covered with oak, beech, and hickory . . . It struck me as extraordinary that the best and most fertile land was on the hill tops, where in other places, it is generally the worst; here grew black walnut, wild cherry, with stems sometimes twenty inches in diameter, black locust, and sugar maple, trees which generally grow only on the richest soils” (p. 282).

PREVIOUS STUDIES BASED ON GLO SURVEY NOTES

General Land Office (GLO) notes of the original land survey of the Ozarks from 1818 to the 1850’s provide quantitative data on forest composition at that time. Surveyors traversed the east and south sides of each 6 mile by 6 mile township and then the east and south sides of each mile-square section within each township. Direction and distance from each section corner and quarter-section corner (that is, halfway along each section side traversed) to two or four bearing trees were measured and species were identified (Bourdo 1956). Diameter of each tree was also recorded. Location of additional line trees and qualitative descriptions of the topography, soil, forest, and undergrowth along each mile line surveyed were also recorded. Although there were no doubt biases in the selection of bearing trees and sometimes errors in measurements, these surveys are the most complete quantitative data set on vegetation in the early 19th Century.

These surveys offer several ways to characterize vegetation: (1) Compilation of numbers of trees by species can provide information on composition, (2) Diameters of bearing trees can provide estimates of size, (3) Distances to bearing trees can provide estimates of total density and density by species, (4) Diameter and distance combined can provide estimates of basal area or dominance, (5) Mile notes can provide qualitative assessment of land, timber and undergrowth, and (6) Plat sheets of each township provide maps of notable features such as streams, prairies, fields and ridgelines.

Prairies are often well delineated both in the notes and on plat sheets because these were considered valuable in land selection decisions. Other measures must be determined from the written data and notes.

Of particular interest in the present study is the density of trees in the non-prairie areas. Most previous studies have used methods developed in Illinois to characterize the openness of the areas with trees based on average distance of bearing trees from the corner (Anderson and Anderson 1975, Rodgers and Anderson 1979). According to these studies, savanna is defined as having less than 50 percent canopy cover of trees, a density of 1 tree per 5 acres to 19 trees per acre, and average distance from the corner greater than 32 feet (48 links). Open forest varies from 19 to 40 trees per acre, average distance from 22 feet (33 links) to 32 feet, and closed forest has a greater density. This definition of savanna as having an arboreal crown cover of less than 50 percent follows Curtis (1959). Curtis defined the lower limit of tree density for savanna at 1 tree per acre rather than 1 tree per 5 acres as Anderson and Anderson did.

As in Missouri, the notes have been used to characterize the vegetation of the Arkansas Ozarks. In most instances, these studies were conducted by anthropologists and archeologists to examine settlement patterns, and therefore forest composition and structure were secondary to the main interest.

The dominant trees in the Lee Creek watershed of Crawford County in the Lower Boston Mountains Subsection in 1837-1843 were white oak, black oak and post oak, with appreciable numbers of hickory. White oaks most commonly occurred on steep slopes and higher elevations. Post oaks were most common on high elevations, upper stream valley floodplains and intermediate flat uplands. Black oak and hickories were distributed across all landform types (Harmon and others 1996, Lockhart and others 1995).

Tree species distribution and density were characterized within three townships along War Eagle Creek in Madison County (Upper and Lower Boston Mountain subsections and Springfield Plateau Subsection) by Joyce (1981). The study area was mapped into SCS (now NRCS) land capability classes and average density, dominance and frequency of all trees within each class were calculated. Trees of all capability classes except one were classed as closed forest using criteria of Rodgers and Anderson (1979). Trees of Class III, having severe limitations that reduce the choice of crops or require conservation practices or both, had an average density (18.4 trees per acre) that classed them as savanna. Approximately 18 percent of the study points fell within this class. Using a different approach, the instances in which the surveyor used such terms as "very little timber" or "no timber of any value or size" in the mile notes were mapped. This occurred in 20 of the 216 total miles surveyed, but all of these occurred on the 52 lines (38 percent) within the Springfield Plateau; none occurred in the Boston Mountains. She concluded that these were the actual "barrens" referred to in narratives. The lines of the Class III areas were often described as "open woods". The average distance to trees on the lines with "barrens" are not provided, nor are the locations of the Class III areas.

Red oaks and white oaks were the most frequently recorded tree species groups within the study area at 374 and 365 trees respectively, and post oak was third with 145 trees. The Class III savanna areas that contained 18 percent of the total trees contained 29 percent of the total post oaks, 0.6 percent of the white oaks and 24 percent of the red oaks. Thus post oak and the red oaks were more important than average in these areas and white oak much less important.

The vegetation of Benton and Washington counties, in the Springfield Plateau and both Upper and Lower Boston Mountains subsections, was mapped from the GLO notes interpreted with the assistance of topographic maps by Miller (1972). Five generalized communities were interpreted and mapped: (1) oak barrens (also called open woodlands and prairie woodlands), (2) lowland forest, associated with streams, (3) lowland or bottomland prairie, in the floodplain of major streams, (4) upland forest, and (5) upland prairie. The oak barrens were "basically grass covered with interspersed trees and brush". They "were most often located on relatively flat lands at moderate elevations (1100-1400 feet), or steep rough slopes." Predominant trees were post oak and blackjack, with a few occurrences of black oak and black hickory. Lowland forest was diverse, with red oak, bur oak, black walnut, ash, slippery elm, shagbark hickory and others. Species of the prairies were not listed. Upland forest generally occurred at elevations from 1400-1700 feet. It was dominated by white oak, black oak, red oak, post oak, walnut, chinkapin oak, and others. At some places it was more open, with more xerophytic species, and difficult to distinguish from barrens without clues from topography. He concluded, "...it seems that this area was largely Oak Barrens and Prairie with the forest restricted to the highlands and stream bottoms." This agreed with the historic description of Owen (1858).

NEW ANALYSIS OF GLO SURVEY NOTES

The purpose of the current study is to characterize the original plant community mosaic of the Arkansas Ozarks. Using field notes of General Land Office surveyors, I analyze the distributions of dominant species, along with density of trees along survey lines. Because of the limitations of available data, the study concentrates on structure of vegetation rather than processes that maintained it, such as fire.

METHODS

In order to provide broad characterization of the vegetation of the Arkansas Ozarks, I analyzed GLO data along north-to-south transects. These transects crossed each of the ecological sections and subsections of the Ozark Ecoregion (fig. 1). This provided a sample of the entire region. I recorded the following data at each section and quarter section point: (1) species of bearing trees and (2) average distance in links to the bearing trees. I summarized mile notes if they provided insight into community structure (e.g., "barrens", "thinly timbered", "oak-hickory" etc.). I grouped species recorded in the notes based on reliability of identification and ecological insight provided. The groups pine, white oaks and red oaks characterize the overall vegetation of broad areas. I recorded post oak and blackjack oak separately since they might indicate more xeric areas and/or more frequently burned areas, beech as an indicator of

more mesic areas, and cedar since it is easily killed by fire and its presence in large numbers could indicate lack of fire. All other species were recorded as "other".

The density of trees in the non-prairie areas can be estimated from the surveyor's data on distance to the bearing trees. The square of the average distance to bearing trees in links (1 link=2/3 foot) provides an estimate of the average area in square feet occupied by each tree (Anderson and Anderson 1975). From this figure the density of trees per acre can be calculated. This approach is equivalent to the correction factor provided by Cottam and Curtis (1956) for utilizing the point-centered quarter method with two, rather than four sampled trees. In a few instances the GLO surveyors recorded the distances to 4 bearing trees, generally at the corners of each township. In calculating density at these corners, the point centered-quarter method should use the square of the average distance in feet to determine area occupied by each tree (Cottam and Curtis 1956). In this study, basal area was calculated as the average basal area of the bearing trees multiplied by the calculated density.

Tree density categories used in Illinois (Anderson and Anderson 1975, Rodgers and Anderson 1979) were used in this study as well, and have already been stated. The terms savanna and barrens are used in this analysis to maintain consistency with the earlier studies cited here. However, an additional distance criterion was chosen to approximate a cover of 25 percent using a density half that of the maximum "savanna" criterion of Anderson and Anderson (1975). This distance of 67 links or 45 feet gives a density of 9.5 trees per acre and a canopy cover of 25 percent. A corner with lower density of trees than this is termed here "open savanna". The term "savanna" is favored here over "barrens" since the former term may be given a simple and objective definition, whereas no such definition for "barrens" exists; it may have meant different things to different observers.

In addition to defining classes using density only, a second method of calculation is used that includes both density and diameter. Since the class definitions are actually based on tree canopy coverage, a given density of small trees will have less canopy coverage than the same density of large trees. The older techniques were empirically derived, based on typical densities and sizes of trees in woodlands of Illinois. The newer method allows measured diameters and basal area to be used along with density to provide an estimate of canopy coverage, which is the actual criterion on which definitions of savanna or forest are based. It is derived from formulas and tables widely accepted by foresters to distinguish "fully stocked" timber stands, that is, those whose crowns are just touching and therefore are fully utilizing the available sunlight, from those that are too open or too dense (Gingrich 1967). Law and others (1994) used the same equations to provide a graphical technique for estimating the percentage of total area covered by oak crowns based on knowledge of basal area, tree diameter and density. Strictly speaking, these equations and the resulting charts only apply to oak forests, but both the authors and most users apply them to mixed forests where oaks make up the largest component. This applies to the forests encountered in the GLO surveys of the Arkansas

Ozarks. This method estimates percent canopy coverage for any combination of tree density, diameter and basal area, which can then be grouped into classes based on any desired definition.

Definitions of open wooded communities other than those cited already have been used. Current efforts to create a U.S. National Vegetation Classification System by The Nature Conservancy, NatureServe, The Ecological Society of America, the Federal Geographic Data Standards Committee and others do not use the terms savanna or barrens. The nearest equivalent term is woodland, and is defined to be a community with a canopy cover of trees of from 25 to 60 percent (Grossman and others 1998). Nuzzio (1986) provided an alternative definition of "oak savanna" as having a tree canopy cover of 10 to 80 percent. Since the method proposed by Law (1994) produces an estimate of actual canopy cover, corner points can be grouped and analyzed using any definition. Therefore, this method was used in conjunction with these two definitions as well as with the Anderson definitions.

These techniques for recording and analyzing data minimize surveyor bias in at least two ways: (1) species identification is simplified since the species groups could be easily identified by the surveyor, (2) exact locations of corner points are not a concern since they are grouped by broad but ecologically meaningful ecological regions. Bias in selection of species would under-represent the species selected against and over-represent the species selected for. Bias in selection would also overestimate the distance to bearing trees, since other trees had been ignored. The use of broad density classes minimizes this effect. The use of several openness categories simply shifts the corner to the next lower openness class, rather than a much lower openness class.

Results are reported by subsection and include frequency of each species group, average density, and openness class of woody cover (prairie, open savanna, savanna, woodland, open forest and closed forest). Nomenclature throughout follows Smith (1988).

RESULTS

The surveyors of the lines used in this study identified 27 taxa among the 792 trees at 379 corners (table 1). White oak and black oak were the most common trees named, making up 29 and 24 percent of the total sample, respectively. Post oak, pine and hickory followed in abundance, each with over 6 percent of the total trees. The white oak species group, consisting of white oak and post oak, was the most abundant, with 41 percent of the total number. The red oak group, consisting of black oak, blackjack oak, Spanish oak (southern red oak), red oak, pin oak and chinquapin oak, followed with 31 percent of the total.

The red oak group (without blackjack oak) was consistently abundant across all subsections, varying from 38 percent of the total bearing trees in the Upper Boston Mountains and 35 percent in the Springfield Plateau to 24 to 26 percent in the other subsections (table 2). Blackjack oak occurred only in the subsections of the Ozark Highlands, comprising a maximum of 16 percent of the bearing trees of the Central

Table 1—Tree names recorded by the surveyors, with presumed species, analysis group, and number of individuals recorded

Surveyor name	Presumed species	Group	Total	Percent
Ash	<i>Fraxinus</i> sp.	Other	10	1.3
Beech	<i>Fagus grandifolia</i> Ehrh.	Other	7	0.9
Black jack (oak)	<i>Quercus marilandica</i> Muench.	Red oak	26	3.3
Blackgum	<i>Nyssa sylvatica</i> Marsh.	Other	32	4.0
Black oak	<i>Quercus velutina</i> Lam.	Red oak	191	24.1
Cedar	<i>Juniperus virginiana</i> L.	Cedar	8	1.0
Cherry	<i>Prunus serotina</i> Ehrh.	Other	1	0.1
Chinquapin	<i>Castanea pumila</i> (L.) Mill.	Other	7	0.9
Chinquapin oak	<i>Quercus muehlenbergii</i> Engelm.	Red oak	1	0.1
Dogwood	<i>Cornus florida</i> L.	Other	8	1.0
Elm	<i>Ulmus</i> sp.	Other	14	1.8
Gum elastic	<i>Bumelia lanuginosa</i> (Michx.) Pers.	Other	1	0.1
Gum	uncertain species	Other	3	0.4
Hickory	<i>Carya</i> sp.	Hickory	48	6.1
Maple	<i>Acer</i> sp.	Other	7	0.9
Mulberry	<i>Morus rubra</i> L.	Other	1	0.1
Pin oak	<i>Quercus palustris</i> Muench.?	Red oak	1	0.1
Pine	<i>Pinus echinata</i> Mill.	Pine	55	6.9
Post oak	<i>Quercus stellata</i> Wang.	Post oak	95	12.0
Red, slippery elm	<i>Ulmus rubra</i> Muhl.	Other	2	0.3
Red oak	uncertain species	Red oak	21	2.7
Sassafras	<i>Sassafras albidum</i> (Nutt.) Nees	Other	4	0.5
Spanish oak	<i>Quercus falcata</i> Michx.	Red oak	10	1.3
Sugar tree	<i>Acer saccharum</i> Marsh.	Other	3	0.4
Sweetgum	<i>Liquidambar styraciflua</i> L.	Other	3	0.4
Walnut	<i>Juglans nigra</i> L.	Other	2	0.3
White oak	<i>Quercus alba</i> L.	White oak	231	29.2
Total			792	100.0

Plateau Subsection. The greatest abundance of white oak was in the Central Plateau where it made up 57 percent of the total trees. Its abundance was intermediate in the Boston Mountains (32 to 38 percent) and lowest in the Springfield Plateau and White River Hills (13 to 15 percent). The abundance of post oak was almost the inverse of white oak in that it was the most named-bearing tree in the White River Hills (28 percent). It was of intermediate abundance in the Upper Boston Mountains and Springfield Plateau (11 and 16 percent) and it comprised only 2 percent of the trees in the Lower Boston Mountains and 1 percent of the trees in the Central Plateau (table 2).

Pine was most commonly selected in the Springfield Plateau (14 percent) and was of intermediate abundance in the Lower Boston Mountains and White River Hills (8 percent of each). It made up only 1 percent of the Central Plateau total and was not recorded in the Upper Boston Mountains. Hickory was recorded in all subsections except the Central Plateau and reached its highest levels in the Boston Mountains at 9 percent. Eight cedars were used as bearing trees only in the White River Hills, making up 4 percent of the total. Seven beech trees occurred only in the Lower Boston Mountains, comprising 3 percent of the total. "Other" trees consistently made up 11 to 15 percent of the total in each subsection, but comprised only 1 percent of the total in the Central Plateau (table 2).

The Boston Mountains subsection corners were dominantly white oak and red oak, but with pine, hickory and other at the next level in the Lower Boston Mountains and post oak, hickory and other in the Upper Boston Mountains. The Central Plateau Subsection was dominated by white oak with red oak as a distant second and blackjack oak as a distant third. The White River Hills Subsection was dominated by post oak and red oak, with white oak and other at the next level, and the Springfield Plateau was dominated by red oak, with post oak, white oak, pine and other sharing the next level (table 2).

Average density over the entire study area was 52 trees per acre (table 3). Density varied from 38 trees per acre in the Central Plateau to 76 trees per acre in the Upper Boston Mountains. Density in the Boston Mountains and Ozark Highlands sections were comparable at 52-54.

As expected, the Anderson method, which used density alone, generally placed corners into more closed classes than the Law method, which used both density and diameter of bearing trees (tables 3 and 4). While Anderson's method classed 38 percent of all corners as closed forest, the Law method classed only 21 percent as closed forest. The open forest and savanna classes were not greatly different between the two methods, but the Anderson method classed only 13 percent of the corners as open savanna,

Table 2—Number and percentages of tree species groups in each subsection

Section/subsection	White oak		Red oak		Post oak		Pine		Hickory		Black-jack		Cedar		Beech		Other		Total	
	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%
Lower Boston Mountains	101	38	68	26	6	2	20	8	23	9					7	3	40	15	265	100
Upper Boston Mountains	33	32	39	38	11	11			9	9							12	12	104	100
Boston Mountains total	134	36	107	29	17	5	20	5	32	9					7	2	52	14	369	100
Springfield Plateau	21	15	47	35	22	16	19	14	6	4	3	2					18	13	136	100
White River Hills	25	13	48	24	55	28	15	8	10	5	9	5	8	4			27	14	197	100
Central Plateau	51	57	22	24	1	1	1	1			14	16					1	1	90	100
Ozark Highlands total	97	23	117	28	78	18	35	8	16	4	26	6	8	2			46	11	423	100
Total	231	29	224	28	95	12	55	7	48	6	26	3	8	1	7	1	98	12	792	100

Table 3—Average density, and number and percentages of corners in structural classes using method of Anderson and classes selected to maintain consistency with previous studies

Section/subsection	Density no./ac	Closed For.		Open For.		Savanna		Open Sav.		Prairie		Forest		Open		Total	
		no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%
Lower Boston Mountains	44.8	49	40	42	34	25	20	6	5	0	0	91	75	31	25	122	122
Upper Boston Mountains	75.7	26	53	17	35	4	8	2	4	0	0	43	88	6	12	49	49
Boston Mountains total	53.7	75	44	59	35	29	17	8	5	0	0	134	78	37	22	171	171
Springfield Plateau	61.8	27	41	11	17	17	26	10	15	1	2	38	58	28	42	66	66
White River Hills	47.4	30	32	20	21	22	23	17	18	5	5	50	53	44	47	94	94
Central Plateau	38.5	12	25	3	6	15	31	13	27	5	10	15	31	33	69	48	48
Ozark Highlands total	49.9	69	33	34	16	54	26	40	19	11	5	103	50	105	50	208	208
Arkansas Ozarks total	51.6	144	38	93	25	83	22	48	13	11	3	237	63	142	37	379	379

Table 4—Number and percentages of corners in structural classes using method of Law and classes selected to maintain consistency with previous studies

Section/subsection	Closed For.		Open For.		Savanna		Open Sav.		Forest		Open		Total no.
	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	
Lower Boston Mountains	28	23	34	28	42	34	18	15	62	51	60	49	122
Upper Boston Mountains	11	22	11	22	16	33	11	22	22	45	27	55	49
Boston Mountains total	39	23	45	26	58	34	29	17	84	49	87	51	171
Springfield Plateau	17	26	9	14	14	21	26	39	26	39	40	61	66
White River Hills	17	18	18	19	20	21	39	41	35	37	59	63	94
Central Plateau	5	10	2	4	7	15	34	71	7	15	41	85	48
Ozark Highlands total	39	19	29	14	41	20	99	48	68	33	140	67	208
Arkansas Ozarks total	78	21	74	20	99	26	128	34	152	40	227	60	379

while the Law method placed 34 percent in this class. There is no criterion in the Law method for defining prairie, but the Anderson method placed over 3 percent of the corners in this structure class. Overall, the Anderson method classed 63 percent of the corners as closed or open forest (table 3), while the Law method placed about 60 percent of the corners into the open classes (table 4).

Although the Law method predicted much less closed forest in each subsection than Anderson, the relative amounts are similar (tables 3 and 4). Based on the Anderson method, the Upper Boston Mountains had the greatest percentage of corners classed as closed forest at 53 percent, with the Springfield Plateau and Lower Boston Mountains ranked next. Using the Law method, the Springfield Plateau has the highest percentage of corners classified as closed forest at 26 percent, with the Lower Boston Mountains and Upper Boston Mountains ranked next. Interestingly, the Upper Boston Mountains, with the highest density, dropped from first to third in the two rankings. Since the Anderson method only considers density and Law adds diameter, this is an indication that the diameters of trees in the Upper Boston Mountains were smaller than those of the other two subsections.

The Law method predicted a similar or lower percentage of open forest in each subsection than the Anderson method,

with Upper and Lower Boston Mountains showing the greatest declines, and with savanna becoming predominant in those subsections. Open savanna increased greatly using the Law method, and is the predominant class in the subsections of the Ozark Highlands with the highest proportion in the Central Plateau Subsection at 71 percent. The Anderson method defined prairie only in the Ozark Highlands subsections.

Combining closed forest and open forest into “forest”, and savanna, open savanna and prairie into “open”, using the Anderson method, the Boston Mountains subsections are dominantly Forest, the Central Plateau is dominantly Open, and the Springfield Plateau and White River Hills are approximately evenly divided (table 3). Using the Law method, the Boston Mountains subsections are approximately evenly divided between forest and open, the Central Plateau is dominantly open, and the Springfield Plateau and White River Hills subsections are somewhat more open than forest (table 4).

Using the cover estimates from Law and the class definitions of Grossman, the percentage of forest (>60 percent cover) varied from 40 percent in the Lower Boston Mountains to 15 percent in the Central Plateau, with the other subsections clustering around 34 percent (table 5). The herbaceous class of Grossman is equivalent to the open savanna class

Table 5—Number and percentages of corners in structural classes using method of Law and classes of Grossman

Section/subsection	Forest		Woodland		Herbaceous		Total no.
	no.	percent	no.	percent	no.	percent	
Lower Boston Mountains	49	40	56	46	17	14	122
Upper Boston Mountains	16	33	25	51	8	16	49
Boston Mountains total	65	38	81	47	25	15	171
Springfield Plateau	23	35	18	27	25	38	66
White River Hills	32	34	27	29	35	37	94
Central Plateau	7	15	8	17	33	69	48
Ozark Highlands total	62	30	53	25	93	45	208
Arkansas Ozarks total	127	34	134	35	118	31	379

Table 6—Number and percentages of corners in structural classes using method of Law and classes of Nuzzio

Section/subsection	Forest		Savanna		Herbaceous		Total no.
	no.	percent	no.	percent	no.	percent	
Lower Boston Mountains	33	27	83	68	6	5	122
Upper Boston Mountains	14	29	31	63	4	8	49
Boston Mountains total	47	27	114	67	10	6	171
Springfield Plateau	18	27	36	55	12	18	66
White River Hills	22	23	46	49	26	28	94
Central Plateau	5	10	22	46	21	44	48
Ozark Highlands total	45	22	104	50	59	28	208
Arkansas Ozarks total	92	24	218	58	69	18	379

used before, except that a canopy cover of exactly 25 percent is classed as woodland under the Grossman definition and herbaceous under the open savanna definition used here.

Using cover estimates from Law and class definitions of Nuzzio, the highest percentage of forest (>80 percent cover) was 29 percent in the Upper Boston Mountains, with Lower Boston Mountains and Springfield Plateau closely following (table 6). The Nuzzio herbaceous class (<10 percent cover) varied from 44 percent in the Central Plateau to 5 and 8 percent in the Lower and Upper Boston Mountains, respectively.

The average cover of corners described as “barrens” or “thinly timbered” by the surveyors was 28 percent and the average density was 39 trees per acre. These indicate open conditions but not greatly so.

DISCUSSION

The criteria proposed by Law and others are based on those widely accepted in forest management and therefore should be preferred, particularly for distinguishing closed forest from open forest. These criteria become more difficult to implement as the structure becomes more open, however, partly because the structure of the charts allows less precise definition of lower canopy coverage. Also, there is no criterion under this method for distinguishing prairie. This method generally defines more open communities for a specified density than the criteria proposed by Anderson and Anderson, but where tree diameters are large it can predict more closed communities.

Guldin and others (1999) analyzed Ozark and Ouachita timber by ecological Section based on USDA Forest Inventory and Analysis data. They showed a density of trees greater than 6 inches d.b.h. of 153 per acre in the Boston Mountains Section and 116 per acre for the Ozark Highlands Section. Density of trees in the early 19th Century in these Sections was 54 and 50 per acre, respectively. Although the modern and GLO numbers are not strictly comparable, this indicates a substantial increase in density of trees in the Ozarks over this period. This agrees with others such as Ladd (1991), who attributed this increase to fire suppression.

The various methods and class definitions generally agree that the Upper and Lower Boston Mountains subsections and the Springfield Plateau Subsection had more closed forest than the other subsections but that the amount, particularly based on the Law method, was much less than today. The subsections of the Ozark Highlands all had high coverage of the most open communities (open savanna and herbaceous).

Based on findings of earlier studies (Joyce 1981, Miller 1972), it is likely that the location of transects used in this study causes an overestimate of the amount of forest in relation to open structure in the Springfield Plateau, in that both of those studies demonstrated more open conditions than data from transects in this study. Both of their study areas were located west of the westernmost transect in this study, where the Springfield Plateau is broader and more level than the places where these transects crossed. The broader and flatter sites, combined with the level-bedded strata of the Ozark Mountains, would have been more exposed to wind, more droughty and more susceptible to frequent fire. The high amounts of pine along the transects studied here are indicative of steep, cherty slopes in contrast to the often level plains underlain by limestone further west.

Although geologic substrate and topography exert control directly over plant communities of the Ozarks, they probably also exert indirect control through precipitation since the Upper Boston Mountains are higher and moister than the other subsections and have up to 10” per year greater precipitation than subsections to the north within the Arkansas study area.

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THE FOREST AS A RESOURCE: FROM PREHISTORY TO HISTORY IN THE ARKANSAS OZARKS

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Abstract—Study of past human land use in the Lee Creek Unit of the Ozark National Forest challenges the existence of “pristine” forests predating the arrival of historic Americans. The distribution of early nineteenth century American settlements corresponds closely to the distribution of late prehistoric Native American archeological sites. One explanation for this finding is that pioneer American settlers occupied lands already altered by earlier Native Americans. To test this hypothesis, we used historical accounts and Geographic Information Systems approaches to develop a model of late prehistoric land use, emphasizing agricultural field clearing practices and wood consumption for building and fuel use. The extrapolated impacts of these Native American activities may well account for the forest environment encountered by historic American settlers. The major implication of this study is that long-term dynamics of forest ecosystems are best understood when human populations are included as components of those systems.

INTRODUCTION

Prehistoric Native Americans entered North America more than 12,000 years ago. Archeologists and paleoecologists have documented the important role Native Americans played in shaping forest ecosystems through use of fire, harvest of timber, tree stand management, plant domestication, and agricultural land clearing (Delcourt 1987, Denevan 1992, Hammett 1992). As a result, we now believe that European explorers entered environments already modified by native land use practices (Cronon 1983, Silver 1990).

Cooperative efforts by the Arkansas Archeological Survey and the Ozark-St. Francis National Forests begun in 1993 provide an opportunity to examine these issues in detail (Harmon and others 1997, Lockhart and others 1995). We discuss here research that addresses one issue in particular: How did prehistoric Native American land use practices impact Ozark forest ecosystems?

LEE CREEK STUDY AREA

Our study area in the Lee Creek Unit of the Ozark National Forest covers an area of approximately 404 square kilometers located in the Boston Mountains province of the Ozark Plateau (fig. 1). Narrow, V-shaped valleys bordered by steep slopes and vertical bluffs rise from clear, gravel-bedded streams. Flat ridge tops separate adjacent valleys. The vegetation today is upland hardwood dominated by oak and hickory with scattered pine and brushy undergrowth.

Lee Creek and its tributaries flow in a southwesterly direction from higher elevations in the northeastern corner of the study area. Valley bottoms are less than a kilometer wide. Sediments are thin and rocky, with narrow bands of moderately fertile soils extending along the streams. Bottomland floods create conditions suitable for limited agriculture.

ENVIRONMENTAL AND CULTURAL HISTORY

Three major climate events affected the region during the period of human occupation: (1) the Pleistocene/Holocene transition, which began about 12,000 years ago and

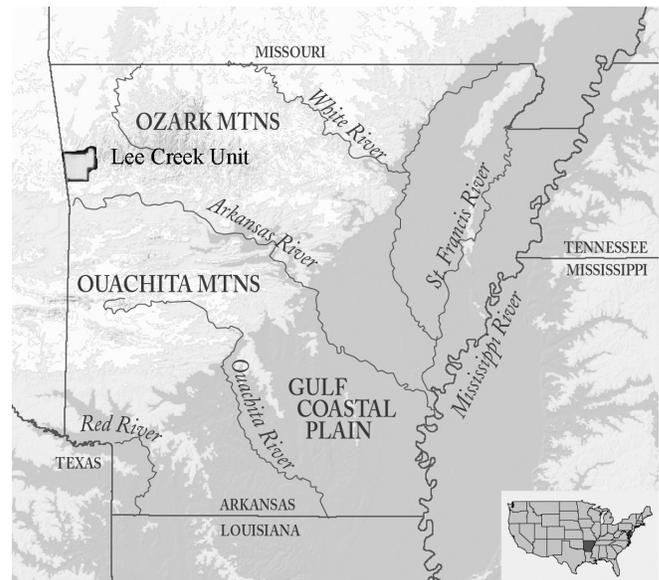


Figure 1—Location of the Lee Creek Unit.

brought an end to Ice Age conditions; (2) the mid-Holocene Climatic Optimum or Hypsithermal episode from 9,000 to about 5,000 years ago, during which warmer and drier conditions prevailed; and (3) the Late Holocene Neo-Boreal episode, which began about 500 years ago and brought cooler and less stable conditions. Tree rings studies indicate that our region experienced frequent and protracted drought conditions during the Neo-Boreal era (Cleveland and Stahle 1996).

Known archeological sites occur in our study area in sufficient number and distribution to permit study of prehistoric land use strategies, especially for the period covering the past 5,000 years (Harmon and others 1997, Lockhart and others 1995). Evidence from these sites and others located in the Pine Mountain area farther downstream (Raab 1976, Trubowitz 1980) makes it possible to identify general trends of prehistoric cultural development.

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The first human occupants of the Lee Creek valley arrived about 12,000 years ago, when a late Pleistocene spruce-jack pine boreal forest was giving way to an early Holocene oak-hickory forest (Delcourt and Delcourt 1981). The solitary archeological site dating to this era represents the presence of small groups of mobile hunters and gatherers who probably did not have much impact on local environments.

The region remained sparsely populated during the next few thousand years; only two sites have been discovered that date to the mid-Holocene era. The region had been encroached by open oak savannah when those sites were occupied (Delcourt and Delcourt 1981). Deer and other forest animals, fish and shellfish, birds, and wild plant foods including nuts, seeds, and fruits were the primary food resources supporting those groups. A slight increase in local environmental impacts probably resulted from the increased use of plant foods.

Native populations expanded after 5,000 years ago, as indicated by the presence of 48 sites in the study area that were occupied between 5,000 and 500 years ago. We recognize three types of sites: rock shelters (n=18) used for temporary camping, burial of the dead, and storage of perishable foodstuffs; small, special-purpose sites (n=15) located in a wide variety of settings; and residential sites (n=15) covering areas larger than 1,000 square meters that were occupied year-round by several extended families for long periods of time. The people who lived at these sites were engaged in the production of locally domesticated plants including lambs-quarters, little barley, knotweed, sumpweed, and several varieties of squashes. Corn, a tropical cultigen domesticated in Mexico, was also grown in small amounts. The advent of plant domestication, coupled with significant population growth, increased the level of human impact on the forest ecosystem.

Northwest Arkansas was part of the Osage Indian hunting territory during the late seventeenth and early eighteenth centuries. French hunters and traders entered the region toward the end of that period, and Euro-American settlement began after Fort Smith was built along the Arkansas River in 1817. A series of treaties signed during the following decade forced the removal of Native Americans from the region.

METHODS

Our investigation of the environmental impacts of past land use strategies in the Lee Creek valley involves three tasks: (1) creation of environmental models using Geographical Information System (GIS) techniques; (2) reconstruction of past land use strategies from archeological and historical evidence; and (3) analysis of the geospatial impacts of reconstructed land use practices on Ozark forest ecosystems.

Several environmental models were developed as GIS data layers for this project: elevation, slope, aspect, hydrography, soils, and line and witness tree locations recorded by nineteenth century General Land Office (GLO) surveyors. These initial models were used to create a series of derived products. Elevation and slope gradients and hydrography were used to create a terrain model based on a drainage class technique that specifies ten landforms. The addition

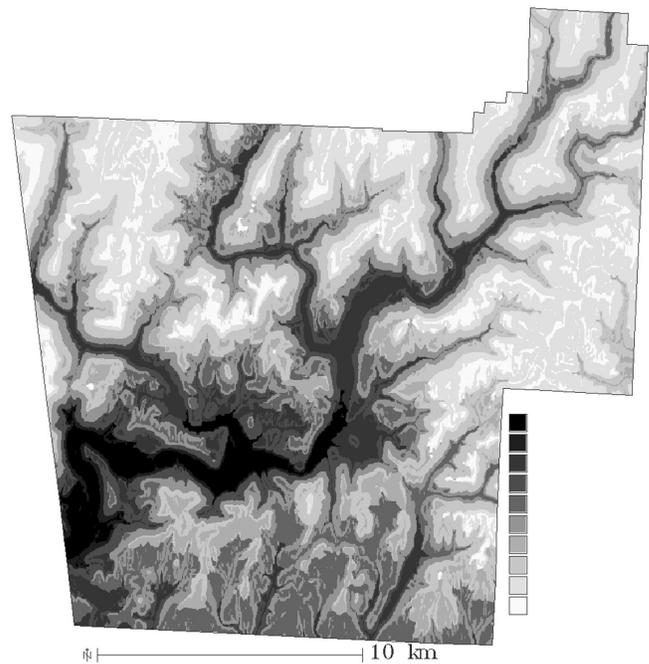


Figure 2—Terrain model for the Lee Creek Unit showing ten landform classes top to bottom: lower, middle, and upper stream floodplains; lower, middle, and upper stream slopes and bluffs; intermediate and high slopes and bluffs; intermediate and high flat uplands.

of a fourth variable — aspect (defined in terms of four 90° quadrants plus a fifth category for flat surfaces) — yields an expanded model comprised of 50 landform classes. The accuracy of both models was confirmed through extensive testing in which the expected and actual distributions of several cultural and environmental features were compared (Lockhart and others 1995: 8-20). For the sake of simplicity, we use the ten-class model here (fig. 2).

Analysis of archeological data within an “adaptation type” model provides a way to reconstruct ancient land use patterns with respect to past environmental features (Sabo and others 1989:1-2). These models define relationships that connect social, technological, and economic practices with the abundance, distribution, and predictability of environmental resources such as food and raw materials. Two prehistoric adaptation types are represented in the archeological data from the Lee Creek Unit: semisedentary hunting/gathering/gardening and semisedentary agriculture. In both of these models, local groups occupy year-round base camps, but part of the resident group spends part of each year engaged in seasonal subsistence pursuits elsewhere.

Geographical Information System applications are used to reconstruct the spatial impacts of past land use strategies on Ozark forest ecosystems. Here we illustrate the use of historical analogs and catchment analysis to estimate environmental impacts in the Lee Creek study area.

THE FOREST AS A RESOURCE

Let us turn now to an examination of three prehistoric land use practices to estimate their impact on Ozark forest environments.

The first practice is timber harvest for construction purposes. In excavated dwelling structures in northwest Arkansas, hardwoods such as red oak, white oak, and hickory were preferred for wall posts, which typically measured 10-30 cm in diameter. These structures average four to eight meters on a side and required about 50 stems for the walls, and half again as many stems for the roof timbers, interior roof supports, and interior bench supports.

Wood charcoal from archeological hearth features provides evidence of a second practice for firewood collecting. A breakdown by species of samples recovered from excavations at the Dirst site along the Buffalo National River reveals that oak species were by far the most preferred fuel woods, followed by sycamore, pine, hickory, and maple (Guendling and others 1992, Sabo and others 1990).

The advent of gardening and, later, more intensive field agriculture created a need for cleared areas, possibly in excess of land cleared through timber harvest and firewood collecting. We'll consider this hypothesis shortly.

How can we estimate the cumulative environmental impacts resulting from these three activities over several centuries of human occupation in the region? That is the question to which we turn next.

PREHISTORIC LAND USE IN GEOSPATIAL PERSPECTIVE

Since early historic Osage lifeways correspond to both of our target adaptation types, we can search historical records for useful analogs to the more ancient ecosystems.

Several visitors to Osage settlements during the early nineteenth century left observations indicating that wood, water, and fertile soils were important limiting factors in settlement location choices. For example, in 1819 Thomas Nuttall observed: "The river lands are no less extensive and luxuriant between the Verdigris and the Arkansa, and would apparently support a condensed settlement; but the prairies will only admit of settlements along their borders, in consequence of a scarcity of wood and water" (Nuttall 1999:211-12). Victor Tixier described an Osage village he visited in 1839: "Hunting lodges had been erected in a bend of the stream. Water and wood were near at hand" (McDermott 1940:159).

To quantify wood consumption and land clearing requirements, it is necessary to consider settlement population size. Here again, historical sources provide guidance. On December 30, 1819, Henry Rowe Schoolcraft happened upon three recently abandoned Osage hunting camps along Swan Creek in southwest Missouri, in an environmental setting similar to the Lee Creek Valley. Schoolcraft described these camps as "all very large, arranged with much order and neatness, capable of quartering probably 100 men each" (Rafferty 1996:78). Using a conservative 1:4 ratio of hunters to overall population, we estimate a group size of 400 individuals. A similar contingent of Little Osages encamped near Fort Osage along the Missouri River were living in 60 lodges "circular in form, not more than ten or fifteen feet in diameter" when they were visited in 1811 by

Henry Marie Brackenridge (Brackenridge 1814:217). These numbers suggest that each family of 4-8 members occupied its own lodge. The total floor area of those lodges, estimated at 480 to 985 square meters, could be accommodated at our large open archeological sites in the Lee Creek study area.

Since Lee Creek is narrower than the Verdigris and Missouri Rivers along which Nuttall's and Brackenridge's observations were made, we need to evaluate the 400-person village size in relation to estimates of regional population densities. For the early historic era, these range from 0.05 and 0.64 persons per square kilometer (Guyette and others 2002). These densities translate to a range of 20 to 259 people for our study area. The late prehistoric population in the Lee Creek valley undoubtedly was distributed among several settlements, so the existence of 15 large, permanent settlements is consistent with the higher population density figure, considering the likelihood that only a few of those sites were occupied simultaneously. Furthermore, the Native American occupants of that area made seasonal visits to other areas, such as the prairie-plains region to the west, for economic activities that included hunting buffalo. These considerations suggest that our study area probably was "home" at any particular time to several extended families representing a total population of no more than 250 people. The use of conservative wood consumption and land clearance estimates is appropriate in view of seasonal fluctuations affecting the resident population size.

What was the annual timber consumption of this community? Unfortunately, our otherwise keen observers of nineteenth century Osage village life fail us on this question, necessitating an appeal to other sources of information. Robert Heizer's (1963) calculation of 83 pounds of wood per family per day for Native Americans living in northern California (where comparable annual temperature ranges prevail and where hardwoods were likewise the major fuel source) provides a yearly per capita figure of 2.3 tons that seems reasonable for our study area. From this, the annual firewood requirement for 250 people is calculated at 575 tons. Using U.S.D.A. figures of ten cords of mixed hardwood per acre and with each cord weighing about 1.5 tons (Graves 1919), our 575 tons represents the timber resources of roughly 38 acres.

How much wood was required for construction and for manufacture of other items? If each dwelling required about 75 stems (adding roof and bench supports to the 50 wall stems mentioned previously), then the 40 structures required to shelter 250 people would consume about 3,000 stems. Using modern figures from the Lake Winona Research Natural Area in Arkansas, timber of 10-30 cm diameter in this quantity would clear an additional 12 – 15 acres at 250 stems per acre, more or less (Fountain 1991). These structures, however, would not need to be replaced every year. French colonists at Arkansas Post complained in the early eighteenth century that wall posts set into the damp, frequently flooded sediments of eastern Arkansas had to be replaced every eight to ten years, so we can estimate that the wall posts of structures built along Lee Creek would last at least that long. Even with additional timber requirements for ancillary structures, dugouts, and

other items, the total quantity of timber required for construction and manufacturing represents but a small fraction of the annual firewood requirement. We therefore decided to use the 575-ton figure as a conservative estimate of total annual wood needs for all purposes.

The area of Ozark forests impacted by this magnitude of wood harvest can be calculated through site catchment analysis. That is, an occupied settlement has a surrounding “catchment area” from which residents harvest resources like firewood. The overall dimensions of site catchments are usually set in relation to the maximum distance people are willing to travel to acquire those resources. How far were Osages willing to walk to collect firewood? Again, our keen observers don’t provide exact figures, but in 1819 Thomas Nuttall accompanied an Osage hunter “about 9 or 10 miles over the alluvial lands of the Grand river” (Nuttall 1999:211). They were not burdened by heavy loads of firewood, but it would be unwise to underestimate the capacity of Osage women who, according to Nuttall, were “accustomed to perpetual drudgery,” and were “stouter and lower in stature than the men” (Nuttall 1999:216). Still, it seems unlikely that the range for firewood collecting would have extended beyond one-third of the range of fast moving hunters. A 5-kilometer catchment area surrounding each Lee Creek settlement seems reasonable in view of these considerations, and is consistent with worldwide ethnographic data on human foraging ranges.

A second issue concerns the overall shape of the catchment area. Most applications use a “concentric circle” approach, which assumes that a person can move with equal ease in every direction. That is not the case in the highly dissected Ozark terrain of the Lee Creek valley. Our solution involves defining catchments in relation to estimated travel costs, where costs accumulate in relation to incremental increases in the slope angle of the ground. Put simply, it is more difficult or “costly” to travel up (or down) a steep slope than it is to travel across flat land.

Catchment areas were calculated for three of the large, open sites in the Lee Creek Unit. All of the Late Holocene semisedentary sites (representing both hunting-gathering-gardening and agricultural adaptation types) occur on the lower and middle stream valley classes of our terrain model. Therefore, we selected one site from the lower stream valley class, a second site from the middle stream valley class, and a third site from the boundary where these two units join.

The areas encompassed within 1-, 3- and 5-kilometer catchments surrounding these sites are shown in figure 3 (see also table 1). These catchments yield fairly consistent estimates on the availability of local wood supplies: the 1-kilometer catchments contain less than four years’ supply, the 3-kilometer catchments expand the supply to one or two decades, and the 5-kilometer catchments contain timber sufficient to meet demands for roughly four decades, or about two generations.

We are not suggesting, of course, that Native American groups in the Lee Creek valley were clear-cutting 38 acres of timberland per year. More likely, they were cutting some

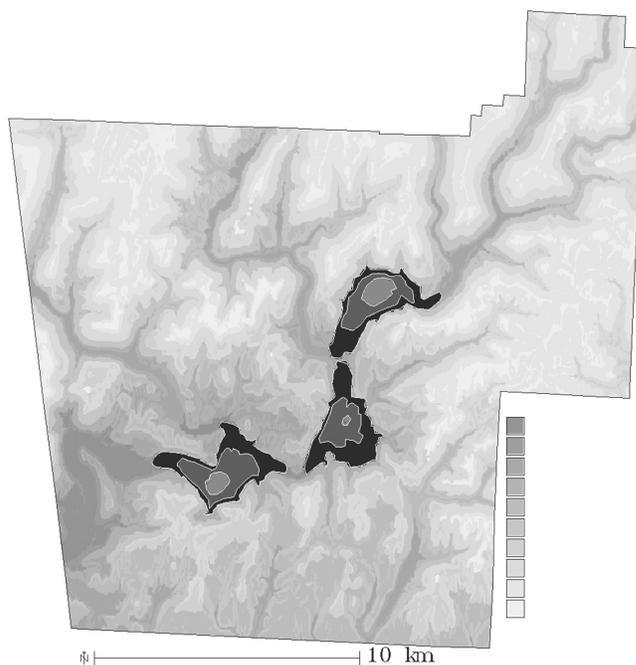


Figure 3—Catchment areas for three archeological sites in the Lee Creek Unit calculated in relation to travel cost surfaces. The light gray (smaller) areas represent 1-km catchments, the intermediate gray areas represent 3-km catchments, and the dark gray (larger) areas represent 5-km catchments.

Table 1—Catchments and estimated wood supplies for archeological sites in the Lee Creek Unit

Site	Catchment range <i>km</i>	Area <i>acres</i>	Wood supply <i>years</i>
3CW42	1	133.3	3.5
	3	832.2	21.7
	5	1,675.9	43.7
3CW119	1	15.8	< 1.0
	3	512.7	13.4
	5	1,521.3	39.7
3CW132	1	216.3	5.6
	3	785.9	20.5
	5	1,499.0	39.1

trees to acquire building timbers and wood for other manufacturing purposes (i.e., dugouts), collecting deadwood to use as fuel, and culling both young and old trees from nut tree groves to increase the room for crown breadth development of productive middle-aged trees – thereby producing additional firewood supplies. The immediate result of these activities was thinning of local tree stands, but over several years cleared areas were likely produced, especially in the bottomlands surrounding larger settlements. The number and distribution of large open sites in our study area therefore probably represents a series of generational relocations

prompted by exhaustion of local wood supplies within adjacent catchment areas. The distribution of these sites in addition to the time span they represent (roughly 4,000 years) further suggests a cyclical pattern of movement in which abandoned sites were reoccupied following reestablishment of forest vegetation.

Under a hunting, gathering, and gardening economy, requirements for cleared land would be modest; a figure of 0.25 acres per person per year is a reasonable approximation. At this amount our 250-person community might require as much as 62.5 acres of garden space. With the emergence of more intensive field agriculture, cleared land requirements in the Lee Creek valley, as elsewhere in eastern North America, increased to something on the order of 0.5 acres per person per year. This produced an overall requirement for as much as 125 acres of croplands, coupled with an increased rate of soil exhaustion.

To determine annual requirements for cleared land, we also need to consider the effects of field rotation. We can never be certain about prehistoric rotation cycles; however, many Southeastern and Southern Plains groups shifted to new fields after old ones had been used for about five years (Moore 1987:143-44, Silver 1990:50-51). If one of every five fields were rotated in this manner in any given year, then old fields would have at least a 25-year recovery period – a time interval during which trees would grow to about the right size for use in dwelling construction but would not have grown so large that they would be difficult to remove (Silver 1990:50). At this rate, annual field expansion requirements would range from roughly 12.5 acres (gardening) to 25 acres (agriculture) per year. If these estimates correspond to prehistoric circumstances in the Lee Creek valley even approximately, then the annual requirement for newly cleared lands for either gardening or field agriculture would fall well within the annual amounts of land from which firewood was collected.

In sum, these estimations suggest that firewood collecting by the late prehistoric occupants of the Lee Creek valley produced the single most extensive impact on local forest resources. Garden and agricultural field production were probably embedded within the areas cleared as a result of timber harvest and firewood collecting. The calculated catchment areas suggest that wood supplies were obtained from the bottomlands, terraces, and adjacent hill slopes along Lee Creek. Over several generations, a community of 250 persons would have cleared extensive tracts of bottomlands in an area the size of the Lee Creek Unit, even with cyclical return to favored sites.

FROM PREHISTORY TO HISTORY

The extent of prehistoric land clearance reconstructed here suggests that Euro-American settlers entered Ozark forests that were already modified by previous groups of Native Americans, who had been living in the region for many thousands of years. Plotting the locations of the first white settlements on a map along with the late prehistoric sites provides additional support for this suggestion (fig. 4). The major implication of this study is that long-term dynamics of forest ecosystems are best understood when human populations are included as components of those systems.

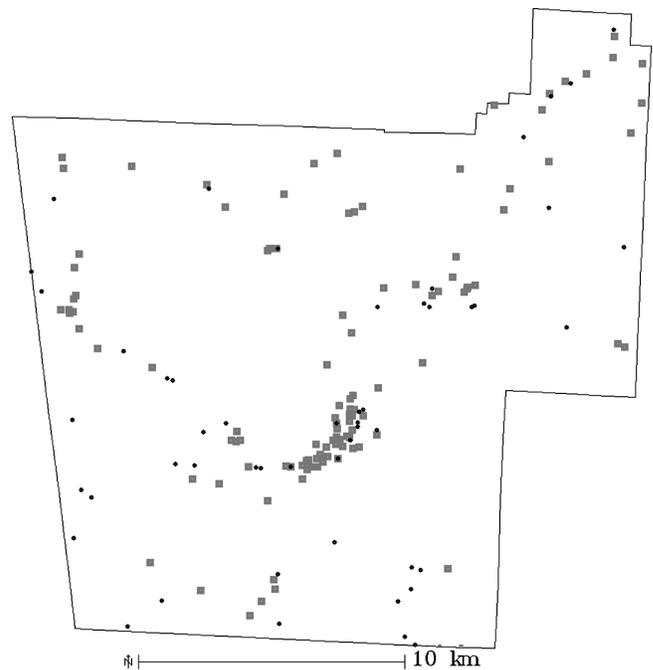


Figure 4—Late prehistoric Native American sites (gray squares) and early historic Euro-American sites (black circles) in the Lee Creek Unit.

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HISTORY OF MISSOURI FORESTS IN THE ERA OF EXPLOITATION AND CONSERVATION

David Benac and Susan Flader¹

Abstract—The era of timber exploitation and early conservation in the Missouri Ozarks occurred roughly from 1880 to 1950, beginning when large timber companies moved into the region to harvest the pine and oak of the valleys and ridgelines. Pine was largely depleted by 1910, but oak harvest continued. Resident Ozarkers, who came largely from a tradition of subsistence hunting, gathering, and basic farming, frequently resisted the efforts of both timber companies, such as the Missouri Lumber and Mining Company, and governmental agencies to bring modernization and industrial productivity to the region. As a result, governmental conservation developed later in Missouri than in neighboring states. The federal government created its first national forests in Missouri in 1933, and the state did not establish a permanent agency devoted to forestry until 1937. The struggle to control access to the region's forest resources and culture remained a prominent issue throughout the era. The legacy remains today in forests with an abnormally high percentage of cull and continued resistance of Ozarkers to governmental regulation.

INTRODUCTION

The forests and the people of the Missouri Ozarks experienced waves of change from the 1880s to the 1940s. During this era large-scale timber operations moved into the region and began to harvest timber. After the collapse of the timber industry local Ozarkers worked to re-establish an independent society free of outside interference. After a decade of failed efforts the federal and state governments finally succeeded in establishing a presence in the Missouri Ozarks during the 1930s. This entire succession of events occurred in an atmosphere of tension between Ozarkers and outsiders over the control of natural resources and the character of Ozark society.

PRE-TIMBER ERA

Ozarkers' heritage shaped the society that existed before the arrival of the timber industry. Many residents of the region traced their lineage through the upland South to Scotland. Scots-Irish who migrated to the United States in the 18th century brought a pragmatic approach to life and a distrust of authority. As residents of the frontiers of Virginia, North Carolina, Kentucky, Tennessee, and, later, the Missouri Ozarks, they honed their love of independence and their ties to the wooded hills on which they depended. (Stevens 1991).

Geographically and culturally isolated, Ozarkers depended on their ability to extract a living from the natural world, roaming the woods in search of game, fruits, nuts, berries, and herbs to supplement their small farms. They used the forest as a commons where livestock roamed free and firewood and timber belonged to whoever cut or collected it. They burned the forest each spring to improve forage for their livestock and reduce ticks and snakes. The issue of woodburning would be at the center of conflicts between Ozarkers and outsiders from the 1880s to the 1940s and beyond.

THE TIMBER BOOM

The Missouri Ozarks experienced a timber boom from approximately 1880 to the 1910s, as railroads penetrated the region. During these years large firms such as the Missouri Lumber and Mining Company, the Ozark Land and Lumber Company, and the Cordz-Fisher Lumber Company bought land and built mills throughout the region. They sought mostly the shortleaf pine on some 6.6 million acres of the eastern Ozarks but also tapped the white and red oak with which it was mixed.

The control of resources emerged as a primary issue as the timber industry began to dominate the region. The Missouri Lumber and Mining Company (MLM) obtained 30,000 acres of pineland in Carter County years before it moved a single employee or piece of machinery there. As timber companies bought and cut land throughout the Ozarks, traditional residents of the region lost some of their access to the resources they had depended on for survival.

The firms sought not only to prevent trespass but to establish a productive, and dependable, labor force. The MLM met this need by creating a company town in Carter County named Grandin (fig. 1), after one of the firm's initial investors; its sawmill at its peak was reputed to be the largest in the nation. Interactions between the MLM and the residents of Grandin and the surrounding hills demonstrate the conflicting visions of society during the years of the timber boom in the Missouri Ozarks. The MLM worked to control the lives of its employees to ensure consistent production while Ozarkers tried to maintain elements of their traditional lifestyle and relationship with the woods. Tensions developed over schedules of work, religion, education, and leisure activities.

The MLM attempted to get as much work out of its employees as possible despite workers' desire to set their own schedules. Ozarkers resisted the MLM's inclusion of

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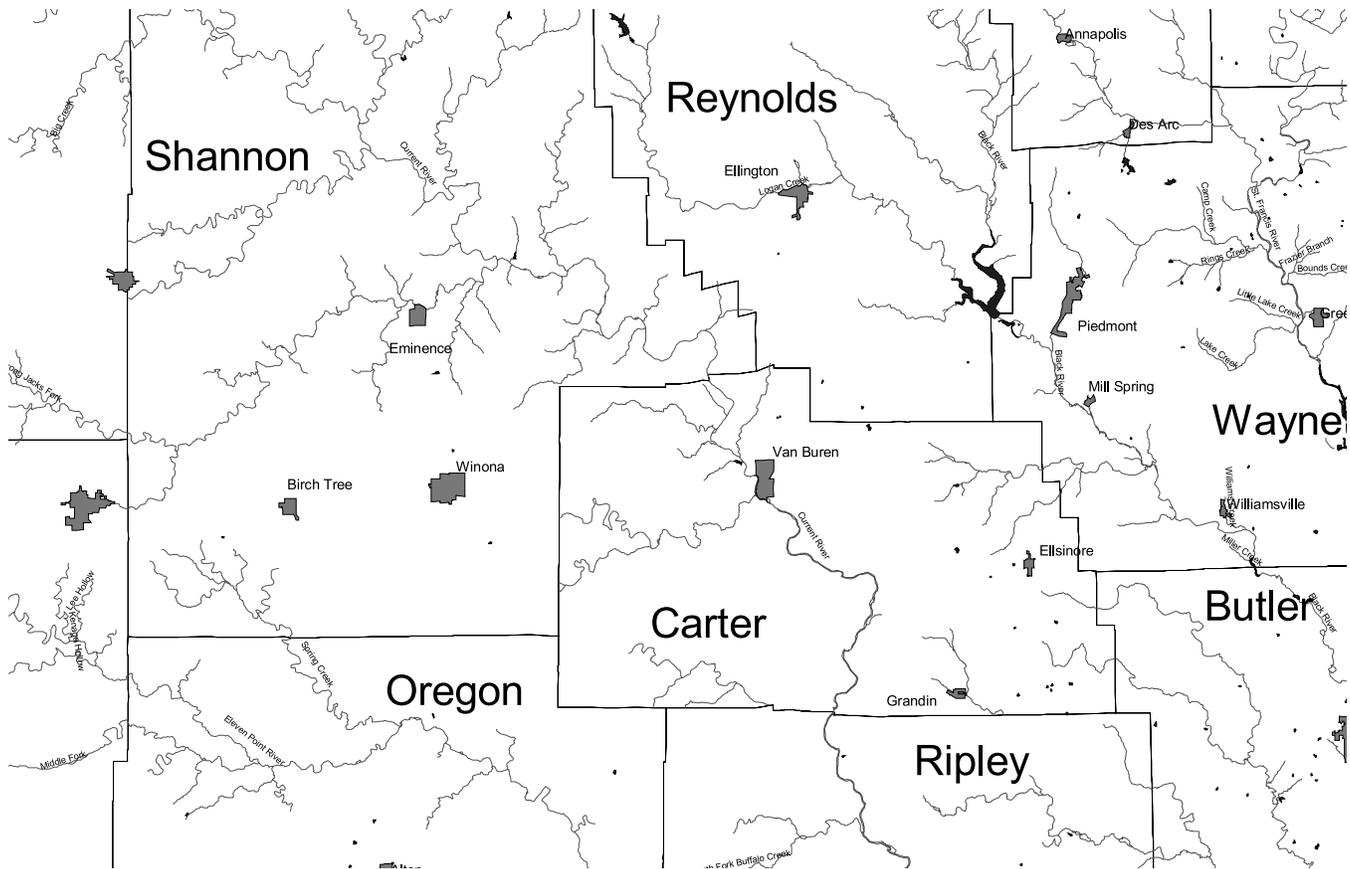


Figure 1—Carter County and surrounding area.

Sunday in the regular workweek as it expanded its operations beyond Carter County. When the firm faced local opposition over Sunday work as it began logging in Reynolds County in 1905, it offered the county's prosecuting attorney \$300 per year if he would discourage people from using legal means to resist. But when MLM expanded into Shannon County in 1907, the prosecuting attorney there sided with the locals. MLM's Ozark manager C.C. Sheppard reported to company president J.B. White that "there is nothing we can do at present, except discontinue this [Sunday] work." [On Reynolds County see J.B. White to W.B. Pettibone (Jan. 12, 1906), folder 57. On Shannon County see C.C. Sheppard to J.B. White (Feb. 12, 1907), folder 364. All letters are in the Missouri Lumber and Mining Papers (hereafter cited MLM Papers) at Western Historical Manuscripts Collection, Ellis Library, Columbia, MO (hereafter cited WHMC)]. Ozarkers and the MLM had different ideas about work. Ozarkers entered the timber boom from a subsistence lifestyle grounded in the cycle of the seasons, while MLM attempted to institute an industrial view of labor based on production quotas and a time clock. Conflicts over this basic element of society reflected the larger tensions of the era.

One of the most effective methods of social control throughout history has been religion. The MLM made every effort to serve as the patron of Grandin's religious institutions throughout the company's tenure in the town. The MLM claimed to

remain open to all doctrines and there is no evidence that the company attempted to influence the sermons of its preachers. While in Grandin the MLM paid the salaries of the preachers at no fewer than three churches—Methodist, Baptist, and Congregationalist. The Congregational Church established a particularly close relationship with the MLM. C.E. Slagle, who ran the company store, occasionally served as a deacon, and the church created an association, the Knights of King Arthur, devoted to teaching young men vocational skills useful in a timber economy as well as the dangers of alcohol and tobacco, which gained the Congregationalists an extra stipend from the MLM. Ozarkers, however, favored the Baptist church, derisively described by White as having "tobacco stained floors and walls" [J.B. White to G. Andrews (Feb. 26, 1906), folder 111; W. Bosard to J.B. White (Feb. 11, 1907), folder 362; J.B. White to C.C. Sheppard (Aug. 1, 1907), folder 530; J.B. White to E.B. Grandin (Sept. 6, 1907), folder 584; all in MLM Papers]. Ozarkers demonstrated their rejection of the urban and industrial values of the MLM by patronizing the church they felt most comfortable in.

Although the MLM never explicitly stated a desire to shape the minds of children in the region, its combination of programs such as the Knights of King Arthur and the maintenance of company schools served to draw the youth of the Ozarks into the control of the company. The MLM built Grandin's school, paid the teachers, and provided

each graduate with a gift. There is some evidence that these practices paid off. When Leonard Hawn's father left the MLM's employ in 1907, Leonard, a graduate of the Grandin school, chose to seek his future with the MLM rather than with his family [C.C. Sheppard to J.B. White (May 30, 1907), folder 438, MLM Papers].

Leisure activities, especially the use of alcohol, represented yet another arena of tension. Ozarkers drank on the job, bootlegged, and opened illicit drinking establishments, while the MLM consistently fired employees drunk at work whether they were laborers, foremen or doctors. One of the best examples of this is the case of Dr. Rhea, a resident of nearby Oregon County, who was employed to assist while the regular MLM physicians took their vacations. After Rhea spent two weeks at a logging camp, the company discovered he had spent a large portion of the time drinking with the locals and fired him immediately [C.C. Sheppard to J.B. White (June 19, 1906), folder 189, MLM Papers]. Ozarkers, regardless of their position in society, returned to their tradition of relaxing in one another's company with their whiskey when they had the opportunity. As a proponent of modernization and efficiency the MLM could not tolerate drunkenness among its employees.

The timber boom came to a close in the Missouri Ozarks around 1910 (fig. 2), when it was beginning to peak in Arkansas, Louisiana and other states in the South and taking off in the Pacific Northwest. By then Missouri's pine was virtually gone, and it has never recovered; even today it amounts to only about 600,000 acres, less than one-tenth its former acreage. The MLM and other large companies moved their operations to other regions with uncut forests, selling off their cutover land to unsuspecting buyers or simply stopping payment of taxes.

The MLM understood the psyche of its workers. When the company decided to close its operations in Grandin, several Ozarkers confronted J.B. White at the company store with concerns about their future. White pacified the locals when he told them he "considered it much better for them to have a small farm and a garden even if they lived in small log houses and raised their living and have their hogs fattening on the mast, that they would be better off than working around a saw mill and paying rent" [J.B. White to A. Johnston (Feb. 5, 1910), folder 755, MLM Papers]. Whether or not the exchange happened exactly the way White claimed, many locals did turn to farming after the big mills left the Ozarks.

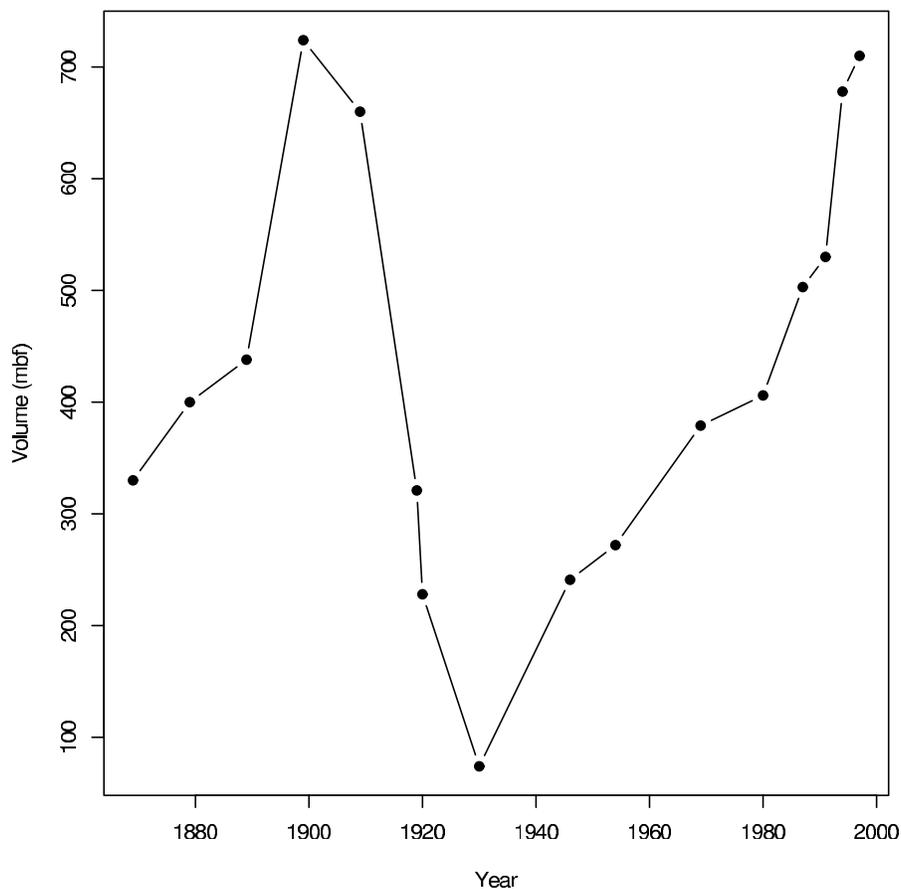


Figure 2—Missouri sawlog production (in million board feet) in selected years, 1860-2000. Figures from 1869 to 1946 are from U.S. Census of Manufactures categories "sawed timber" or "lumber sawed," as reported in Steer (1948). For certain years Steer also includes "estimates" that are somewhat higher, i.e., 1929—260 and 1939—296. Sawlog figures from 1958 to 1997 are from USDA resource bulletins.

THE TRANSITIONAL ERA

The years from about 1910 to the mid-30s were a transitional era in the Missouri Ozarks. While Ozarkers attempted to return to a life of subsistence agriculture, the timber interests still in the area sought to extend the life of the remaining oak and other hardwoods by initiating an industrial style of conservation. Neither group truly succeeded.

With the departure of much of the timber industry, locals tried to meet their needs with family farms. Between 1900 and 1920 the number of farms increased in both Carter and Shannon counties. Despite this growth, both counties stayed near the bottom of the state in terms of percentage of land in farms, meaning that most farms were small (Stevens 1991). Locals purchased what land they could and tried to cultivate the rugged terrain, supplementing their meager produce by hacking oak ties and cutting wood from high-graded stands for stave bolts, charcoal, and firewood. Much of this cutting was from land they did not own but claimed permission to cut, a practice described as “grandmawing.”

As Ozarkers tried to regain their traditional self-sufficiency they also sought to assert their independence from outside forces. They did this in part through opposition to government agencies, which found the Ozarks a less than welcoming region. Although the federal government was active in states bordering Missouri, including Arkansas where the Arkansas (later, Ouachita) and Ozark National Forests were established in 1907 and 1908, it was unable to establish a forestry presence in the Missouri Ozarks during the period. Unlike Arkansas, Missouri had no public domain remaining at the time; but even after passage of the Weeks Act in 1911, which authorized purchase of land for national forests in the eastern states, the Missouri General Assembly, disproportionately representative of rural areas, failed to pass enabling legislation for two forests proposed in 1914.

Nor was the rural-dominated Missouri legislature willing to approve a state forestry agency advocated by several governors, even though more than half the states established such an agency during the Progressive Era. The state passed a game and fish law, including a license and warden system, in 1905, but the Game and Fish Department struggled to establish a presence in the Ozarks, where locals made sport of dodging the regulations and the wardens. In 1917 the legislature authorized five percent of all game and fish license fees to be set aside in a state park fund, a measure in considerable disfavor among both urban sportsmen and Ozarkers, especially after the diversion was increased to 25 percent in 1923 and the state began buying parklands in the Ozarks. The parks would be off limits to hunting, timbering, and livestock.

The state's efforts in forest conservation during the transitional period devolved to the hands of a group of influential timbermen who continued to tie their fortunes to Missouri, where St. Louis was the main crosstie market in the nation and Kansas City still a major distribution point for southern lumber. At a dinner in 1921 sponsored by the Lumbermen's Exchange of St. Louis and the Tie and Timber Division of the St. Louis Chamber of Commerce, they organized a Missouri Forestry Association (MFA) in order to “advance the public understanding of the importance of timber crops”

and insure “a proper area of forests so maintained and cared for as to furnish a supply of timber for future needs” [The organization meeting of the Missouri Forestry Association (Dec. 21, 1921-Jan. 22, 1922), and Missouri Forestry Association: Constitution (Dec. 7, 1921), both in folder 275, Frederick Dunlap Papers, 1891-1937, WHMC.]

The MFA dominated Missouri's efforts to establish control over its forests during the 1920s, advocating fire prevention, tax reform, and reforestation and opposing national forests or regulation at any level, federal or state. Though some urban conservation and recreational interests promoted national forests and other public land at the time, the MFA sought to prevent the U.S. Forest Service from entering the state. They did not favor state forests either, except perhaps as small demonstration areas, though they advocated a state forestry program that could encourage protection of private forests. Missouri was one of only a handful of forested states with no forestry legislation or administration whatever by the 1920s. When the Clarke-McNary Act of 1924 made federal matching funds available to qualified state forestry agencies for fire protection and reforestation, the MFA lobbied for the best they could get in 1925 from a legislature ever attentive to rural voices, a small forestry program under the State Board of Agriculture, provided that they—the timber industrialists in MFA—would pay the salary of the state forester and related expenses [for one demonstration of the MFA's relationship with the Clarke-McNary Act see Minutes of council meeting (Aug. 4, 1925), folder 276, Dunlap Papers].

Despite having achieved some success, the MFA could not change the attitudes of most Ozarkers towards forestry. Both MFA and the new state forester devoted their greatest efforts to the fire problem, but Ozarkers refused to give up the practice of woodburning, an important part of their traditional culture. The new state forester, Frederick Dunlap, and his only assistant, Paul Dunn, who was stationed in the Ozarks to organize local communities to control their own fire, tried valiantly to make inroads. But when funding for their small program dried up entirely in 1931, they gave up in despair and left the state; Dunlap filed a final report concluding that fire control was “impossible” in the Ozarks (Callison 1953, 96) (we have been unable to find the report). The MFA also may have given up on its attempts to control the state's forests by this time, as it seems to have essentially disappeared.

ERA OF GOVERNMENTAL INVOLVEMENT

As the great depression, which had already begun in the Ozarks in the 1920s in the aftermath of the timber boom, deepened over the entire nation during the 1930s, economic, social, and environmental conditions combined to facilitate the entrance of government into the Missouri Ozarks.

At the urging of the governor, the state legislature in 1929 finally passed an act authorizing national forests in Missouri, but an amendment rendered it moot by limiting acquisition to 2000 acres per county. Then a new National Forest Reserve Association, formed by local businessmen and public officials in the eastern Ozarks, won authorization in 1933 for up to 25,000 acres per county—a limitation subsequently removed—and the U.S. Forest Service quickly established eight purchase units in the Ozarks and

began land acquisition. The *National Plan for American Forestry*, issued in 1933, concluded that private owners were responsible for “practically all the major forest problems” and recommended public ownership of *half* the nation’s forest land; state planners in turn recommended that 8 million acres in Missouri be in public ownership and devoted to intensive forestry (Missouri land use problems and policy. Transmitted to National Resources Board May 18, 1935 by E.A. Mayes, research assistant, 141p. tps., in Missouri State Planning Board, 1933-1943, Missouri State Archives, Jefferson City, MO). In fact only about 1.3 million acres would be purchased in Missouri during President Roosevelt’s New Deal.

Even before the acquisition of substantial national forest lands, however, Missouri took advantage of the New Deal’s Civilian Conservation Corps and other work relief programs to develop its state parks, by 1933 totaling more than 40,000 acres. The state’s emphasis on park development, funded in part by diversions from fishing and hunting license fees, coupled with decimated wildlife populations and the ever-political nature of the game and fish warden system, led Missouri sportsmen to launch an initiative petition campaign in 1935 for a constitutional amendment to create a bipartisan conservation commission with full authority for fish, wildlife, and forestry, but not parks (Flader, in press). Though the measure passed overwhelmingly in 1936, most of the 29 counties in which it failed were forested counties in the Ozarks, where residents were still deeply resistant to outside interference (Callison 1953).

With parks now relegated to a separate agency, the new commission in 1938 hired George White from the U.S. Forest Service to develop a state forestry program. White hired five more professionally trained foresters and assigned them to protection districts in the Ozarks. With lookout towermen and high school boys hired locally to help spot and fight fires and with a mobile motion picture unit, they began the long, slow process of educating Ozarkers about the perils of woodburning. Until they could control fire, reforestation and forest management would hardly pay—though, White believed, if landowners could be induced to plant trees, they would become advocates for fire control (Keefe 1987). By late 1938 White had cooperative fire-fighting agreements with 144 private landowners—likely corporations, as they owned between 500 and 37,000 acres apiece. The size of the holdings suggests that, while the forestry program may have had support, it was not from the common Ozarker. As late as 1946, the forestry division admitted that fire protection remained its primary focus [Missouri Conservation Commission, Press Releases, 1937-1939 and 1946-1947 (bound and held by the State Historical Society of Missouri, Columbia), 1-2].

The Missouri General Assembly in 1946 finally passed its first significant forestry legislation, the State Forestry Act, which established a “forest cropland” program and provided penalties for woods arson; and it finally began appropriating funds (\$150,000) from general revenue for forestry purposes, mostly fire control, which enabled the state to receive more matching funds from the federal government. By 1950 Missouri’s 15.5 million acres of forest included 150,000 acres of state forests and 1.3 million acres of national forests,

although the land had only about one-fifth the stocking of sawtimber that could be expected under good management and open range for livestock still prevailed in much of the Ozarks. About 6 million acres, public and private, were organized in forest protection districts, only about two percent of which burned annually, compared with an estimated one in three acres before fire control (OM 1951-52: 341-43). The state was on its way to a more effective forestry program.

CONCLUSION—THE LEGACY

The growing success of the U.S. Forest Service and the Forestry Division of the Missouri Conservation Commission marked the beginning of permanent governmental involvement in the Ozarks. Later generations would establish the Ozark National Scenic Riverways (1964), end the practice of open range grazing (1967), begin to recognize the region’s ecological significance, and even appreciate and begin to mimic the ecological role of natural fire.

By the close of the 20th century, Missouri’s 14 million acres of forest land, four-fifths of which is in the Ozarks, would remain overwhelmingly (83 percent) in private hands (fig. 3), controlled by more than 300,000 landowners, the vast majority of whom owned fewer than 50 acres. Forest industries would own less than 2 percent (compared with 25 percent in Arkansas and 14 percent in the country as a whole) and public agencies 15 percent, including 1.5 million acres in the Mark Twain National Forest, some 444,000 acres of state forests, and 138,000 acres of state parks. The incidence of wildfire—as opposed to prescribed fire—is down to about 1/10 of 1 percent of Missouri’s forests burned annually, but almost all the fires are human caused, the majority of them still classified as arson—a lingering remnant of the Ozark tradition of woodburning and resistance to outside authority.

More than a century of land abuse by industry and Ozarkers alike, coupled with continued poverty, rugged individualism, and distrust of governmental authority, has left Missouri forests with the highest percentage of cull material (tables 1 and 2)—trees unusable for industrial wood products because of rot, dead material, form, or other defect—of any state in the nation (Shifley 1999). Virtually all of this cull is in hardwoods, much of it in the red oak group that came to dominate the more than 6.6 million acres formerly in shortleaf pine in the wake of heavy exploitation and continued burning, grazing and erosion. This legacy of mistreatment, coupled

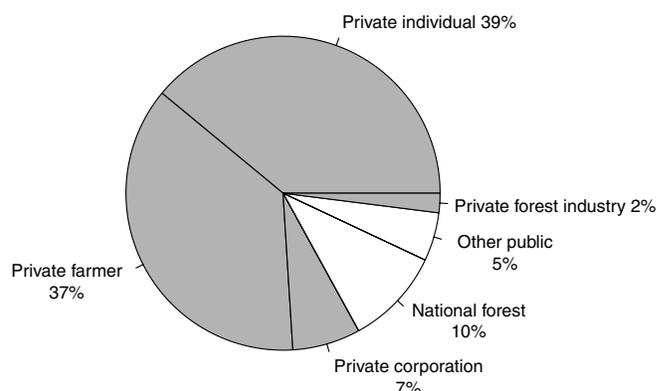


Figure 3—Missouri timber ownership by class.

Table 1—Total cull material

Rank	State	Cull	Growing stock	Cull of total
		<i>billion cubic feet</i>		<i>percent</i>
1	Missouri	4.8	9	35
2	Mississippi	2.9	19.8	13
3	Maine	2.8	24.3	10
4	Virginia	2.4	25.9	8
5	Wisconsin	2.2	16.6	12
6	Texas	1.9	12.9	13
7	N. Carolina	1.9	32.7	5
8	Minnesota	1.9	15.1	11
9	Louisiana	1.9	18.9	9
10	Georgia	1.9	30.7	6

Source: Shifley (1999).

Table 2—Percentage of hardwood cull material

Rank	State	Hardwood cull	Hardwood growing stock	Cull of total
		<i>--- billion cubic feet ---</i>		<i>percent</i>
1	Missouri	4.8	8.1	37
2	Kansas	0.7	1.2	36
3	Oklahoma	0.9	1.6	35
4	Iowa	0.9	1.7	34
5	Nebraska	0.1	0.3	22
6	Arkansas	1.9	12.3	13
7	Tennessee	1.5	13.8	10
8	Illinois	0.5	4.7	10
9	Kentucky	0.6	14.8	4

Source: Shifley (1999).

with drought and the advancing age of many trees, has left the state's forests especially vulnerable to wood-boring insects, fungi, and other manifestations of oak decline.

Yet Missouri still has no forest practices act to guide the treatment of private lands. A broadly representative

Governor's Advisory Committee on Chip Mills that heard testimony for more than a year on the sorry state of Missouri's forests proved unwilling to embrace any sort of regulatory mechanisms for better forest management, largely out of respect for—or fear of—Ozarkers' insistence on private property rights and their resistance to governmental regulation, and the state legislature failed to enact any of the committee's recommended economic incentives (Lewis, in press). The challenge for Missourians to secure better management of their forests remains immense.

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OLD-GROWTH WOODED PASTURE IN THE OZARKS

David H. Journey and David W. Stahle¹

Abstract—Forests in the Ozarks are ancient: the dominance and density of their various arboreal and herbaceous species have fluctuated over time in relation to climatic change and cultural influences. This study examines the nature of the pre-European forest composition in the Ozarks through studies of geology and soils, General Land Office surveys, archeology, and dendrochronology. Examples and a case study on the Wedington Unit are drawn from the Ozark-St. Francis National Forest, where, in some areas, old-growth oak forests remain adjacent to former agricultural fields that are regenerating naturally. This paper also identifies forest management practices that aid in the maintenance of diverse old-growth ecosystems.

INTRODUCTION

Landscapes and vegetation communities are in constant change. The disciplines of geography and archeology, which deal with human-land relationships, can provide us with ecological models of plant change related to human use of the available natural resources. This paper identifies archeological and historical data that can be used to confirm or disprove changes in ecosystem models of the Arkansas Ozarks. Such changes are relevant to our understanding of the cycling of species with different life spans in response to climatic drought episodes, insect infestations, and fire regimes. A case study is provided on the Wedington Unit, Boston Mountain Ranger District, Ozark-St. Francis National Forests.

STUDY AREA

The Wedington Unit (fig. 1) lies west of Fayetteville in the extreme northwestern corner of Arkansas, where Ozark Plateau remnants of the Boston Mountains form outlying ridges over the Springfield Plateau. The Unit falls on the divide between Benton and Washington Counties, and is bounded on the north and east by the Illinois River. Wedington Mountain, an erosional remnant of the Ozark Plateau, runs generally north-south through the study area.

GEOLOGY AND SOILS

The rocks of the Ozarks are primarily sedimentary in origin, formed by deep sea and near-shore sediments laid down during the Paleozoic era (Sabo and others 1982). The Wedington Unit consists of the northward extension of the sandstone formations of the Boston Mountains onto the limestone-dominated Springfield Plateau. The Boston Mountains are capped by the Mississippian era Wedington sandstone unit of the Fayetteville shale formation (Haley 1976). These generally level-bedded strata are warped by domal uplift and deeply incised by streams, giving the region a mountainous relief.

The Springfield Plateau consists of gently sloping Mississippian limestones and contains the Boone limestone/chert formation. This formation is important for the readily available chert that was heavily exploited by Native Americans

for the manufacture of stone tools. Dickson (1991) divides chert from the Boone formation into St. Joe, Reeds Spring, Keokuk, and Moorehead varieties.

The dominant soils of the Wedington study area were developed under hardwood vegetation (Harper and others 1969, Phillips and Harper 1977). In the uplands, the soils are Allegheny, Apison, Enders, Hector, Mountainburg, Steprock, and Nella—all primarily stony and gravelly sandy loams. Soils on the mountaintops are generally < 3 feet deep, while soils on slopes and benches may range to 7 feet deep. Soils on the lower uplands of the Springfield Plateau in the study area are primarily Captina, Nixa, Pickwick, and Tonti. These are silt loams and cherty silt loams that range from 3.5 to 5.5 feet deep. Soils in the flood plains of the study area include Britwater, Captina, Razort, and Secesh. These are silt loams and gravelly silt loams that range from 4 to > 7 feet deep.

No typical mollic (black surface horizon, thickened) prairie soils (Carytown, Jay, Mayes, Newtonia, Sogn, Taloka) have been mapped within the Wedington study area (Phillips and Harper 1977). In fact, the nearest known soils in Benton County that developed under prairie vegetation (Jay) are at least 2 to 3 miles north of the area. In Washington County, Taloka soils have thickened surface epipedons typical of prairie soils and are found south of the study area (Harper and others 1969). These soils are frequently found in association with the Captina soils that do surround the Wedington study area; however, Captina soils have shallower surface horizons and are thought to have developed under hardwoods (Phillips and Harper 1977).

GENERAL LAND OFFICE RECORDS

Today, there are only a few areas of the Ozarks that still contain the full range and proportion of plant and animal species that flourished prior to European settlement. Land managers need statistically sound models of presettlement plant distributions over entire landscapes to understand vegetation potential and historical changes in vegetation (Foti and Glenn 1991, Warren 1984, Warren and O'Brien 1984). The original land surveys made when the public

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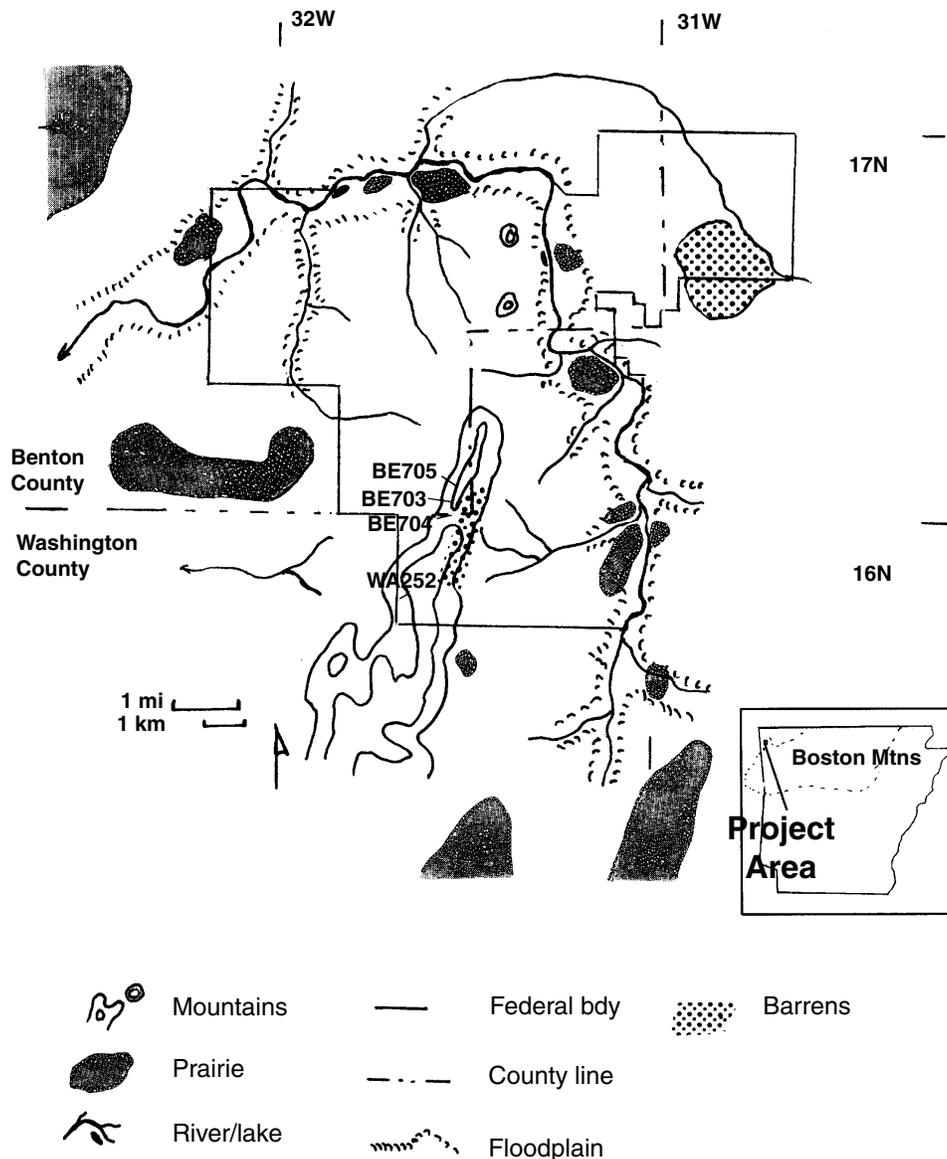


Figure 1—Wedington Unit prairie and forest reconstructed from Government Land Office surveys, 1832 to 1833.

domain was sold or given to private individuals or entities are excellent sources of these data. In these surveys, the observations of prairie-forest boundaries and witness trees recorded at each land tract corner provide quantitative information that can be used to reconstruct arboreal communities and their interfaces with prairies (Bourdo 1956; Curtis 1959; Delcourt 1976; Delcourt and Delcourt 1974, 1977; Journey 1982, 1987; Sears 1925).

Surveyor bias has been analyzed by several researchers (Bourdo 1956; King 1978, 1984; Sears 1925; Warren 1984) and appropriate methods developed to address these biases (Journey 1982, 1987; Siccama 1971). Since land surveys are legal documents, General Land Office (GLO) surveyors were instructed to record the nearest tree to each corner of a tract as a witness tree, so that the corner itself could be relocated over time (Dodds and others 1943, McKittrick

1918, McMahon 1941, Shine 1969). As early as 1806, witness trees were required to be as close as possible to the land tract corner (White 1982), and in 1831 this was specifically mandated in Tiffin's instructions to all Federal land surveyors (Dodds and others 1943). In the 20th century, this stipulation was changed toward selection of more permanent corners (Bragg 2002, Stewart 1935). Tharp (1941, 1948) presents discussions on the tree-ring dating of witness trees in order to provide legal witness for land tract corners and "follow the footsteps of the surveyor." Generally speaking, the closer the tree to the corner, the easier it is to locate again by subsequent surveyors laying out land grants from the public domain. It was also easier and more cost effective for the field crews of the original surveyor to mark nearby trees rather than selecting certain species at greater distances.

GLO surveyors noted and marked from one to four trees at each corner of a tract, describing each tree, its diameter, and the direction and distance to it from the corner. When land lines were being run, trees falling on a line were also noted and marked, and the boundaries between forest and prairie recorded; all of which provide evidence for the extent of fire-dependent ecosystems. Occasionally, observations such as “burned over,” “barrens,” or “burned tree” provide direct evidence of fire in the forests (Weniger 1984, 1996). In Texas, these direct observations were recorded in Hill and Falls Counties (Weniger 1984), and tree sizes and densities have been used to determine fire return effects on community development along the interface of Blackland Prairies and the Post Oak Savannah (Jurney 1987, 1988a, 1988b, 1988c). In Arkansas, the term “barrens” appears to reflect a fire-dependent ecosystem; the term has also been found in notes from Johnson, Benton, and Washington Counties (Lockhart and others 1995, Miller 1972, Sabo and others 1982). This term is definitely correlated with “burned over” areas in Jackson County, MO, where prairie fires had burned into forested areas and killed former witness trees (Jurney 1982).

The usefulness of correlating GLO witness tree distributions to soil and topographic settings is demonstrated by two studies in the Ozarks: Chaney (1990) on the Middle Fork of the White River in Washington County, and the Arkansas Archeological Survey on the Lee Creek Unit of the Boston Mountain Ranger District in Crawford County (Lockhart and others 1995). Both studies observed that although post oaks (*Quercus stellata*) favored moderately to well-drained soil, they were absent from poorly drained soils. White oaks (*Q. alba*) were distributed across the foothills and upper slopes and nearly absent from the flood plains of the interior Ozarks. Red oaks (*Q. falcata*, *Q. pagoda*) were more frequent on well-drained slope soils and the flood plains. Black oaks (*Q. velutina*, *Q. schumardii*) and hickories (*Carya* spp.) were evenly distributed across all soils. Historic settlement has disrupted the vegetation patterns, introducing red cedars (*Juniperus virginiana*) and pines (*Pinus* spp.) into many areas and allowing the spread of other species such as maple (*Acer* spp.), sycamore (*Plantanus occidentalis*), walnut (*Juglans nigra*), cottonwood (*Populus deltoides*), and hackberry (*Celtis laevigata*) in all areas.

The GLO studies have direct relevance to historic vegetation regimes, and the U.S. Department of Agriculture (USDA) Forest Service is currently developing a witness tree geographic information system (GIS) layer for all the Ozark-St. Francis National Forests. Until this is completed, individual study areas have been selected to demonstrate the potential for land management. One of these is the Wedington Unit.

We reconstructed the presettlement vegetation for the entire Wedington Unit of the Ozark-St. Francis National Forest and peripheral areas surrounding the unit, comprising 24,320 acres (9 846.2 ha). Figure 1 illustrates the interface of prairies and forests in the Wedington study area. Some areas, such as barrens, identify fire-prone areas, in addition to the prairie areas. Since many of the areas shown as prairies are located on soil types developed under forests, it is assumed that most of these prairies were produced by wild-

fires. A long linear prairie is located along the road from Fayetteville to Rogers, while others appear to be associated with agricultural fields. Prairies are found in upland, slope, and flood plain settings.

Table 1 lists 25 canopy species and 5 understory species observed by 3 individual surveyors in the Wedington Unit and adjacent forests and prairies during 1833 and 1834. The witness tree matrix consists of 334 trees (table 1). The original surveys were plotted on U.S. Geological Survey 7.5-minute quadrangles and were sorted according to six physiographic/topographic zones (flood plain, flood plain prairie, slope, slope barrens, upland, upland brushy prairie). Common names for trees were used by the land surveyors. Exact scientific nomenclature cannot be determined with confidence for all species, but the best-guess scientific names are presented in table 1.

The flood plain contained 52 witness trees. The dominant species included post oak (15.4 percent), black walnut (13.5 percent), hickory and sycamore (9.6 percent each), and white oak and blackjack oak (*Q. marilandica*) (5.8 percent each). The next most common species were black oak, elm (*Ulmus* spp.), hazel (*Corylus americana* or *Hamamelis virginiana*), sumac (*Rhus* spp.), and locust (*Gleditsia* spp. or *Robinia pseudoacacia*) with 3.8 percent each. Incidental species (1.9 percent each) included overcup oak (*Q. lyrata*), black gum (*Nyssa sylvatica*), cherry (*Prunus serotina*), hackberry, honey locust (*Gleditsia* spp.), box elder (*Acer negundo*), ash (*Fraxinus* spp.), red bud (*Cercis Canadensis*), and spicewood (*Lindera benzoin*).

The flood plain prairie contained nine trees, dominated by hickory (44.4 percent) and blackjack oak (22.2 percent). Incidental species included plum (*Prunus* spp.) and cane (*Arundinaria gigantea*).

The slope contained 122 trees, dominated by black oak (31.9 percent), blackjack oak (27 percent), post oak (23.7 percent), and white oak (7.3 percent). Incidental species included hickory, black gum, cherry, hazel, sumac, vines, and briers. The only red oak tree in the Wedington Unit was recorded in the slope zone. The slope barrens contained single observations of white oak, black oak, blackjack oak, chinquapin (*Castanea pumilia*), and hazel.

The upland contained 144 trees, dominated by black oak (33.3 percent), post oak (27.7 percent), blackjack oak (25 percent), and white oak (5.5 percent). Incidental species included hickory, elm, maple, hazel, sumac, whortleberry (*Vaccinium* spp.), huckleberry, vines, and briers. The brushy upland prairies included single observations of elm and plum.

No pines or cedars were recorded in the original notes. Both species have regenerated naturally in an early 20th century field on the top of Wedington Mountain. The cedars were introduced by settlement, the pines by the USDA Forest Service.

The distance from the land tract corner to the witness tree provides a point-specific distance index that is highly variable. We used these data to calculate an average density

Table 1—Listing of General Land Office witness trees^a from the Wedington Unit, Boston Mountain Ranger District, Ozark-St. Francis National Forest (T16-17 N, R 31-33 W), surveyed in 1832-1833

Species common name	Scientific name	Zone						Total
		Flood plain	Floodplain prairie	Slope	Slope barrens	Upland	Brushy prairie	
Ash	<i>Fraxinus</i>	1	0	0	0	0	0	1
Black gum	<i>Nyssa</i>	1	0	1	0	0	0	2
Black oak	<i>Quercus veluntina</i>	2	0	39	1	48	0	90
Black walnut	<i>Juglans nigra</i>	7	1	0	0	0	0	8
Blackjack oak	<i>Q. marilandica</i>	3	2	33	1	36	0	75
Box elder	<i>Acer</i>	1	0	0	0	0	0	1
Cherry	<i>Prunus</i>	1	0	0	0	0	0	1
Chinquapin	<i>Castanea</i>	0	0	0	1	1	1	3
Elm	<i>Ulmus</i>	2	0	0	0	1	0	3
Hackberry	<i>Celtis</i>	1	0	0	0	0	0	1
Hazel	<i>Corylus</i>	2	0	1	1	1	1	6
Hickory	<i>Carya</i>	5	4	3	0	4	0	16
Honey locust	<i>Gleditsia</i>	1	0	0	0	0	0	1
Locust	<i>Robinia</i>	2	0	1	0	0	0	3
Maple	<i>Acer</i>	0	0	1	0	0	0	1
Overcup oak	<i>Q. macrocarpa</i>	1	0	0	0	0	0	1
Pawpaw	<i>Asimina</i>	1	0	0	0	0	0	1
Plum	<i>Prunus</i>	0	1	0	0	0	0	1
Post oak	<i>Q. stellata</i>	8	0	29	0	40	0	77
Red bud	<i>Cercis</i>	1	0	0	0	0	0	1
Red oak	<i>Quercus</i> spp.	0	0	1	0	0	0	1
Spicewood	<i>Lindera</i>	1	0	0	0	0	0	1
Sumac	<i>Aralia</i>	2	0	1	0	1	0	4
Sycamore	<i>Plantanus</i>	5	0	0	0	0	0	5
White oak	<i>Q. alba</i>	3	0	9	1	8	0	21
Understory								
Briers		0	0	1	0	1	0	2
Cane	<i>Arundinaria</i>	1	1	0	0	0	0	2
Huckleberry	<i>Vaccinium</i> spp.	0	0	0	0	1	0	1
Vines		0	0	1	0	1	0	2
Whortleberry	<i>Vaccinium</i> spp.	0	0	1	0	1	0	2
Total		52	9	122	5	144	2	334

^a Witness trees were noted and marked to facilitate subsequent location for dispersal of public domain, and denotes their legal status as a court witness.

index in each physiographic/topographic zone. The densest area is the flood plain (17.7 feet), followed by the slope and upland (25.3 feet each). The brushy upland prairies yielded a point density index of 104 feet, followed by the flood plain prairie (105.6 feet) and the slope barrens (119.1 feet). The slope barrens correspond to the old-growth post oak stands along the benches and intact uplands of Wedington Mountain. This yields an estimate of 72 trees per acre during the 1832–33 period. Due to fire suppression, the stands are denser today, averaging up to 148 trees per acre (see Tom Foti, in press).

PREHISTORIC ARCHEOLOGY

Archeological surveys of approximately 25 percent of the Ozark-St. Francis National Forests have yielded the 1,472 prehistoric sites shown in table 2 (Jurney 2001). The largest single category is undifferentiated prehistoric lithic scatters (73.6 percent), followed by undifferentiated Archaic (9 per-

cent), Woodland (4.8 percent), Mississippian (3.7 percent), and Late Archaic (3.5 percent). All other categories are represented by few sites.

The majority (14.5 percent) of the identified cultural components date to the Archaic (1,500+ YBP). This indicates a relatively low intensity of human occupation and use of the Ozarks throughout most of prehistory. Sedentary populations are represented by the Mississippian, Woodland, and phase categories (11.1 percent). Sedentary groups are marked by semipermanent villages, mound building, and incipient agricultural practices (Davis and Limp 1994).

Native Americans lived light-on-the-land in the Ozarks for nearly 9,000 years. During this time, the primary hunting strategy was the group surround; fire may have been used to drive game or alter local habitats. Some wild plants were domesticated near the end of this era, probably due to

Table 2—Prehistoric sites on the Ozark-St. Francis National Forest compiled from the Automated Management of Archeological Site Data in Arkansas (AMASDA) database kept by the Arkansas Archeological Survey

Years ago	Culture/period	Count	
		<i>no.</i>	<i>percent</i>
12,000+	PaleoIndian	10	0.7
9,500	Dalton	6	0.4
9,499	Early Archaic	12	0.8
	Middle Archaic	8	0.5
5,000	Mid-Late Archaic	1	0.1
	Late Archaic	52	3.5
	Undifferentiated Archaic	133	9
1,800	Early Woodland	9	0.6
	Late Woodland	4	0.3
	Woodland	71	5
1,100	Middle Mississippian	1	0.1
	Late Mississippian	2	0.1
	Mississippian	54	3.7
	Kent Phase	3	0.2
	Caddo I.	1	0.1
	Caddo	1	0.1
	Neosho	1	0.1
410	Contact	3	0.2
	Contact pre-1800	1	0.1
150	Protohistoric	5	0.3
	Undifferentiated	1,077	73.6
Total		1,455	100.0

increasing land disturbances around bluff shelters and riverine base camps (Fritz 1985, 1990). Around 1,500 years ago, garden agriculture, probably using slash-and-burn strategies, intensified the human alteration of the landscape. Many flood plain forests were also cleared for villages, mound centers, and agricultural fields. Hunting strategies shifted to more solitary strategies, but there appear to have been attempts to gather food and natural resources in the interior Ozarks and transport them to regional population centers in the Arkansas River valley and the lower valleys of major streams incised into the Ozark dome (Schambach 2001).

Few major excavations and sporadic archeological surveys have been conducted in the Wedington Mountain area shown in figure 1. The most extensive excavations have been conducted at the Moss Shelter (3WA252) located on private land approximately 1 mile south of Wedington Gap (Stahle 1986), and at the Albertson site (3BE174) located on Spavinaw Creek approximately 15 miles north of the project area (Dickson 1991). Moss Shelter was formed by dissolution of shales and sandstones by water and wind action. Albertson was formed by riverine undercutting of

limestone beds. Cultural manifestations at Moss and Albertson range from transitional Paleo-Indian to Mississippian (ca. 10,000 to 500 years ago). The majority of the diagnostic materials date to the Middle and Late Archaic, ca. 8,000 to 1,500 years ago (Dickson 1991, Stahle 1986).

Moss Shelter represents the typical formation of upland bluff shelters (fig. 2). The basic process begins with the dissolution of the shale beds that lie under more resistant sandstone layers. Block faulting from freeze-thaw cycles and root penetration also contribute to the formation of sediment traps along the benches of the mountains. Cultural deposits were recovered > 2 m deep at this site, and similar deposits have been found along the upper benches of Wedington Mountain. Other shelters on the northern end of Wedington Mountain were formed by block fracturing of the sandstone as well as water and wind action. Cultural deposits extend along benches and down slopes from all known rock shelters in the vicinity.

A number of archeological surveys recording prehistoric open sites and rock shelters have been conducted in the vicinity by USDA Forest Service archeologists. Two prehistoric lithic scatters were discovered and recorded during our investigation of the Wedington Unit. One (3BE703) is located on the southern point of the ridge overlooking Wedington Gap. The site consists of several bifacial thinning flakes observed on a deflated area of the sandstone outcrop. The area appears to have been used as a tool refurbishing station and provided a superb vantage point with a view to the west, southwest, and southeast on both sides of the gap. The second prehistoric site (3BE704) is located in the bottom of Wedington Gap. This area is marked by erosion of the overlying sandstone to the underlying shale; the vegetation consists of a suite of xeric plants, including blackjack oak. The site consists of a highly disturbed scatter of Boone chert debris. Artifacts collected included five chert cores, four large decortication flakes, two bifacial tool fragments, and one heat-treated lamellar flake. The site has been severely damaged by illegal off-the-road vehicle traffic.

The two prehistoric sites in the Wedington study area represent two different types of activity. One (3BE704) was a staging area for transforming chert cores imported from the adjacent Springfield Plateau into tools. Apparently heat-treatment of these cores was practiced here. The second site (3BE703) appears to be a hunting or territorial lookout, based on the vantage point that provides visual coverage of several miles. The only activity represented in the material culture here is the resharpening of tools that were manufactured in another locality. Neither site represents a habitation locus.

Plant remains, mostly acorns, from 10 sites in the dry bluff shelters of the Ozarks provide information on the cultural selection of oak species (Cande 1997, Hilliard 1986). Acorns were quantified in these studies, but carbonized hickory nut shells and other plant remains were not quantified. Of the 10 sites listed in table 3, only 3 had more acorns from white oaks than from red oaks. Comparing the archeological data with the GLO data, this relative frequency of red oak species to white oak species (87 to 21 percent, column 3 in table 3) is to be expected.

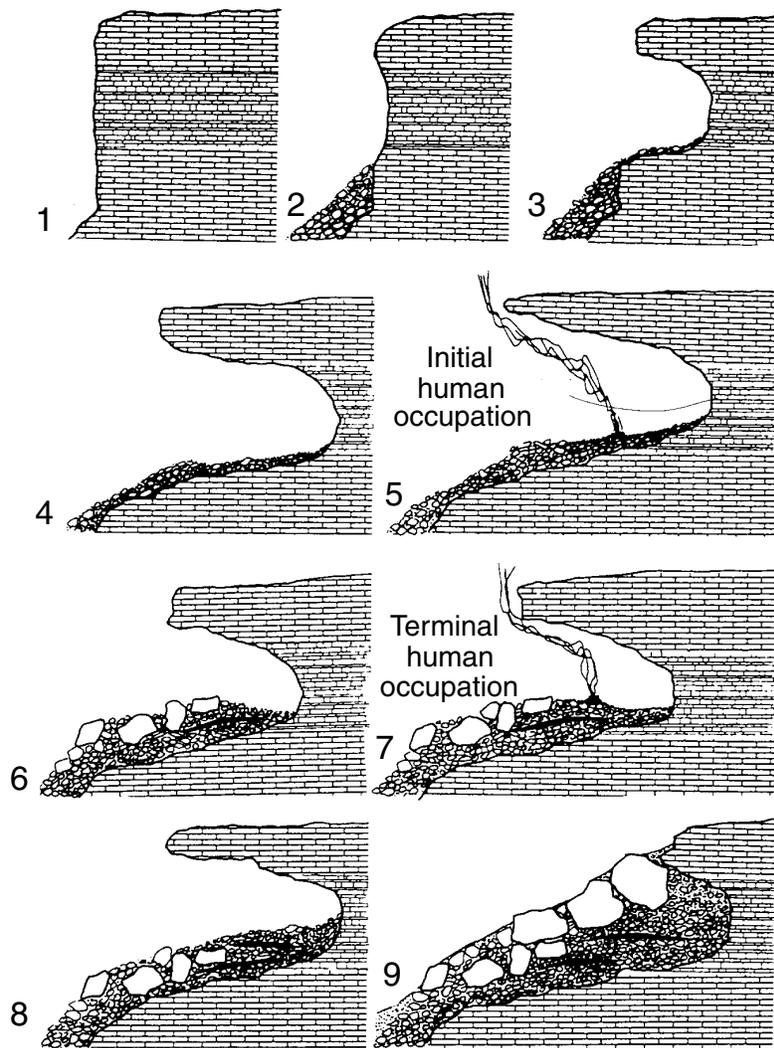


Figure 2—Schematic of Ozark bluff shelter formation processes (Cande 1997, Laville and others 1980).

Table 3—Listing of red oak and white oak acorns from Ozark archaeological sites in Arkansas

Site	Red oak no.	Red oak percent	White oak no.	White oak percent	Total no.
3BE1	749	65.1	402	34.9	1,151
3WA4	173	39	266	61	439
3BE10	211	85.5	36	14.5	247
3CR8	35	21	131	79	166
3BE6	41	63	24	37	65
3BE11	22	60	15	40	37
3MA5	13	54.2	11	45.8	24
3NW624	51	66	26	34	77
3NW625	5	31	11	69	16
Total	1,300		922		2,222

BE = Benton; WA = Washington; CR = Carroll; MA = Madison; NW = Newton.

Analyzed by Hilliard (1986) and Cande (1997).

In some of these sites, large conical pits were excavated and filled with over a gallon of acorns, in order to parch the contents. Parched acorns have also been found across the Ozarks in woven bags that served to reduce insect infestation, preserve the nut meat, and make the shells more removable (Fritz 1985, 1990, 1997). Red oaks may have been considered a more dependable food source since they do not germinate until spring and are less susceptible to insects, and the acorns have a slightly higher caloric value than white oaks (Hilliard 1986).

HISTORIC ARCHEOLOGY

Archeological surveys (Jurney 2001) of approximately 25 percent of the Ozark-St. Francis National Forest have recorded 2,535 historic sites (table 4). The largest single category is developed settlement-rural agriculture (73.9 percent), followed by pioneer settlement-agriculture (9.1 percent), developed settlement (7.6 percent), developed settlement-rural nonagriculture (3.5 percent), Anglo-American (1.8 per-

Table 4—Listing of historic sites on the Ozark-St. Francis National Forest compiled from the Automated Management of Archeological Site Data in Arkansas (AMASDA) database kept by the Arkansas Archeological Survey

Years ago	Site category	Count	Percent
450	Late Holocene semi-sedentary	24	0.9
150	Pioneer settlement	20	0.8
	Pioneer settlement-agriculture	231	9.1
110	Developed settlement	193	7.6
	Developed settlement-rural agriculture	1,877	74.0
	Developed settlement-rural-nonagriculture	90	3.6
	Developed settlement rural plantation	7	0.3
	Developed settlement-city/town	44	1.7
	Developed settlement-rural forager	1	0.1
	Anglo-American	45	1.8
	Developed settlement-African American	3	0.1
Total		2,535	100.0

cent), and developed settlement-city/town (1.7 percent). All other categories are represented by only a few sites (table 4).

The significance of these data is that the majority (89.2 percent) of the identified cultural components date to the developed settlement era of the late 19th and 20th centuries (ca. 1890 to 1940). This indicates a tremendous increase in human impacts to the landscape that tied to population growth and improved transportation (see Guyette and others, in press).

The historic archeological data (Jurney 2001) provide a minimum estimate of 9,452 farmsteads on the Ozark-St. Francis National Forests (total area 1,158,289 acres) that were occupied between 1890 and 1940. Using 110 acres as a mean farm size with 43 acres under cultivation (Schalm 1973), 1,039,720 acres (89.7 percent) of the forest could have been occupied between the late 19th and early 20th centuries, 406,436 acres were cleared and cultivated, and the remaining 633,284 acres were used as wooded pasture. Based on these interpolations, the unoccupied portion of the Ozark-St. Francis National Forests (188,569 acres) may have been used by free-range herders.

One historic site (3BE705) investigated as part of the present study consists of a 20-acre cleared field on the top of Wedington Mountain. The access road to the field passes through the rock escarpment in a narrow cleft. Rock fences had been constructed in all low areas along the escarpment

to prevent free-ranging livestock from entering the field on the top, the fence and escarpment providing an approximate 4,592-foot perimeter. The rock wall, which comprises about 15 percent of the total perimeter, is 4 feet tall and measures 3 feet thick in places. It is estimated that 8,265.6 cubic feet of stone (approximately 1,836.8 tons) were removed from the field and rock outcrop to build this rock fence, a significant investment in labor to achieve a protected cultivated area. If the escarpment wall were not in place, the investment would have been much greater to protect the field crops from free-ranging livestock.

Old-growth trees were removed from the cultivated field but were left in place along the bench below the escarpment wall, where livestock were allowed to free-range. Since it was abandoned, the old field has been reclaimed by red cedars, pines, and mixed hardwoods. We cored these trees using a Swedish increment corer. The red cedars are at least 68 years old, indicating that the field was abandoned or converted to fallow ground around 1933. The bench and side slopes of this area retain old-growth characteristics. Tree-ring collections on the south end of the mountain by Wedington Gap have yielded one of the best records of frost rings (false spring events) in all of Arkansas and Oklahoma (Stahle 1990).

Based on our examination of the Benton County Deed Records in the Bentonville Courthouse and the Forest Service tract acquisition files, the land containing the field and old-growth wooded pasture on Wedington Mountain is part of a homestead land grant to Harry and Lizzie Beck dated November 3, 1899. The land falls on the dividing line between Washington and Benton Counties. The 80-acre parcel in Benton County was sold to Thomas Dunn in October 1905. The land was acquired by S.C. Peacock in a tax sale and was resold to Clarence S. and Cora Rankin July 12, 1913. They sold the land, including the portion in Washington County, to A.L. and Doris McCulley (134 acres total) on October 14, 1922. Doris and her son J.H. (wife Carrie E.) and daughter May sold the land to the U.S. Resettlement Administration on November 13, 1938. At that time, two dwellings, a poultry house, a barn, a well, and a spring were located at the core of the farm. The upland pasture was cultivated on the south end and wooded on the north end. Based on our courthouse and tract acquisition file research for this paper, little improvement and expansion was done to the farm from 1899 to 1907. During the Peacock ownership in 1908, a central barn was built. The McCulley ownership in 1922 marked the expansion of the farm with the construction of two houses, followed by a poultry house in 1933. The upland pasture was most likely cleared and cultivated around 1922. At least five serial occupations worked the land in this area. The McCulley occupation from 1922 to 1933 was the most intense.

DENDROCHRONOLOGY

Since the late 1950s, tree-ring samples have been collected from stands of living trees across Arkansas and adjacent States. A series of chronologies has been developed for the region from these collections (Stahle 1990; Stahle and Hehr 1984; Stahle and others 1984, 1985b). The five longest Arkansas chronologies established are for baldcypress (*Taxodium distictum*) and span the period 1322 to 1990.

The mean germination date is 1498, and the stands range in age from 214 to 668 years. The nine second-longest chronologies are for white oak. White oak spans the period 1598 to 1993, with a mean germination date of 1697 and an age range of 89 to 395 years. Thirty-four post oak chronologies span the period 1626 to 1993, with a mean germination date of 1671 and an age range of 257 to 372 years. Five shortleaf pine (*Pinus echinata*) chronologies span the period 1649 to 1982, with a mean germination date of 1760 and an age range of 71 to 333 years. Two black oak chronologies span the period 1870 to 1959 and are similar to red oak in growth patterns and ages (< 100 years longevity).

The significance of these data revolves around the maximum ages of various species. Baldcypress, the longest lived at 650 years, is restricted to aquatic habitats of large rivers and swamps. Several stands are present on the St. Francis Division of the Ozark-St. Francis National Forests. Post oak and white oak have approximately the same life spans (350 years), while the life span of shortleaf pine is slightly less. These three species generally reach old age between 300 and 350 years. Black oak and red oak have much shorter life spans, rarely reaching 100 years. Because of this range in life spans, it is to be expected that species dominance should vary across the landscape. It is our opinion that the apparent decline of red oak in the area may be a result of an overly mature species dying out, while longer-lived species such as shortleaf pine, white oak, and post oak remain viable.

We have collected fire-scarred trees and stumps in the southern Ozarks as part of ongoing fire and ecosystem studies conducted by the USDA Forest Service. In the southern Ozarks, continuous fire scar records have been compiled on the Bayou and Pleasant Hill Ranger Districts for three time periods: 1747 to 1764, 1804 to 1906, and 1916 to 1954. From 1747 to 1764, the fire return interval ranged from 1 to 3 years with a mean return interval of 2.43 years. From 1804 to 1906, the fire return interval ranged from 1 to 9 years with a mean return interval of 4.4 years. From 1916 to 1954, the fire return interval ranged from 1 to 12 years with a mean return interval of 5.3 years (D.H. Journey. 2002. Historic fire regime. 19 p. On file with: Ozark-St. Francis National Forests, 605 W. Main, Russellville, AR 72801). This suggests a general trend toward decreasing fire returns with increasing historical settlement and fragmentation of the landscape (R. Guyette. 2000. Notes on fire history at three sites in the Lower Atoka Hills adjacent to the Arkansas River. On file with: School of Natural Resources, I-30 Agriculture Building, University of Missouri, Columbia, MO 65211).

CONCLUSIONS

Natural pollen traps—sediment deposits containing fossilized pollen—have not been found in the Wedington study area, or, more generally, in the Ozark-St. Francis National Forests. This discussion presents a broad-brush comparison using data from adjacent regions. Pollen and geological studies suggest that over the last 40,000 years, climate has been the major driving force behind changes in plant communities across the landscape (Bousman 1991). Around 16,000 years ago, dominant tree species included pine (29.3 percent), oak (16.9 percent), willow (16.5 percent), and hickory (10.1 percent), with about 50 percent canopy

cover. Current landforms developed around 7,500 years ago; since then, there have been at least five periods alternating between aggradation and erosion (Jacobson and Primm 1997). Around 9,000 years ago, vegetation was dominated by oak (63.8 percent) and pine (9 percent), with 40 percent canopy cover. Early Indians were highly mobile and apparently followed large herds of now-extinct animals. They may have used large fires to drive animals into traps or to attract grazing herds to certain locations. Human population was low, and the extent of human-caused and natural disturbances remains unknown.

Around 5,000 to 6,000 years ago, the current climate and suite of natural ecosystems developed and included the most extensive grasslands and lowest percentage of canopy cover (10 percent, minimum). Oaks continued to grow in dominance (72 percent) and remain at this level today (Bousman 1991). Pines decreased to 5 percent; hickories comprise 6 percent. Indian populations increased during the same period; they appear to have settled into specific ecological niches where their activities were concentrated. The Ozark bluff shelters received extensive settlement at this time and appear to have been bases for seasonal rounds of plant and animal exploitation. Human-caused environmental disturbances increased around base camps and gardens and led to the domestication of wild plants in the Ozarks (Fritz 1985, 1990, 1997). Around 1,500 years ago, tropical cultigens imported from Mexico provided the basis for the development of sedentary life ways. Indians developed large population centers with settlement concentrated in the flood plains. Bluff shelters appear to have been used for mortuary practices and food storage. Fire scar records from trees indicate a mean fire return interval of 2.43 years during the late 1700s (R. Guyette. 2000. Notes on fire history at three sites in the Lower Atoka Hills adjacent to the Arkansas River. On file with: School of Natural Resources, I-30 Agriculture Building, University of Missouri, Columbia, MO 65211) (D.H. Journey. 2002. Historic fire regime. 19 p. On file with: Ozark-St. Francis National Forests, 605 W. Main, Russellville, AR 72801). Based on Texas pollen studies (Bousman 1991), around 1,000 years ago the canopy cover was 20 percent. Today, the percentage of canopy cover has returned to the level of 8,000 years ago (40 percent).

With the advent of European settlement in the 19th century, the trend toward nucleated settlement in the flood plains increased. The rectangular land survey system forced land grants into shapes oriented north-south, and the average grant ranged from 40 to 160 acres, arbitrarily chosen from the available public domain. This pattern of public land distribution forced dispersed settlement into 40- to 160-acre parcels. Land was first chosen along larger streams where cultivation was possible, then less suitable land was chosen by later settlers. By the late 1800s, most of the Ozarks had been claimed by settlers, and farmsteads dotted the landscape (1 per 110 acres). During this period, a mean fire return interval of 4.4 years was recorded in fire-scarred trees (R. Guyette. 2000. Notes on fire history at three sites in the Lower Atoka Hills adjacent to the Arkansas River. On file with: School of Natural Resources, I-30 Agriculture Building, University of Missouri, Columbia, MO 65211) (D.H. Journey. 2002. Historic fire regime. 19 p. On file with: Ozark-St. Francis National Forests, 605 W. Main, Russellville,

AR 72801). The increased population density contributed to a reduction in forest fire spread but increased the impacts to specific land parcels through logging, plowing, construction of rock fences, and soil depletion from increased erosion. Certain trees such as red cedar, bois d'arc (*Maclura pomifera*), and walnut were transplanted for food and economic purposes to locations where they had formerly been rare (Jurney 1994).

Acquisition of worn-out farmlands by the USDA Forest Service in the early 20th century led to the rehabilitation of many eroded fields and the planting of trees that could provide a sustained yield of wood products. Fire suppression became a primary concern, and fire was taken out of the ecosystem. Fire-scarred trees indicate mean return intervals ranging from 5.3 to 22 years during this period (R. Guyette. 2000. Notes on fire history at three sites in the Lower Atoka Hills adjacent to the Arkansas River. On file with: School of Natural Resources, I-30 Agriculture Building, University of Missouri, Columbia, MO 65211) (D.H. Jurney. 2002. Historic fire regime. 19 p. On file with: Ozark-St. Francis National Forests, 605 W. Main, Russellville, AR 72801). The fire atlases for the Bayou and Piney Ranger Districts from 1935 to 1972 yield data on fire occurrence at the time. Because fires were immediately suppressed, the atlases cannot provide extent information, only the area of the District and number of fires for each period of record. Dividing the District area by the number of fires and the number of years in the record, lightning fires ranged from zero on the St. Francis in the Mississippi Delta, 150 miles from Wedington, to 111 on the Bayou at the eastern edge of the Ozark Dome, 50 to 80 miles southeast of the Wedington study area. This yields a minimum estimate of 6 to 18 lightning fires per million acres per year. Human-caused fires ranged from 91 on the St. Francis to 672 on the White Rock (50 miles southeast of Wedington) (D.H. Jurney. 2002. Historic fire regime. 19 p. On file with: Ozark-St. Francis National Forests, 605 W. Main, Russellville, AR 72801). This yields a minimum estimate of 87 to 114 human-caused fires per million acres per year.

Today, forests resembling presettlement conditions are rare. The wooded pastures of Wedington Mountain are examples of old-growth post oak forests, barrens, and savannahs that have received fewer disturbances by historic settlement than adjacent areas. It is important that such areas are managed for their old-growth characteristics to retain the diverse ecosystems in which they are located. In our opinion, old-growth wooded pastures exhibit long-term resiliency, and perhaps maintenance of this ecosystem will reduce forest susceptibility to infestations such as the red oak borer and oak decline.

Specific recommendations to preserve and maintain diverse old-growth ecosystems are presented here for consideration by forest managers. First, we recommend using the GLO records to develop a GIS layer showing potential historic vegetation prior to extensive European disturbances. The correlation of GLO vegetation types to soils, slope/aspect, and land type associations will enhance the silvicultural prescriptions that are used to plan future forests. Dendrochronological analysis is recommended to develop spatial models of natural old-growth distributions of

multiple tree species. Point-specific fire scars should also be collected from old trees and snags to improve our understanding of the frequency, intensity, and extent of wildfires in the presettlement ecosystem. Finally, there is a need to correlate lightning strikes and lightning-caused wildfires with weather parameters to improve modeling of fire spread across the Ozark landscape.

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AGE DISTRIBUTION OF OAK FORESTS IN NORTH-CENTRAL ARKANSAS

Rick Soucy, Eric Heitzman, and Martin A. Spetich¹

Abstract—We used tree ring analysis to reconstruct the tree establishment patterns in four mature white oak (*Quercus alba* L.)-northern red oak (*Quercus rubra* L.)-hickory (*Carya* spp.) forests in the Ozark Mountains of north-central Arkansas. Cross sections were removed from the stumps of 321 recently harvested trees and total age determined for each. All four stands originated between 1900 and the 1920s following a stand-level disturbance(s) such as timber harvesting and/or wildfire. Oak establishment was abundant for 10-30 yrs following the disturbance(s) but steadily declined thereafter. There was no oak establishment at the study sites over the past 50-60 yrs. Establishment since the 1940s and 1950s was dominated by shade tolerant species such as flowering dogwood (*Cornus florida* L.) and red maple (*Acer rubrum* L.)

INTRODUCTION

The Ozark Mountains are the dominant physiographic feature in northern Arkansas. They include over 15 million ac of oak-dominated forests. Oaks have been important species in the region over the past 6,000 yrs (Delcourt and Delcourt 1991), and there are compelling financial and ecological reasons for maintaining a significant oak component in the landscape. Species such as northern red oak (*Quercus rubra* L.), white oak (*Quercus alba* L.), and black oak (*Quercus velutina* Lam.) have historically been, and continue to be, sources of valuable timber. The harvesting of these prized species provides economic benefits to the rural people and communities involved with the logging industry. From a wildlife perspective, acorns are an essential seasonal food supply for a variety of game species such as deer, bear, and turkey.

Despite the current abundance of mature oak forests, the long-term sustainability of oak is uncertain in northern Arkansas and much of the eastern United States. Difficulties in naturally regenerating oaks have been documented in the Lake States (Crow 1988, Lorimer 1993), the northeast (Abrams 1997), the Appalachians (Carvell and Tryon 1961, Loftis 1990), and the central hardwood region (including northern Arkansas) (Graney 1989, Sander 1972, Sander and Graney 1993). In the Arkansas Ozarks, oak generally is succeeded by species like blackgum (*Nyssa sylvatica* Marsh.), flowering dogwood (*Cornus florida* L.), red maple (*Acer rubrum* L.), and black cherry (*Prunus serotina* Ehrh.).

There are several possible contributing factors to the oak regeneration problem. These include acorn predation (Bowersox 1993), damage to oak seedlings by insects and diseases (Oak 1993), and excessive tree competition resulting from decreased fire frequency (Abrams 1992, Brose and others 1999, Van Lear and Waldrop 1989). The latter hypothesis, that shade tolerant non-oak species accumulate beneath mature oaks in the absence of fire and inhibit the recruitment of oak seedlings, has been cited as a dominant factor by the research community. Yet any of these factors would hinder or eliminate the development of advance oak seedlings and saplings. Regardless of the

cause(s), traditional silvicultural practices that simply involve cutting the overstory without regard to these factors can lead to upland forests that are compositionally and structurally different from the previous forest.

The abundance of mature oak forests in northern Arkansas demonstrates that oak regeneration has not always been a problem. Indeed, previous disturbance conditions appear to have facilitated successful oak establishment and development. To better understand current oak regeneration difficulties, it is important to gain information on when and how today's mature oak forests regenerated. We selected four oak stands in north-central Arkansas for detailed study. The objective was to use tree ring analysis to reconstruct the patterns of tree establishment in each stand.

METHODS

Study Areas

Four mature white oak-northern red oak-hickory (*Carya* spp.) stands in north-central Arkansas were selected for study. The stands, located in the White River Hills and Springfield Plateau subsections of the Ozark Mountains (USDA Forest Service 1999), were on the Sylamore Ranger District of the Ozark-St. Francis National Forest in Stone County and Baxter County, AR. Sites were no closer than 0.5 miles from each other; the distance between the two most widely spaced stands was 12 miles. Elevations ranged from 700 to 1400 ft. Soils were Clarksville and Noark very cherty silt loams (Ward 1983, Ward and McCright 1983), and slopes were 8 to 40 percent. Site index for upland oak was 70 ft at base age 50 (Ozark-St. Francis National Forest, unpublished data).

All four stands had been commercially harvested from 1998 to 2000 using the group selection system. With this method, approximately one-sixth of the area in each stand was regenerated in 0.25–1.0 ac scattered openings. All merchantable trees in the openings were harvested and removed, while non-merchantable trees greater than 1-in in d.b.h. (diameter at breast height) were killed by stem injection with herbicide (glyphosate). In addition, a commercial thinning from below was conducted in some parts of the forest matrix between the openings.

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Data Collection

In 2000 and 2001, we established one transect in each stand and systematically selected three openings for further study. Depending on stand size, the distance between the openings chosen was 500 to 2000 ft. In each opening we established one 0.25-ac circular plot. Using chainsaws, a cross section was cut from all non-rotten stumps within the plots that possessed a ground line diameter larger than 2 in. The cross sections were tallied by species or species group (e.g., red oak). In most of the openings, at least several unmerchantable trees were not felled during harvesting. We felled and removed cross sections from the stumps of these trees if their ground-line diameters exceeded 2 in. In all, we collected 321 sound cross sections.

To calculate the pre-harvest tree density and basal area in each stand, we sampled the forest matrix between the openings. Two 0.05-ac overstory/midstory plots were established 100 ft north and south of the northern and southern boundaries of each opening sampled; 6 plots were established in each stand. Plots were offset if they included skid trails or areas that had been commercially thinned. Within each plot, species and d.b.h. were tallied for all living trees greater than 4.5 in d.b.h.

Laboratory Procedures

Tree cross sections were transported to the University of Arkansas – Monticello for preparation and analysis. Each cross section was sanded with progressively finer sandpaper so that individual tree rings were clearly visible. Tree age for each cross section was determined by counting the tree rings under a dissecting microscope. About ten percent of the samples were independently recounted to check the precision of our work. The mean difference between the original counts and recounts was 2.1 yrs. Tree ages were grouped by decade to reconstruct tree establishment and stand development patterns at each site.

RESULTS AND DISCUSSION

Stand Structure

The four stands were similar in terms of total overstory/midstory tree density and basal area (table 1). Densities ranged from 193 to 204 trees per ac, and basal areas varied

from 114 to 122 ft² per ac. White oak, red oak (including northern red oak and black oak), and hickories were the dominant species. In each stand, they combined for at least 92 percent of the tree density and at least 96 percent of the basal area. There were more white oak stems than red oak or hickory in all four stands. Associated species included flowering dogwood, red maple, eastern redcedar (*Juniperus virginiana* L.), and shortleaf pine (*Pinus echinata* Mill.).

Age Distribution

The age distributions of the study areas exhibited a number of similarities (figs. 1A through 1D). First, there was an abrupt pulse of tree establishment beginning in the 1900s (fig. 1C) or 1910s (figs. 1A, 1B, and 1D). It is likely that a disturbance such as timber harvesting and/or wildfire triggered this regeneration response by removing all or portions of the forest canopy. Separate age distributions of each 0.25-ac plot (not depicted) indicate that disturbances were likely stand-level in scale. That is, an establishment pulse during a particular decade in one plot was also evident in the other two plots in that stand.

Second, few of the trees we sampled originated prior to 1900. Although red oaks are not particularly long-lived – for example, physiological maturity of black oak occurs near age 100 (Sander 1990) – white oak is a long-lived species with rotation ages of 120+ yrs (Rogers 1990). Therefore, some older trees probably were killed by the same disturbance(s) responsible for the regeneration pulse. The near-absence of older trees also suggests that post-disturbance establishment was dominated by either germinating seedlings or the release of advance regeneration.

Third, tree establishment was particularly abundant for 10 to 30 yrs following disturbance, but steadily decreased with increasing stand age. Perhaps the initial disturbance in each stand was the sole disturbance, or subsequent disturbances were relatively small and had little effect on establishment. Lorimer (1985) observed that examining age distributions alone may be insufficient to reconstruct stand disturbances. We are currently analyzing tree radial growth patterns to more accurately describe disturbance history of the study areas.

Table 1—Stand characteristics of trees greater than 4.5 in dbh at the four study sites

Species	Stand 1		Stand 2		Stand 3		Stand 4	
	Density <i>trees/ac</i>	Basal area <i>ft²/ac</i>						
White oak	93	46	80	46	87	48	110	73
Red oak ^a	73	60	47	44	53	63	43	32
Hickories	20	7	60	21	43	10	37	11
Flowering dogwood	—	—	10	2	7	1	3	1
Other ^b	10	5	7	1	3	< 1	7	1
Totals	196	118	204	114	193	122	200	118

^a Includes northern red oak and black oak.

^b Includes red maple, eastern redcedar (*Juniperus virginiana* L.), and shortleaf pine (*Pinus echinata* Mill.).

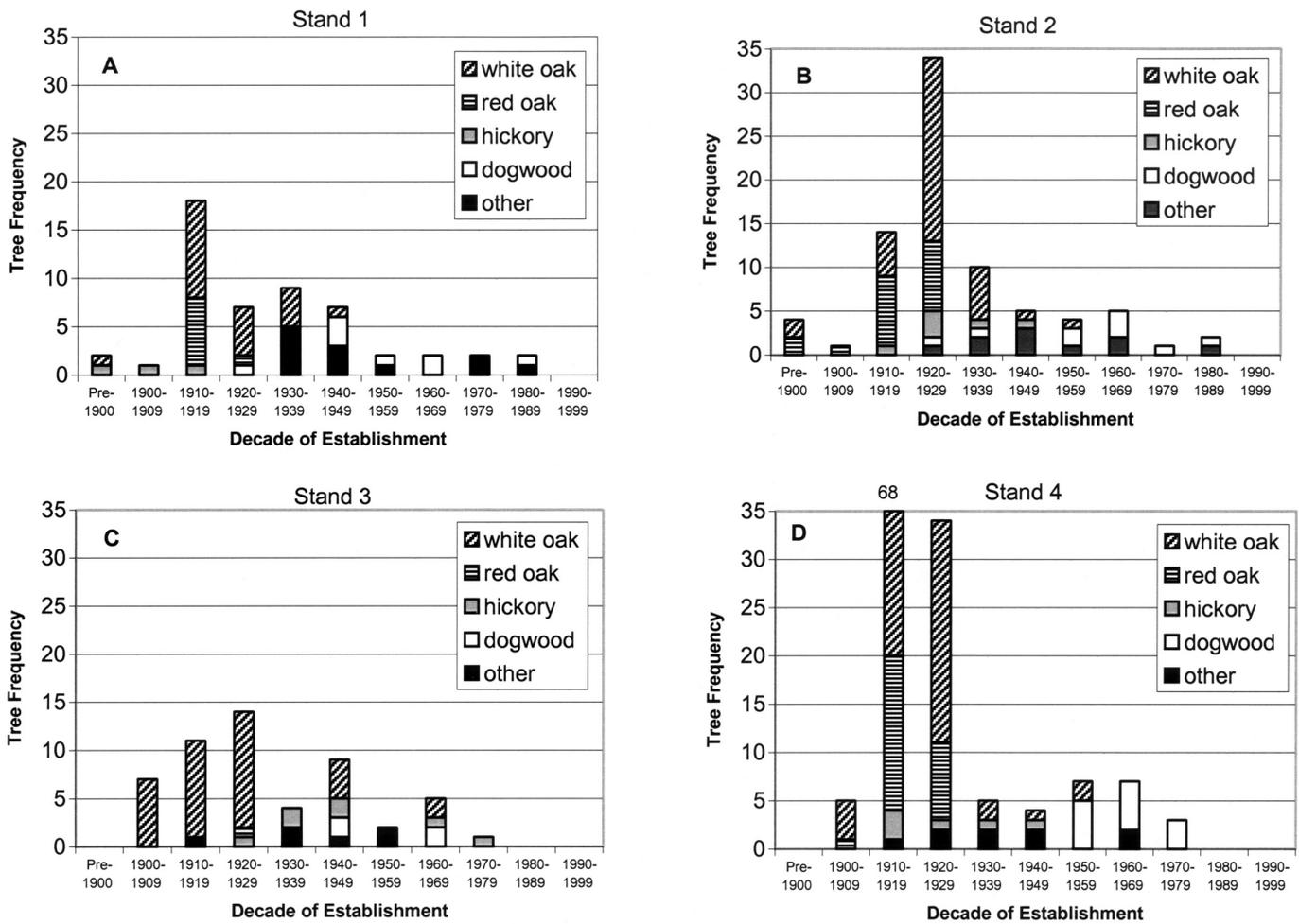


Figure 1—Age distributions for trees greater than 2 in at ground-line diameter at (A) Stand 1, (B) Stand 2, (C) Stand 3, and (D) Stand 4. Note that the “Other” category includes blackgum, red maple, and sassafras (*Sassafras albidum* (Nutt.) Nees).

Finally, different species established at certain times. White oak and red oak aggressively colonized the disturbed study areas from the 1900s through the 1920s (fig. 1A-1D). In the 1930s, white oak continued to establish, albeit at reduced levels, but red oak establishment ceased and never resumed. Although white oak is considered intermediate in shade tolerance, it is more tolerant than northern red oak and black oak, and is most tolerant as a seedling or sapling (Rogers 1990). White oak was clearly able to establish in the shaded conditions of the developing stands better than red oaks. Yet after the 1930s, white oak establishment also decreased and ceased by 1950 to 1970. Coincident with the cessation in oak establishment was an increase in establishment of shade tolerant species such as flowering dogwood and red maple (fig. 1A-1D). These species consistently established from the 1930s through the 1970s and 1980s; field observations at the study sites indicated they were abundant in seedling and sapling size classes not sampled in this study.

CONCLUSIONS

The four mature oak stands we studied in north-central Arkansas originated following stand-level disturbances that occurred between 1900 and 1930. Following the disturbances, oak establishment continued for decades, with the

more tolerant white oak establishing for a longer period than red oaks. Few white oaks, and no red oaks, established at the study sites over the past 50 to 60 yrs. Instead, establishment became dominated by shade tolerant species. These results demonstrate that disturbance is a prerequisite for successful oak regeneration. Current investigations into tree radial growth patterns should provide additional information on the type and frequency of disturbances at the study sites.

ACKNOWLEDGMENTS

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PATTERNS OF OAK DOMINANCE IN THE EASTERN OUACHITA MOUNTAINS SUGGESTED BY EARLY RECORDS

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Abstract—Many years of human influence across the Interior Highlands have caused profound changes in forest composition, disturbance regimes, and understory dynamics. However, information on the historical condition of these forests is limited. General Land Office (GLO) records, old documents, and contemporary studies provided data on the township encompassing the Lake Winona Research Natural Area (LWRNA). The study area was first surveyed between 1821 and 1838, and few settlers had settled this mountainous region by the 1930s. A 1987 ecological assessment of the LWRNA, coupled with other reports, supplemented the GLO descriptions. The original surveys tallied at least 15 species of witness trees, primarily white oak (*Quercus alba* L.), black oak (*Q. velutina* Lam.), shortleaf pine (*Pinus echinata* Mill.), blackgum (*Nyssa sylvatica* Marsh.), and post oak (*Q. stellata* Wang.). A 1931 resurvey identified at least 14 taxa, but by then the witness trees had become overwhelmingly shortleaf pine, with much less oak. Forest composition in the LWRNA is shifting once again toward oak dominance, with a prominent pine supercanopy.

INTRODUCTION

Humans have dramatically changed forest composition, disturbance regimes, and understory dynamics across most of North America. Very few stands remain that retain sufficient ecological integrity to use as standards for restoration, and new perturbations continually alter these remnants. This challenges stewards and researchers who desire to maintain certain features of the natural environment, especially when the management objects are isolated parcels in a matrix of unprotected forests.

To describe how the forests of Arkansas have changed, researchers have examined narratives of early explorers (Strausberg and Hough 1997), historical documents and photographs (Smith 1986), and General Land Office (GLO) survey notes (Bragg 2003, Foti and Glenn 1991). All of these sources can contribute to our understanding of forest composition and structure. However, the quality of any historical information must be thoroughly evaluated before inferring definitive ecological conclusions (Forman and Russell 1983, Noss 1985). Reliable information is critical when assessing long-term change in remnant stands of old-growth forest.

The 113-ha Lake Winona Research Natural Area (LWRNA) has been preserved as a relic old forest in the Ouachita Mountains of central Arkansas (Fountain and Sweeney 1987). Little is known about the developmental history of the LWRNA, limiting its utility as a case study of forest change. This study is intended to supplement existing ecological research on the eastern Ouachita Mountains including the LWRNA, with special emphasis on long-term patterns of overstory oak dynamics.

METHODS AND MATERIALS

Study Area

Located in the Ouachita Mountains of western Saline County, the study area lies approximately 50 km west of Little Rock and encompasses the whole GLO-surveyed area of

Township 2 North, Range 18 West (T2N R18W). The LWRNA (fig. 1) falls entirely within T2N R18W. Since the whole township is relatively uniform in landform and vegetation, and rather than abbreviating the already limited GLO data to the small area encompassed by the LWRNA, the data for the LWRNA will be considered detailed enough for comparison with the larger GLO results. In terms of relative species composition and stand development patterns, this assumption should not be too problematic.

Fountain and Sweeney (1987) described the environment of the LWRNA, which is typical of the region as a whole. The landscapes are predominately steep hills and low mountains, with slopes ranging from gentle (5 to 10 percent) to very steep (> 50 percent). Sandstones and shales dominate the bedrock of the region, and the colluvial-origin soils are primarily Typic Hapludults. Alum Fork, a major tributary of the upper Saline River, and many small creeks drain the township.

Data Sources

This comparison was taken from three main sources: the original land survey (GLO) notes (Daniels 2000), an ecological assessment of the LWRNA (Fountain and Sweeney 1987), and a trade journal report on the lumbering potential of the region (Anonymous 1904). These reports, coupled with other historical and modern references, describe the forest conditions of the LWRNA region from the early 1800s to the present.

For many years researchers have used GLO survey notes to describe presettlement vegetation patterns, e.g., Bourdo 1956, Delcourt 1976, and Lutz 1930, although there are some challenges with their interpretation related to surveyor bias, scale incompatibility, and species clarity (Bragg 2003, Schulte and Mladenoff 2001, Whitney and DeCant 2001). For example, Bragg (2003) reported on the uncertainties related to surveyor species delineations, including the timing of most survey work (November to March, during the dormant season), the surveyors' lack of formal taxonomic

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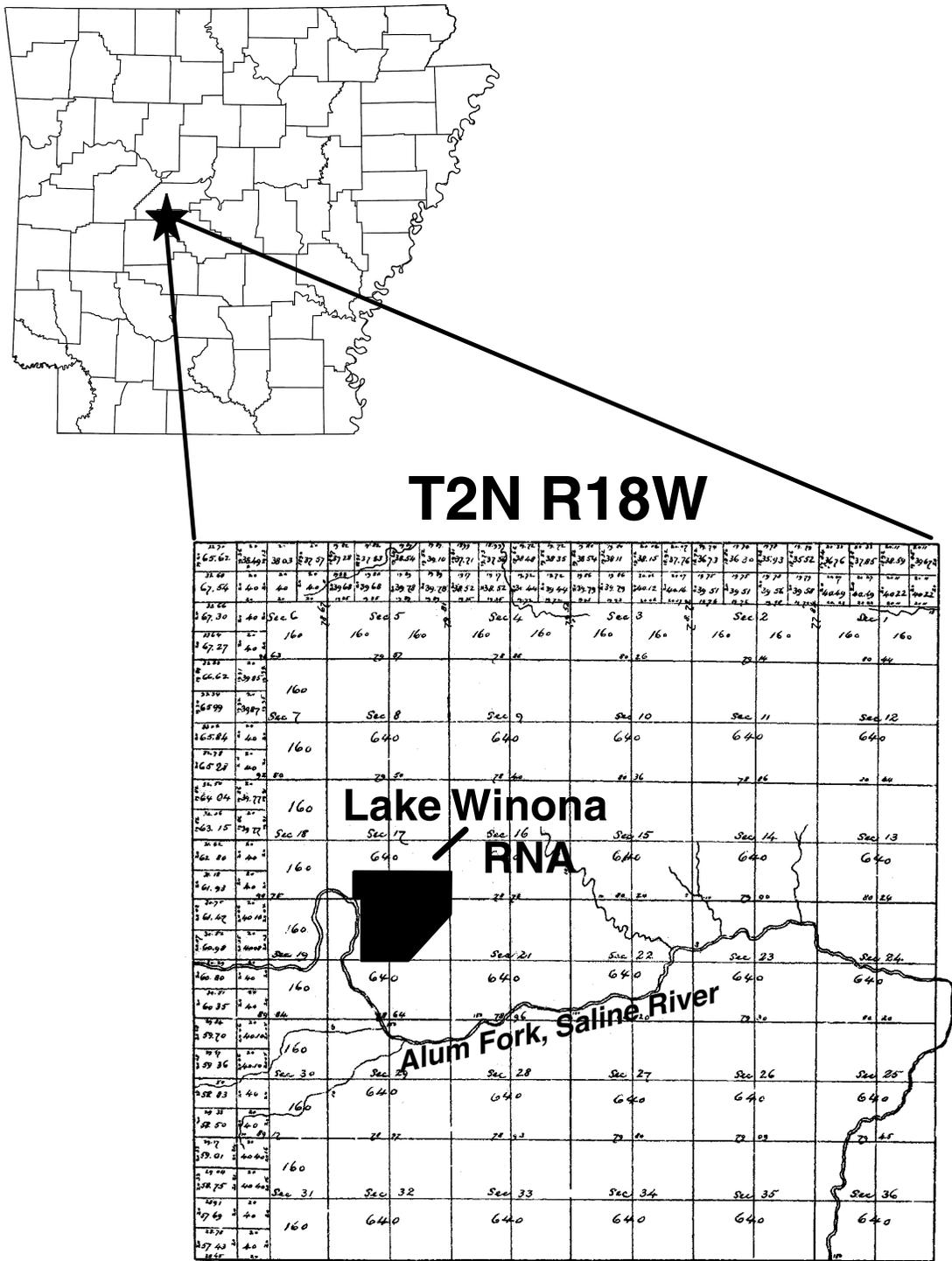


Figure 1—The 1840 plat map of T2N R18W, showing the approximate location of major drainages and the LWRNA.

training, and their use of nonspecific or obscure common names. Though these concerns may limit interpretation of GLO records, the survey notes still represent the best available quasi-quantitative information on presettlement vegetation conditions.

The township and range lines of T2N R18W were surveyed as early as 1821, with most of the interior section lines

completed in early 1838. For simplicity, I refer to these data as the “Original 1838 data” since the GLO completed the vast majority of the interior lines during that year. As an aside, John R. Conway surveyed much of the study area. A member of an early regional political dynasty, Conway’s father, John S., was the first governor of Arkansas, his older brother Henry was an Arkansas congressman, brother Frederick was the surveyor-general of Missouri, brother

William was an Arkansas supreme court justice, and brother Elias became governor of Arkansas in 1852 (Herndon 1922).

By 1931, a resurvey of T2N R18W was commissioned. The notes do not give any justification for this effort, although it could be related to an ownership dispute. Arthur W. Brown, a federal surveyor, undertook the resurvey of T2N R18W between August and December of 1931 and relocated approximately half of the original corners. Many of the witness trees had died or been cut since the original GLO survey, so most corners required remonumentation. Another resurvey of a portion of the township was completed in the mid-1970s when the U.S. Department of Agriculture Forest Service requested a survey of the Lake Winona spillway elevation. However, I did not include this traverse because of the very limited area surveyed within T2N R18W.

The Ouachita National Forest established the LWRNA in 1977 to preserve a remnant of the pine-hardwood forest that once dominated much of the Ouachita Mountains. In a baseline ecological assessment, Fountain and Sweeney (1987) reported an overstory of > 100-year-old shortleaf pine (*Pinus echinata* Mill.) and a mid- and understory overwhelmingly dominated by oaks (*Quercus* spp.), hickories (*Carya* spp.), gums (*Liquidambar* sp. and *Nyssa* sp.), and shrubs. They predicted that the lack of fire, coupled with individualistic pine mortality from disease, insects, wind, and lightning, would eventually lead to a hardwood-dominated overstory.

I searched the GLO records for any witness or line trees with the surveyors' assignment of species and an estimated diameter. The common names given by the surveyors (table 1) are probably reliable to species for the most obvious taxa, e.g., white oak (*Q. alba* L.), but are only accurate to genera for others, e.g., hickory. The 1987 assessment of the LWRNA was conducted by trained ecologists and foresters using modern equipment and measurement protocols, and hence better reflects the true distribution of vegetation. The taxonomic assignments by Fountain and Sweeney (1987) were assumed to be accurate to species. For broad discussion, species groups have been used to simplify the naming conventions. Hence, the white oak group includes white oak and post oak (*Q. stellata* Wang.); the red oak group consists of southern red oak (*Q. falcata* Michx.), black oak (*Q. velutina* Lam.), blackjack oak (*Q. marilandica* Muenchh.), and spotted oak (*Q. shumardii* Buckl.); the hickory group probably contains several *Carya*; the gums consist of blackgum (*N. sylvatica* Marsh.) and sweetgum (*L. styraciflua* L.); the conifer group includes eastern redcedar (*Juniperus virginiana* L.) and shortleaf pine; and other hardwoods contain all other minor hardwood taxa.

RESULTS

The original GLO survey of the LWRNA region in the early 1800s described a largely untouched wilderness, with oaks and pine dominating the overstory (table 2). The 1838 survey reported at least 15 taxa. Witness trees were mostly white oak, black oak, shortleaf pine, blackgum, and post oak. Blackjack oak, commonly found in open, fire-dominated sites, was used several times as a witness tree. Other minor shade-tolerant species such as flowering dogwood

Table 1—Common names of trees used by the 1821–1838 and 1931 surveyors in T2N R18W, and their probable taxonomic equivalents

Surveyor name	Probable scientific name ^a
Pignut hickory	<i>Carya cordiformis</i> (Wang.) K. Koch
Hickory	<i>C.</i> spp.
Chinkapin	<i>Castanea pumila</i> (L.) Mill. var. <i>ozarkensis</i> (Ashe) Tucker
Dogwood	<i>Cornus florida</i>
Ash	<i>Fraxinus</i> spp.
Holly	<i>Ilex opaca</i>
Cedar	<i>Juniperus virginiana</i>
Sweetgum	<i>Liquidambar styraciflua</i>
Gum	<i>L. styraciflua</i> , <i>Nyssa sylvatica</i>
Mulberry	<i>Morus rubra</i> L.
Blackgum	<i>N. sylvatica</i>
Pine	<i>Pinus echinata</i>
Cherry	<i>Prunus serotina</i> Ehrh.
White oak	<i>Quercus alba</i>
Red oak	<i>Q. falcata</i> , <i>Q. rubra</i> , <i>Q. velutina</i>
Blackjack oak	<i>Q. marilandica</i>
Spotted oak	<i>Q. shumardii</i>
Post oak	<i>Q. stellata</i>
Black oak	<i>Q. velutina</i> , <i>Q. rubra</i> L., <i>Q. falcata</i>
Elm	<i>Ulmus</i> spp.

^a Multiple species are listed if several options are possible.

(*Cornus florida* L.) and American holly (*Ilex opaca* Ait.) were mentioned, but their infrequent usage suggests that their presence in the early 1800s was limited.

The intervening century found the region gradually settled, logged, and farmed. Most witness trees in the 1931 resurvey were small-diameter shortleaf pine (fig. 2), followed by white oak, blackgum, and post oak. Surveyor A.W. Brown noted much of mature pine and oak had been removed, although some areas still contained virgin timber. Brown placed the hickory, gum, elm (*Ulmus* spp.), ironwood [*Ostrya virginiana* (Mill.) Koch.], and holly along the creek bottoms implying that their presence in upland areas was limited. Brown's report also stated that "[p]ractically the entire township produces a very good growth of native grasses, but the efforts of the Forest Service to get settlers to launch more extensively into the cattle business have so far proved rather fruitless," and later "timber on the hillsides is quite free of undergrowth" (Brown 1931).

During the next half-century, much of the township experienced timber harvest and fire suppression. The 1987 LWRNA inventory indicated a decline in pine dominance and a resurgence of oak importance. Conifers (mostly shortleaf pine) had decreased from almost 74 percent of surveyed stems to < 35 percent of trees in the LWRNA inventory (fig. 2). White and red oaks, gums, and other hardwoods increased noticeably and dominated the understory (Fountain and Sweeney 1987), which had virtually no shortleaf pine or eastern redcedar. The white oak group comprised nearly one-third of the stems in the LWRNA, and the red oak group increased to almost 11 percent, or over five times their

Table 2—Common names of species (and counts) noted in the GLO surveys of T2N R18W and the LWRNA

1838 GLO ^a	1931 Resurvey ^a	1987 LWRNA inventory ^b
White oak (135)	Pine (299)	Shortleaf pine (456)
Black oak (91)	White oak (58)	White oak (408)
Pine (78)	Blackgum (19)	Blackgum (108)
Blackgum (13)	Post oak (14)	Red maple (75)
Post oak (11)	Black oak (5)	Black oak (71)
Hickory (8)	Sweetgum (3)	Post oak (58)
Sweetgum (5)	Ash (2)	Hickory (48)
Blackjack oak (4)	Cedar (2)	Blackjack oak (37)
Dogwood (3)	Blackjack oak (1)	Dogwood (40)
Elm (3)	Gum (1)	Southern red oak (34)
Gum (3)	Hickory (1)	(many other hardwoods present)
Holly (2)	Holly (1)	
Red oak (2)	Pignut hickory (1)	
Cherry (1)	Red oak (1)	
Chinkapin (1)	Spotted oak (1)	
Mulberry (1)		

^a Common names as provided by the surveyors; count totals are for the entire T2N R18W.

^b Trees per hectare for the “dominant” species on the LWRNA.

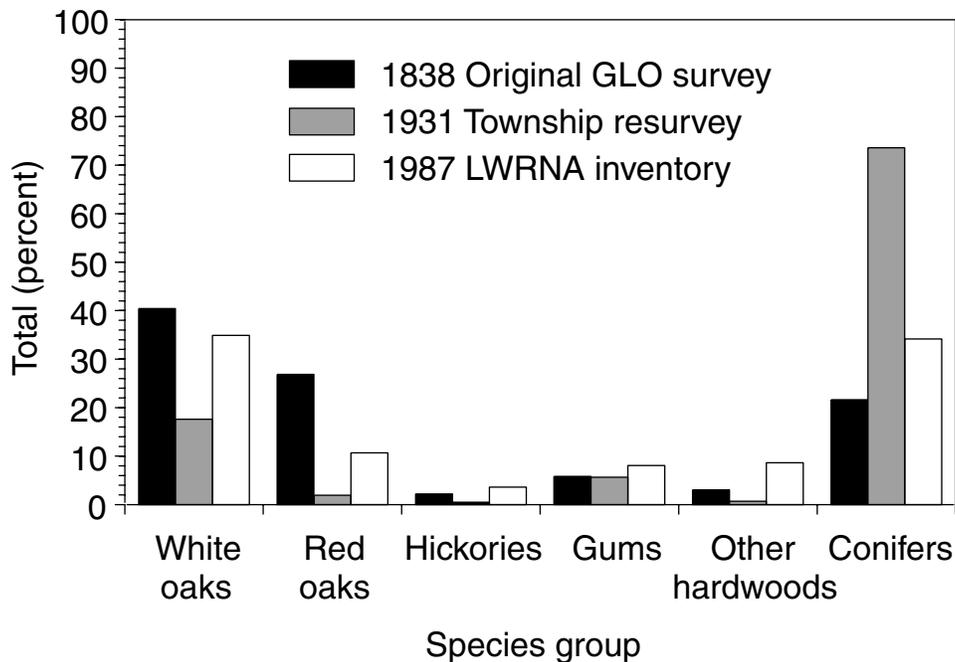


Figure 2—Frequency distribution of major species groups in the original Government Land Office surveys and the 1987 LWRNA inventory (see text for group delineations).

presence just 50 years earlier. Hickories, gums, and other minor hardwood species also increased their stocking, although they still represent a minor component (about 20 percent) of the stand.

DISCUSSION

Comparison of GLO data with Fountain and Sweeney’s work suggests that pine gained more prominence between the early 1830s and 1930, with a concurrent decrease in

oak. Regional forest dynamics changed markedly during this period, especially after commercial logging began early in the 20th century (Shelton and Murphy 1990, Smith 1986). The frequency of hardwoods in the 1838 GLO notes suggests that these hills had undergone a remarkable transformation by the 1930s. Harvesting and fire, coupled with land clearing, probably improved shortleaf pine establishment, resulting in large numbers of small pine being utilized as witness trees by the 1931 resurvey.

However, because of uncertainty in how surveyors actually selected their witness trees, I did not further quantify oak and pine composition. Even though the oldest GLO notes suggested the prominence of oaks and other hardwoods, the surveyors' preferences may have biased tree selection. For example, it is possible that hardwoods were chosen more frequently than shortleaf pine because they contrasted with a pine overstory (Bourdo 1956, Bragg 2003). If so, the abundance of some hardwood species from the initial GLO surveys may exceed their true historical representation.

Other reports, e.g., Smith 1986, disagree with the relative dominance of hardwoods suggested by the GLO notes. Early (pre-1900) observations on the study region indicated shortleaf pine was the dominant overstory species. For instance, Anonymous (1904) reported pine sawtimber volume five times that of hardwoods in the eastern Ouachita Mountains. However, Anonymous (1904) alone is not definitive proof of an informational discontinuity, because this nonrefereed (and even promotional) source may reflect biases that emphasize the commercial potential of the region. Additionally, merchantable sawtimber does not directly translate into stocking proportions, especially if the hardwoods were predominantly small-diameter, poorly formed stems.

Oaks and other hardwoods have probably long held subordinate positions in the Ouachita Mountains of central Arkansas, especially on exposed sites in fire-prone areas. However, given the absence of large-scale catastrophic disturbances like fire or timber harvesting, it is likely that the mixed pine-hardwood overstory of the LWRNA will gradually revert to a hardwood-dominated stand. In a second-growth pine-oak stand near the LWRNA, Shelton and Murphy (1990) reported a noticeable decline in smaller pine size classes and increased representation by white oak, southern red oak, and other hardwoods. However, if borers, sudden oak decline, drought, or similar destructive agents arise, then the LWRNA may develop a greater prominence of hickory, gum, red maple (*Acer rubrum* L.), and other hardwoods.

CONCLUSIONS

Barring a major disturbance, the dominance of closed-canopy hardwood under- and midstories means the existing supercanopy of shortleaf pine will not replace itself. Unless constrained by decline, oaks (especially white and black oak) are poised to replace shortleaf as the pines succumb to age, insects, lightning, and other causes. The long-term preservation of current conditions, i.e., shortleaf pine dominance, at the LWRNA is highly unlikely, but whether or not oaks will reach and maintain their expected importance is less certain.

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**Upland Oak Forest Ecology
and Wildlife Ecology**

UPLAND OAK ECOLOGY AND MANAGEMENT

D.H. Van Lear¹

Abstract—Of the many disturbance factors that shaped hardwood forests in the eastern United States, fire was perhaps the most important. Fires ignited by Native Americans and lightning played a dominant role in sustaining oak (*Quercus* spp.) forests throughout the Central Hardwood Region. Prior to logging at the turn of the last century, fires in the region were mostly light to moderate intensity surface fires. Exclusion of frequent surface fires for over 70 years has changed the character of these previously open forests and contributed to the gradual invasion of oak stands by shade-tolerant, fire-intolerant species. Although upland oaks are more easily maintained on poor quality sites, sustaining oak species on good quality sites is difficult. When canopy-gap type disturbances occur on good sites, oak regeneration is not competitive enough to grow into the mid- and upper canopy. If there is a major disturbance in the overstory of these mixed stands, pioneer shade-intolerant species such as yellow-poplar (*Liriodendron tulipifera*) out-compete oak regeneration and dominate the next stand. Periodic underburning in mixed hardwood stands creates conditions similar to those prior to fire exclusion and are conducive to oak regeneration and establishment. A shelterwood-burn technique has recently been developed that can be used on productive upland sites to enhance the competitive position of oaks in the advance regeneration pool. Oaks are well adapted to tolerate fire and benefit from fire at the expense of their competitors. Foresters can use prescribed fire where feasible to sustain oaks in a variety of ecosystem conditions ranging from fully stocked timber stands to open oak woodlands.

INTRODUCTION

As the Wisconsin ice sheets retreated to the North toward the end of the Pleistocene Epoch, tundra and boreal vegetation that had dominated the Central Hardwood Region began to be replaced by hardwood species. Spurred on by the warming climate and the widespread use of fire by Native Americans, oaks (*Quercus* spp.) gradually dominated the region (Abrams 2002, Carroll and others 2002).

Fire, early man's only tool to manipulate the landscape, has been a major ecological process shaping the pattern, composition, and structure of vegetation in the eastern United States. Frequent fires set by man and lightning kept the forests open and park-like. Fire regimes characterized by frequent, low-intensity burns favored plants adapted to survive these types of fires. Oaks and other fire-adapted species benefitted from this fire regime and were able to out-compete less fire-adapted species and dominate much of the Central Hardwood Region.

Regenerating oaks on productive upland sites has been a major silvicultural challenge for decades in eastern hardwood forests (Carvell and Tryon 1961, Clark and Watts 1971, Loftis and McGee 1993). Could land-use history tell us why oaks cannot be regenerated on good quality sites? We know that fire was a much more dominant factor historically than it is today. In fact, foresters had long considered taboo the use of fire in hardwood management. However, in the last two decades, the use of fire by Native Americans to manage the landscape has become more appreciated (Pyne 1982, Buckner 1983, Pyne and others 1996, Bonnicksen 2000, Carroll and others 2002).

Recent books about oak ecology and management provide excellent treatments of these broad topics (Hicks 1998, Johnson and others 2002, McShea and Healy 2002). Therefore, I will confine my remarks to the fire ecology of upland

oaks and how fire can be used silviculturally to sustain oak forests in various ecological conditions.

LAND-USE HISTORY AND ITS ROLE IN SUSTAINING OAK FORESTS

Man is intimately linked to the distribution and dominance of oak in the Central Hardwood Region. About 12,000 years ago, Native Americans made their way into North America (Williams 1989, Bonnicksen 2000, Carroll and others 2002). They used fire in many ways because it helped them survive and improved their quality of life. Over thousands of years, the American Indian became expert in using fire for various purposes, e.g., for hunting, to concentrate game in convenient areas, to encourage fruit and berry production, to keep the woods open along major corridors of travel, to fire-proof their villages, and for many other uses (Williams 1989, Pyne and others 1996, Bonnicksen 2000). Anthropogenic burning was certainly more important than lightning-ignited fires in shaping the vegetative character of the Central Hardwood Region.

The Native American population of North America has been estimated as high as 18 million at the time of Columbus (Dobyns 1983). Their influence on the eastern forest was far out of proportion to their population density, primarily because of their use of fire (Hudson 1976). Because of their high populations and burning activities, Native Americans ensured that much of the Central Hardwood Region was relatively open woodlands, savannahs, and prairies. The eastern United States in 1500 was a managed landscape and had been for thousands of years (Buckner 1983, Williams 1989, MacCleery 1992, Pyne and others 1996, Carroll and others 2002).

Indians burned frequently, complementing lightning as an ignition source. Their burning extended the fire season beyond the "natural" lightning-fire season of summer. After

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Indian populations plummeted in the 16th and 17th centuries from exposure to European diseases, their level of burning declined and the forest became uncommonly dense (Carroll and others 2002).

Early European settlers displaced the Indians, but continued using fire for many of the same reasons, i.e., to clear the woods of underbrush, to expose nuts, to clear agricultural fields, and to enhance grazing. Not until the early decades of the 20th century were there serious efforts to exclude fire as an ecological process in eastern North America. However, burning was still a common practice into the 1940s and 50s in the Southern Appalachian Mountains and the Ozark Highlands (Pyne and others 1996, Carroll and others 2002).

Widespread attempts to exclude fire, combined with exploitive logging of early successional species, e.g., shortleaf pine (*Pinus echinata*) from the Ozark highlands, enabled the modern oak forest to develop rapidly across much of eastern North America (Dey 2002). An era of fire exclusion had begun that would produce different environments from those that had existed in previous millennia and which would have numerous unexpected consequences (Brose and others 2002).

Now oaks are not being sustained on good quality sites (Healy and others 1997, McWilliams and others 2002). Land-use history — a history based not only on written history (Hudson 1976, Dobyns 1983, MacCleery 1992) but also on nature's history as recorded in sediment cores showing pollen and charcoal distribution for thousands of years (Watts 1983, Delcourt and Delcourt 1987, Carroll and others 2002), clearly demonstrates the important role fire once played in the eastern United States. It is reasonable to conclude that a policy of fire exclusion over much of the past century is a major cause of our inability to regenerate oaks on better sites today. Of course, there are other factors that are important in certain areas, especially overbrowsing by deer (Lorimer 1993). But exclusion of fire, in my opinion, is the primary reason for the disturbing trend of oaks failing to regenerate on good quality sites throughout much of the Central Hardwood Region.

ADAPTATIONS OF OAKS TO FIRE

Fire has been so ubiquitous and exerts such profound influences on the environment that it is reasonable to assume that natural selection favored individuals in populations that could best survive fire (Pyne and others 1996). Plant species that evolved with fire adapted by developing attributes that increased their chances of survival in those environments.

Among the fire-adaptations of oaks is their tenacious ability to resprout repeatedly, after other species have died, from root collar buds following topkill by fire (Waldrop and others 1987). The ability to resprout time after time after their tops are killed would improve oak survival rates because they would continually occupy the same growing space over long periods of time, beyond the elimination of other species.

Oaks have thick bark which insulates their living cambium from the heat of surface fires (Hare 1965). Competing

species such as maples (*Acer* spp.) and American beech (*Fagus grandifolia*) have thinner bark, especially when young, and are quite susceptible to fire damage or mortality.

Because acorns are often buried by squirrels and/or jays (*Sciuridae* and *Corvidae*) and germination is hypogeal, root-collar buds of oaks are well protected from the heat of surface fires (soil is a poor conductor of heat). Many of oaks' competitors, such as yellow-poplar, have seeds that germinate on the soil surface and thus have exposed buds which are more susceptible to mortality from fire (Brose and Van Lear 1998, Brose and others 1999a, Brose and others 1999b). A major reason why oaks tolerate fire better than most competitors is because oak sprouts often originate beneath the soil surface (Burns and Honkala 1990).

Some adaptations not only allow plants to survive fire but also play a major role in predisposing plant communities to recurrent fire (Mutch 1970). Fallen oak leaves are resistant to decay and curl as they dry, providing a highly aerated fuel bed which encourages frequent surface fires. In contrast, leaves of fire-sensitive hardwoods like American beech, yellow-poplar, and maples lie flat on the ground and decay rapidly, preventing a flammable fuel bed from developing. Unless fire-adapted plant communities tend to promote recurrent fire, they are likely to be replaced by non-flammable communities (Bond and van Wilgen 1996).

MAJOR ECOLOGICAL DISTURBANCES AFTER EUROPEAN SETTLEMENT

Europeans began settling the Central Hardwood Region over 300 years ago. Since then, there have been many types of anthropogenic disturbances, including logging, fuelwood cutting, charcoal production, grazing, agriculture, and development in the region (Buckner 1992, Hicks 1998, Dey 2002). Timber exploitation began in the mid 1800s when the steam engine allowed the entire region to be heavily logged. Often harvests were followed by intense and severe fires in the heavy logging debris, which created coppice forests dominated by oaks (Clatterbuck 1991, Dey 2002). These intense and often severe fires differed from fires of previous millennia which, because of their frequency, were generally low intensity burns in light fuels (Carroll and others 2002).

In the early 1900s the chestnut blight (*Cryphonectria parasitica*) was introduced into New York's Botanical Garden. By the late 1930s, the blight had eliminated chestnut (*Castanea dentata*) as an important component in eastern forests, although its snags and downed logs continue to provide habitat for wildlife to this day. American chestnut was dominant in mixed stands throughout much of the Central Hardwood Region occupying a broad swath from the Appalachian Mountains to Arkansas and south into Georgia, Alabama, and Mississippi. Chestnut was one of the most economically, as well as ecologically, important species in the region and was generally replaced by oak forest associations (Hicks 1998, Johnson and others 2002, McShea and Healy 2002). However, on good quality sites in the southern Appalachians, heavily logged chestnut-dominated stands often succeeded to associations dominated by mesophytic species (Vandermaast and Van Lear 2002).

Catastrophic wildfires around the turn of the last century in the Lake States and Rocky Mountains aroused the country's attention and concern. Cutover forests in the southeastern Coastal Plain burned so frequently that forest regeneration was often impossible. Slash fires following logging in the Appalachian Mountains burned severely with devastating offsite effects, such as erosion, sedimentation, and smoke pollution. The public began to see fire as an enemy to be suppressed at all costs (Pyne and others 1996, Johnson and Hale 2002). In the early decades of the 20th century, a policy of fire exclusion began that created ecosystems different from those fire-dependent ecosystems that had existed in previous millennia.

Over-zealous fire exclusion in ecosystems that had previously been fire dependent is a form of disturbance, i.e., a state of disorder which changes the very nature of those ecosystems. Exclusion of fire had many unexpected and undesirable consequences, including endangerment of fire-dependent ecosystems and many species that live in them (Landers and others 1995, Brennan and others 1998, Brose and others 2002). On good quality sites in the southern Appalachians, rhododendron (*Rhododendron maximum*) has encroached on upland sites and now threatens the diversity and productivity of cove forests (Vandermast and Van Lear 2002). The spread of rhododendron is, in part, related to the exclusion of fire in the mountains.

SUSTAINING OAK FORESTS WITH FIRE

Oak forests are in trouble. They are being replaced by other species, especially on good quality sites because of natural succession trends and because we have been unable to consistently regenerate oak species on these sites following harvest. Fire has been excluded in many areas of the Central Hardwood Region. In some areas, unnaturally high deer herds prevent oak regeneration because oaks are preferentially browsed by white-tailed deer (Healy 1997). Insect pests, e.g., the red oak borer, and diseases, e.g., a root rot caused by the fungus *Armillaria*, contribute to the problem of oak decline in the Ozarks (Lawrence and others 2002). Other papers in the proceedings of this conference cover these latter topics, so I will address the use of fire to regenerate oak-dominated stands.

In the dense shade of mature mixed-hardwood stands, oak seedlings and seedling sprouts do not develop into competitive stems either because of poor initial establishment of oak seedlings or the slow juvenile growth of oak advance regeneration if present (Loftis 1983, Abrams 1992, Lorimer 1993, Loftis and McGee 1993). Overstory removal by either partial or complete cuttings often releases well-established shade tolerant regeneration, such as red maple, or facilitates establishment of fast-growing shade intolerant seedlings like yellow-poplar. Oak species generally become a minor component or altogether absent on good quality sites as the new stand develops (McGee 1979, Abrams 1992, Lorimer 1993). Numerous researchers think this pattern of stand succession is a relatively recent phenomena, developing in the past 75 years or so, and is tied to the exclusion of fire from eastern hardwood forests (Little 1974, Van Lear and Johnson 1983, Crow 1988, Van Lear and Waldrop 1989, Abrams 1992, Lorimer 1993).

Repeated surface fires, especially in the growing season, remove much of the mid- and understory strata in mature mixed hardwood stands, reducing shading and providing growing space for oak advance regeneration. Spring fires are especially effective in killing these lower strata trees (Barnes and Van Lear 1998), some of which die gradually over several years. If oak advance regeneration is >½ inch at ground line, it is likely to survive burning by sending up new sprouts. Fire prepares a favorable seedbed for caching of acorns by squirrels and jays (Darley-Hill and Johnson 1981, Galford and others 1989) and may reduce surface soil moisture, which discourages establishment of meso-phytic species (Barnes and Van Lear 1998). Frequent burning may also control insect predators of acorns and new seedlings (Galford and others 1989). All these fire effects create environments that favor oak regeneration on better quality sites.

Because forest ecosystems are complex and fire regimes vary (season, intensity, severity, fire-return interval, etc.), effects of fire in hardwood stands also vary. Single fires in mixed hardwood stands have occasionally created oak-dominated stands (Roth and Hepting 1943, Carvell and Maxey 1969) but sometimes species composition in young stands has been little altered by single fires (Johnson 1974, McGee 1979, Augspurger and others 1987). Many earlier studies, mine included, failed to adequately document fire behavior characteristics and other features of the treatment fires.

Season of burning and fire intensity are important considerations if oak regeneration is to be favored by fire. Season of burning affects sprouting vigor. In the winter when root reserves are highest, hardwoods have the greatest ability to sprout following topkill. In the growing season, root reserves are lower and sprouting vigor is less. Fire intensity is critical because certain species, such as the oaks, can survive higher intensity fires than their competitors (Waldrop and others 1987, Brose and Van Lear 1998).

Fire is, of course, but one disturbance factor that affects vegetation. Fire often works in combination with other environmental forces, especially with wind or ice storms that break up the overstory canopy. When the upper canopy is reduced or removed by wind or ice, ecosystems are predisposed to fire (Myers and Van Lear 1998). Openings in the overstory increase insolation and drying of fuels, as well as favor growth of fine fuels which help carry surface fires.

UNDERSTORY BURNING TO ENCOURAGE OAK REGENERATION

Van Lear and Watt (1993) described a theoretical silvicultural prescription to encourage oak regeneration in the Piedmont of South Carolina by repeated understory burning in mature mixed hardwood stands near the end of the rotation. Barnes and Van Lear (1998) continued this study and found that oak rootstocks in the regeneration layer were increased, root/shoot ratios of oaks were enhanced, and competitive woody species decreased by repeated burning. Understory and midstory density was reduced by about 50 percent. Although boles of small diameter (5 to 10 inches) trees were often damaged by repeated burning, there was

little visible damage to boles of large overstory oaks from these low intensity fires.

Understory burning must be continued at 2-3 year intervals for perhaps 10 years or so before sufficient oaks of competitive size will be present in the advance regeneration. In addition, seed-producing individuals that are vigorous competitors of oak, such as yellow-poplar, should be harvested at the beginning of the burning program. The initial fire will stimulate germination of yellow-poplar seed stored in the duff but subsequent fires will kill these small seedlings. Repeated underburning is handicapped by the expense and risks of multiple prescribed fires (Van Lear and Brose 2002). Nevertheless, if no oak advance regeneration exists in a stand and prescribed fires are feasible, periodic understory burning provides a means to encourage establishment of oak seedlings and seedling sprouts, while reducing competitors.

THE SHELTERWOOD-BURN METHOD TO REGENERATE OAKS

A shelterwood-burn method was recently developed in the Piedmont of Virginia to enhance the competitive position of oak regeneration in such stands (Keyser and others 1996, Brose and Van Lear 1998, Brose and others 1999a).

Although developed outside the Central Hardwood Region, this method may be effective there and should be tested. The initial shelterwood harvest removes roughly half of the overstory basal area, leaving the best dominant and co-dominant oaks. In this first cut, all yellow-poplars are removed. Following this partial harvest is a 3- to 5-year waiting period, during which time the advance regeneration develops. Generally the advance regeneration on good sites will be dominated by species other than oaks. The third step occurs after the waiting period when a relatively hot growing season burn is run through the advance regeneration.

A growing season fire in early spring kills most of the yellow-poplar regeneration and sets back other competitors. Red maple, for example, requires hotter fires to achieve desired mortality rates (Brose and Van Lear 1998). Oak regeneration is favored because oak seedlings/sprouts, many of which have grown to a ground-line diameter >0.5 inch following the initial shelterwood cut, survive the fire by vigorous resprouting from their relatively large root systems.

Oak seedling/sprouts with large root/shoot ratios are capable of vigorous sprouting and growth after the spring burn if adequate light is available, which the fire provides (Brose and Van Lear 1998). In our study of the shelterwood-burn technique in Virginia's Piedmont, density of free-to-grow oaks exceeded 300 stems per acre with high intensity spring fires, while yellow-poplar density was reduced up to 90 percent. Low-intensity winter burns provided little control of yellow-poplar. Summer fires provided substantial numbers of free-to-grow oaks in the medium-high intensity levels, although many of the smaller oak seedlings were killed because they were not of sufficient size to tolerate the heat.

Additional burns may be prescribed if oak regeneration is not adequate after one burn. In many situations within the Central Hardwood Region and beyond, decades of fire exclusion have allowed oak competitors to become so firmly established that oak regeneration may not be as plen-

tiful as desired. Oak dominance of the advance regeneration should increase with repetitive spring burning if such burns are deemed necessary.

A shelterwood cut is the essential first step in this technique because the shelterwood produces oak litter which creates a flammable fine fuel bed capable of carrying the subsequent fire. Clearcutting would produce a forest floor dominated by less flammable foliage. Shading from the shelterwood also prevents yellow-poplar regeneration from growing so large during the interval before burning that it could not be killed by fire (Hane 1999).

Although research on the shelterwood-burn technique was done in the Piedmont where yellow-poplar is the major competitor, other species are serious competitors in the Central Hardwood Region. Competitive species may exhibit either exploitive or conservative ecological strategies, depending upon the type of disturbance, to enhance their chances of survival (Bormann and Likens 1979, Johnson and others 2002). Most oak species are relatively conservative and do not allocate large portions of photosynthate to top-growth following large-scale overstory disturbances, as do many of their competitors.

Differences in developmental patterns probably explain why oaks benefit from the shelterwood-burn method. Yellow-poplar, for example, usually regenerates prolifically following the initial shelterwood cut. Because its seed remains viable for years in the duff and it is a pioneer species, it grows densely and vigorously during the first few years after disturbance and dominates the advance regeneration pool. During this time yellow-poplar regeneration allocates most of its energy to top-growth. Conversely, oak regeneration allocates much of its energy to root growth during the interval between shelterwood cutting and burning (Hane 1999). Oaks are therefore able to sprout vigorously after burning while yellow-poplar can not. Without burning, oak regeneration could not compete with the fast growing yellow-poplar seedlings.

During the 3 to 5 year waiting period, logging slash decomposes and become less hazardous to burn. Heavy logging slash from the initial shelterwood cut resting against boles of residual trees should be lopped or pulled away to prevent bole damage during burning. Distances between residual trees are generally great enough that directional felling can prevent most tops from being in close proximity to boles of residual trees (Brose and Van Lear 1998, Brose and others 1999a). Residual overstory trees can recover from the shock of the initial cut during the waiting period before they are stressed again by burning.

Management Options with the Shelterwood-Burn Method

There are several management options available to land-owners following completion of the shelterwood-burn technique. The first option would be to harvest the shelterwood and release the oak-dominated regeneration. This method of timber management is economically attractive because the initial cut of the shelterwood method produces immediate income. A small portion of the profit is then used to pay for the prescribed burn a few years later. Removal of

the shelterwood after burning is more profitable than the initial cut because the best oaks were retained and probably increased in value during the intervening years before final harvest. However, the shelterwood-burn method can be used to accomplish objectives other than timber management (Brose and others 1999).

The shelterwood-burn method can be used by wildlife managers to sustain hard mast production and provide palatable browse during the regeneration period. The classic structure of the shelterwood can be maintained while stockpiling oak regeneration with periodic burns (Brose and others 1999b). Many upland game and non-game species utilize the mast, browse, and cover in a regenerating shelterwood (Brose and others 1999b, Lanham and others 2000).

The shelterwood-burn method could be used to restore rare fire-maintained ecosystems (Brose and others 1999b). Frequent (1-2 year intervals) growing season burns after the initial shelterwood cut would favor herbaceous vegetation (Bond and van Wilgen 1996) and would gradually reduce the density and size of woody regeneration and create a hardwood woodland or savannah, two increasingly rare habitats in the eastern United States after decades of fire exclusion (Buckner 1983, Pyne 1982, Van Lear and Waldrop 1989, Abrams 1992).

Would a regeneration technique developed in the Piedmont of Virginia be successful in the Central Hardwood Region? Some fire research suggests that it would. Repeated burning in oak-pine communities on xeric sites in the Cumberland Plateau reduced regeneration of red maple and other non-oak species and promoted chestnut oak regeneration (Arthur and others 1998). Hot fires in mountain laurel thickets in the Northeastern United States opened overstory canopies, i.e., a disturbance similar to a shelterwood harvest, and allowed oak reproduction to grow past the dense shrub layer (Moser and others 1996).

FELL AND BURN SITE PREPARATION FOLLOWING COMMERCIAL CLEARCUTTING

Phillips and Abercrombie (1987) described a site preparation technique used in the Southern Appalachians following commercial clearcutting (removal of merchantable stems only) to develop pine-hardwood mixtures. The technique consisted of spring felling of residual (unmerchantable) stems after leaf-out, followed by an intense, but not severe, summer broadcast burn. Pine species were then planted at relatively wide spacings to maintain a pine component among the sprouting hardwoods.

Spring felling of residuals followed by burning reduced sprout growth of competing hardwood species more than that of oak sprouts. The intense broadcast burns used in this technique often cause new oak sprouts to originate from below the mineral soil surface and result in well-anchored stems. These results indicate that intense broadcast burns following harvest should increase (or at least maintain) the oak component in the new stand.

Care must be used in prescribing broadcast burns on poor quality sites. If the burns consume the entire forest floor,

severe erosion and nutrient loss may result. These negative consequences can generally be prevented if burning is done when the lower layers of the forest floor and root mat are damp. Such conditions often occur in the Southern Appalachians a few days after a soaking rain (Phillips and Abercrombie 1987).

CONCLUSIONS

Until the early decades of the past century, fire played a major role in maintaining oak-dominated forests in the eastern United States. As a result of fire exclusion and, in some cases, other factors, such as deer browsing, oak forests on good quality sites are being replaced by other species. On poor quality sites oaks are maintaining themselves.

Upland oaks are well adapted to regimes of frequent low-intensity surface fires. Because of these adaptations, prescribed fire can be used to accomplish different management objectives, ranging from establishment of oak regeneration to restoration of open oak woodlands. However, foresters have been reluctant to use prescribed fire in hardwood stands because of fear of damaging boles of high-value trees.

Practical silvicultural prescriptions using fire for oak regeneration have been lacking. It is now understood that periodic understory burning in mature mixed hardwood stands creates environmental conditions, such as reduced low shading and less competition, which favor oak regeneration. In addition, a shelterwood-burn method has recently been developed for good quality sites which have proven successful in improving oaks' competitive position in the advance regeneration pool in mixed hardwood stands. This technique reduces the density and vigor of oaks' competitors, especially when growing season burns of relatively high intensity are used, and develops adequate numbers of vigorous free-to-grow oak stems in the advance regeneration pool.

Forest managers will need to use prescribed fire or a fire surrogate (herbicide) to sustain oaks on good quality sites. The land-use history of the Central Hardwood Region and the fire ecology of oaks tell us that fire and oak forests go hand in hand. If we study our history (as recorded both by man and by nature) carefully, we will understand that the region has been a managed landscape for millennia and fire was the primary management tool. It played a major role in sustaining oak forests and will need to be used now and in the future to favor oaks.

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OAK DISPERSAL SYNDROMES: DO RED AND WHITE OAKS EXHIBIT DIFFERENT DISPERSAL STRATEGIES?

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Abstract—We provide an overview of the ecological and evolutionary interactions between oaks and several of their dispersal agents, and review a series of studies that demonstrate how various acorn characteristics affect feeding and caching decisions of these animals, which in turn may influence oak dispersal and establishment. We demonstrate that acorns of red oak species show a marked dispersal advantage over those of various white oak species. From this, we predict that red oaks are likely to establish in a wider range of micro-environments and at greater distances from maternal sources, whereas white oaks should be limited to establishment closer to maternal sources. This in turn should influence the spatial pattern of oak recruitment and seedling physiological traits. We discuss current efforts to test this Differential Dispersal Hypothesis (DDH) and its implications for various aspects of oak ecology including masting, seedling physiology, and regeneration.

INTRODUCTION

Although oaks dominate many forest ecosystems worldwide (Barnes and others 1998), several aspects of oak ecology remain poorly understood including oak regeneration and masting (McShea and Healy 2001). Animals that eat and disperse acorns, such as squirrels, mice, and jays may play a pivotal role in oak forest dynamics (Jones and others 1998, Ostfeld and others 1996), influencing regeneration both positively and negatively through their roles as seed dispersers and predators. The ecology and evolution of oaks is likely to be strongly dictated by the behavioral decisions of these animals. Understanding oak forest ecosystems may therefore require multidisciplinary approaches that determine how the behavioral ecology of animals affects oak forest characteristics including levels and patterning of seedling recruitment and plant physiological traits. Our research attempts to examine such linkages by focusing on behavioral responses to various acorn characteristics as a starting point.

MECHANISMS OF OAK DISPERSAL

Acorn Characteristics and Oak Dispersal

The behavior of most acorn consumers and dispersers follows directly from several key characteristics of the two major subgenera of oaks in North America (Kaul 1985): the white oak group (hereafter WO, subgenus *Quercus*, formerly *Leucobalanus*) and the red oak group (RO, subgenus *Erythrobalanus*). Acorns of WO species contain low levels of both tannins (2 percent by mass) and lipids (5-10 percent) and usually germinate in the autumn, during or shortly after seed fall. Acorns of RO, in contrast, possess more tannins (6-10 percent) and lipids (18-25 percent) and usually require cold stratification to break dormancy, at least in temperate regions. In the following sections we review several lines of

investigation that collectively demonstrate the influence of these acorn characteristics on the feeding and caching behavior of acorn consumers, and ultimately, the reciprocal effect of such behavioral decisions on oak dispersal and establishment.

Acorn Food Preferences

The differences in lipid and tannin levels between WO and RO acorns have long been considered primary determinants of feeding preferences of many avian and mammalian acorn consumers. Lipid levels represent the primary source of digestible energy in acorn cotyledon and are thus the reason that acorns are so highly sought for food by >150 species of wildlife (Van Dersel 1940). However tannins, a group of water soluble phenolic compounds common in acorns, readily bind to salivary and digestive enzymes reducing both their palatability and their digestibility (Robbins and others 1987, Chung-MacCoubrey and others 1997). Thus when selecting between acorn types for food, most species are faced with a trade-off between RO acorns that are high in energy but unpalatable and others (WO) that contain significantly less energy but are far more palatable and digestible (Smith and Follmer 1972).

Attempts to determine whether mammals prefer RO or WO acorns have produced varying results depending on study conditions (Lewis 1980, Smith and Follmer 1972). This controversy was largely resolved in 1986 by Smallwood and Peters who examined the feeding response of eastern gray squirrels to artificial acorns made from ground cotyledon of *Q. alba* acorns to which varying amounts of tannin and lipid were added. By presenting free-ranging gray squirrels with these artificial acorns, they found that gray squirrels selected acorns low in tannin levels in autumn when energy

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requirements were low and food was relatively abundant. In contrast, in the winter when energy requirements were high, squirrels selected artificial acorns with higher lipid levels even when they contained higher amounts of tannin (Smallwood and Peters 1986).

Early Germination in WOs and Embryo Excision

The behavior of early germination in WO acorns presents a second problem for acorn consumers. Rapid autumn germination in many WOs, occurring in some species while acorns are still attached to the tree (Steele pers. obs.), involves the rapid transfer of energy into a taproot that is high in cellulose and indigestible for most granivores (Fox 1974). Early germination in WO species likely represents an adaptation to prevent seed predation by granivorous mammals and birds (Barnett 1977, Steele and Smallwood 2001), and perhaps larval insect predators (e.g., *Curculio*) that begin feeding on acorns before they mature. For mammals, birds, and even some insects early germination greatly limits the availability of WO acorns as food in the autumn. Early germination means that if not eaten soon after seed fall, much of the energy of the WO crop will no longer be available to seed consumers. Moreover, if whole intact WO acorns are stored, it is likely that such energy stores would be lost as these acorns continue to produce taproots during periods of warmer weather.

At least one group of mammals—the tree squirrels (*Sciurus*)—appear to have overcome this problem with the behavior of embryo excision (Fox 1974, 1982; Pigott and others 1991). Eastern gray squirrels, for example, are known to carefully remove the radicle and excise the embryo from the apical end of WO acorns with their incisors prior to caching these acorns (Fox 1982, Pigott and others 1991). Recently we reported that this behavior is quite common, and that WO acorns with excised embryos remain in tact in the scatter hoards of squirrels for up to six months (Steele and others 2001b). Several observations also suggest that this behavior may be an adaptation unique to the genus *Sciurus*. We have observed the behavior in at least two other species of tree squirrels (*S. niger* in the midwestern U.S. and *S. auerogaster* in central Mexico), but have failed to observe any such behavior in at least four other species of small mammals, all of whom otherwise show similar feeding and caching responses to acorns (see below). Recently we presented acorns to naïve captive raised eastern gray squirrels that possessed no previous experience with acorns. The animals cached dormant RO acorns over those of WO, removed the radicles of germinating WO acorns, and on occasion excised or attempted to excise the embryos of WO acorns (Steele and others, unpublished data). We argue that this behavior is likely unique to the tree squirrels and that there is a strong innate basis for the behavior.

Caching Responses and Acorn Perishability

Both the behavior of embryo excision and the selective consumption of WO acorns in autumn suggest that some acorn consumers may be sensitive to acorn perishability due to germination. In fact, Smallwood and Peters (1986), in their analysis of acorn preferences of gray squirrels, predicted that squirrels might selectively cache RO acorns over those of WO, and that they may use tannin as a cue to

identify less perishable RO acorns. Over the last decade, we have fully verified this first prediction with two series of experiments in which we have presented small mammals with RO and WO acorns. In the first, we directly observed free-ranging gray squirrels and recorded their feeding and caching decisions. The second experiment, repeated many times under a variety of conditions, involved selective provisioning of granivorous mammals with metal-tagged acorns (e.g., Steele and others 2001b). Following their dispersal, metal detectors were used to relocate the tags and determine those acorns cached and those eaten, as evidenced by discarded tags. In all such experiments we found that small mammals selectively dispersed and cached RO acorns and consistently ate those of WO species. These experiments, coupled with several others conducted on captive mammals (e.g., southern flying squirrels, white-footed mice) lead us to conclude that selective dispersal and caching of RO is a behavior common to most scatter-hoarding mammals in Eastern deciduous forests. (Although bluejays (*Cyanocitta cristata*) are also important dispersal agents of oak, especially over long distances (>1 km), most studies conclude that they selectively disperse primarily RO species with smaller acorns (Darley-Hill and Johnson 1981, Johnson and Webb 1989, but see Bossema 1979, Monsandl and Kleinert 1988 for dispersal by European jays)).

In another series of experiments we sought to determine specific cues that small mammals use to determine which acorns to eat and which to disperse and cache. Hadj-Chikh and others (1996) addressed this question by presenting free ranging gray squirrels with pairs of acorns that varied with respect to several characteristics (i.e., size, perishability due to germination schedules, fat and tannin levels). They produced overwhelming support that the animals were responding to acorn perishability over any other factor, including tannins. Likewise, in a related experiment, Steele and others (1996) found that tree squirrels selectively cache sound acorns over those infested with insect larvae, which the animals instead consume along with the larvae. Together these results indicate that tree squirrels, and perhaps other acorn consumers, rely on acorn perishability to make caching decisions.

More recently we also have found that tree squirrels can distinguish between dormant and non-dormant RO acorns even when the non-dormant acorns exhibit no physical signs of germination (Smallwood and others 2001, Steele and others 2001a). Moreover, by manipulating acorn chemistry and creating artificial acorns with one type of pericarp (WO or RO) that contain ground RO or WO cotyledon (with varying concentrations of fat and tannin), Steele and others (2001a) showed that squirrels only cache those artificial acorns constructed of RO pericarps, regardless of their contents. However, when these RO pericarps are first soaked in acetone (to potentially control for chemical cues in the pericarp), gray squirrels consistently consume these acorns. These results point to a chemical cue (or the absence of one) in the pericarp that may be used by the animals to identify dormant, non-perishable seeds (Steele and others 2001a). Future efforts are directed at comparing the chemical profiles of dormant and non-dormant acorns and determining whether squirrels detect a dormancy cue or simply respond to damaged packaging (i.e., the pericarp).

Partial Consumption of Acorns

In addition to selectively caching RO acorns, small mammals and several other acorn consumers, selectively consume portions of individual acorns in a manner that may also influence dispersal and establishment of the oaks. Steele and others (1993) found that several vertebrates as well as weevil larvae (genus *Curculio*) selectively feed on the basal portion (proximal end) of several species of RO acorns, especially when acorns and other food are abundant (Steele and others 1993). Each vertebrate species uses a markedly different technique for opening acorns, but each frequently consumes only 10-40 percent of the basal portion of the cotyledon.

Because the acorn embryo (< 1 percent of the biomass of the acorn) is located in the extreme apical end of the fruit, many of these partially eaten acorns can still germinate. In greenhouse experiments, for example, germination rates are as high or higher for partially eaten acorns as they are for intact seeds (Steele and others 1993). In behavioral experiments, Steele and others (1998) also found that gray squirrels often dispersed and cached the potentially viable apical fragments. And, although germination and establishment rates of partially eaten acorns in the field are substantially lower than those of whole acorns, these observations suggest that the ability to survive partial predation may represent a means by which several RO species sometimes escape seed predation. We suggest that in the life of an oak (150 or more years) infrequent establishment as a

result of partial acorn consumption need only occur rarely for this to represent a successful reproductive strategy.

Tests of alternative hypotheses to explain the underlying causes of the behavior point to a suite of chemical and physical traits that may collectively promote partial consumption and subsequent survival of RO seeds. Steele and others (1993) found that tannin levels (as measured by protein binding capacity) are significantly higher in the apical half of the acorns of two RO species, where the embryo is located. More recently, several of us also found that both lipid levels and Na levels are significantly higher in the basal half than the apical half of three additional species of acorns (Steele and others, unpublished data). Consequently, the top of the acorn may not only be more palatable and digestible because of lower tannin levels but may also contain more energy (lipid), and an important nutrient (Na), often limiting for herbivorous mammals such as tree squirrels (Steele and Koprowski, 2001 and references therein). In other experiments, Steele and others (1998) have shown that although partial acorn consumption is not influenced by the thickness or presence of the pericarp, the shape of the acorn can affect the behavior. When acorns are shelled and the cotyledon is carved so the basal and apical ends of the acorn are reversed, tree squirrels begin eating from the true apical end of the seed (which looks like the basal end). Thus it appears several physical and chemical characteristics may act synergistically to promote partial consumption of the basal half of acorns and subsequent survival of these damaged fruits.

Table 1—Overview of characteristics of RO and WO acorns, behavioral responses to these characteristics by acorn consumers, and the influence of these responses on the oaks

Acorn characteristics	Acorn type	Response and influence on oaks	References
Low tannin, low fat	WO	Selective consumption of WO in autumn	Smallwood and Peters 1986
High tannin, high fat	RO	Selective consumption of RO in winter Selective caching of RO for winter	Smallwood and Peters 1986 Smallwood and Peters 1986
Early germination	WO	Consumption of acorns Embryo excision by tree squirrels	Hadj-Chikh and others 1996 Steele and others 2001a Fox 1982, Pigott and others 1996 Steele and others 2001a
Delayed germination	RO	Selective scatter hoarding of RO Potential for far greater dispersal in RO	Hadj-Chikh and others 1996 Smallwood and others 1998
Insect Infestation	RO and WO	Selective consumption of infested acorns Selective scatter hoarding of RO only	Steele and others 1996
Chemical gradients in acorns	RO and WO	Partial consumption of RO only and subsequent survival of damaged seeds	Steele and others 1993 Steele and others 1998
Acorn shape	RO	Partial consumption of RO	Steele and others 1998
Acorn size	RO	Selective long distance dispersal of smaller-seeded RO by jays Selective scatter hoarding of larger-seeded RO by tree squirrels	Darley-Hill and Johnson 1981 Steele and others unpub. data

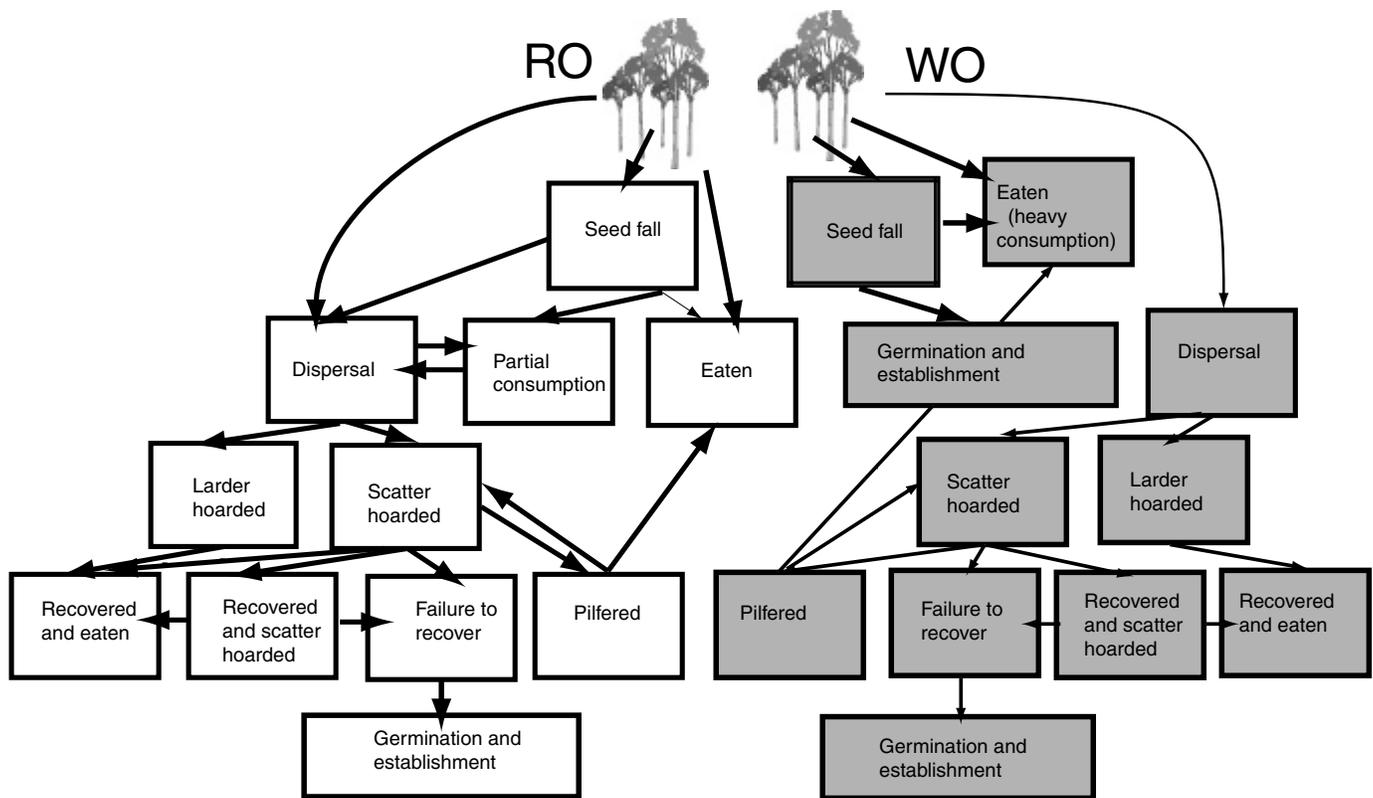


Figure 1—Acorn fate diagram for species of red oak (open rectangles) and white oak (shaded rectangles). The width of arrows is proportional to the probability of the corresponding event.

SYNTHESIS, IMPLICATIONS, AND FUTURE DIRECTIONS

Acorn Fates and The Differential Dispersal Hypothesis (DDH)

The studies reviewed above collectively point to a marked contrast in dispersal strategies of the two primary groups of oaks in North America. Table 1 summarizes the major behavioral responses of avian and mammalian agents of oak dispersal to the different characteristics of RO and WO acorns. Figure 1 is a seed fate diagram that integrates these various responses.

The obvious conclusion to follow from these summaries is that acorns of RO have a significant dispersal advantage. RO acorns are dispersed greater distances from their sources, cached more often in a wide variety of environments, and even show the ability, under some circumstances, to escape partial predation. Acorns of WO, in contrast, should show short dispersal distances and may be in fact adapted for rapid germination near or under parent trees. Although most of our studies have been conducted in eastern deciduous forests, we predict that because of the consistent differences between RO and WO acorns across North America, this phenomenon of differential dispersal is likely to occur throughout temperate forests of North America. If in fact RO and WO species exhibit contrasting dispersal syndromes, several important implications may follow.

Differential Dispersal and the Spatial Arrangement of Oaks

One likely outcome of these contrasting dispersal strategies is a significant difference in the spacing of RO and WO seedlings (Smallwood and others 1998, Steele and Smallwood 2001). RO seedlings are likely to establish at greater distances from parents and thus become more widely spaced; WO seedlings should be clumped near or under parent trees. In an initial test of this hypothesis, Smallwood and others (1998) measured the distribution of seedlings and adult trees of several oak species in the same forest plot to construct best-fit, putative seedling shadows using the computer models of Ribbens and others (1994). The two WO species studied (*Q. alba* and *Q. prinus*) had short truncated seedling distributions and extensive clumping of seedlings within a few meters of the parent. In contrast, the two RO species (*Q. rubra* and *Q. velutina*) showed no clumping and seedling shadows of RO extended much farther than those of WO.

Although results of Smallwood and others (1998) support the DDH, they demonstrate the expected pattern of seedling distribution for only one site. We are currently examining seedling distributions for six additional oak forests throughout eastern North America to determine the consistency of these findings. In addition Smallwood's results are derived from computer models that generate expected distributions in relation to putative, not definitive, parents. To more definitively determine seedling-parent distances, we are currently conducting parentage analysis of seedlings (via microsatel-

lite DNA fingerprinting) in several managed and old-growth stands of oak in the central and eastern U.S. Although the final outcome of these genetic analyses is not yet available one of two general conclusions is likely.

If the molecular analyses ultimately show greater dispersal of RO seedlings than WO as predicted, these contrasting dispersion patterns are likely to result in two sets of alternative cascading effects for the two subgenera of oaks. Assuming the microenvironment beneath parent trees is both more shaded and exhibits less variability in microsite conditions, white oak seedlings would then be expected to be more shade tolerant, less capable of colonizing new micro-environments, and more competitive than RO seedlings (reviewed by Steele and Smallwood 2001). Currently we are testing several of these predictions.

If, on the other hand, the molecular results fail to support the hypothesis by showing white oak seedlings to be widely dispersed, as preliminary results suggest, the most obvious question to follow will be how are white oaks dispersed? Perhaps seedlings exhibit different distributions than seeds because of strong differential survival of rarely dispersed seeds. White oaks may therefore be more dependent than ROs on such rare events, the occasional acorn that is carried and dropped, or the exceedingly rare occasions when whole WO acorns are scatter-hoarded and subsequently forgotten. Perhaps in the life of an oak such rare events are, simply, the rule.

Differential Dispersal and Masting in Oaks

A second implication to follow from our behavioral studies, regardless of the molecular findings, concerns the masting patterns in RO and WO species. Masting is the synchronized, episodic production of seeds by one or more tree species in one year, followed by widespread crop failure in others. Masting is common in oaks and considered by many as a genetically influenced factor affecting their dispersal and establishment (Crawley and Long 1995, Koenig and Knops 2001, Sork and others 1993). In a recent review Koenig and Knops (2001) concluded that masting in oaks is an adaptive response that is best explained by the predator satiation hypothesis. This hypothesis argues that mast failures serve to decrease seed predators, while good crop years result in satiation of seed predators and seedling establishment.

Koenig and Knops (2001) also note, however, that the most significant evidence against the predator satiation hypothesis for oaks "...is the lack of synchronization in masting behavior among species within a community, in particular between species requiring different numbers of years to mature acorns" [e.g., RO and WO species]. We argue that such asynchrony between RO and WO species (especially within a community) is expected because of differential treatment of WO and RO acorns by acorn consumers. Although ROs clearly would benefit from synchronized masting with WOs, since WO acorns could then satiate predators while RO acorns were dispersed, WOs may have no advantage in masting with ROs and may potentially be at a disadvantage of synchronizing its mast with species that are preferred for caching. This could potentially explain some asynchrony in acorn masting as WOs evolve to "escape" masting with RO.

We have tested this prediction by simulating RO and WO acorn abundance and found that significant scatter hoarding of WO acorns only occurs when these acorns are abundant and ROs are not (Steele and others, unpublished data). Because of the extreme susceptibility of WO acorns to predation, we also expect seed fall patterns within a season to differ between the two oak groups, with WO species showing rapid seed fall and RO species extending their release of acorns over longer periods. We are currently testing these hypotheses by conducting a meta-analysis of acorn production studies.

In conclusion, seed consumers have the potential to affect such wide-reaching factors as plant spatial patterns, physiological traits, and degree and timing of acorn masting. Understanding the degree to which these behaviors influence oak dynamics may prove critical for effectively managing oak ecosystems in the face of such threats as forest fragmentation and climate change.

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THE KEYSTONE ROLE OF OAK AND HICKORY IN THE CENTRAL HARDWOOD FOREST

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Abstract—Communities of the central hardwood forest have been dominated primarily by oak and hickory for the past 5000 years. Over this time period, they have become keystone species within the ecosystem and are of major importance in maintaining biodiversity. Not only do the large number of oak and hickory species by themselves contribute to community richness but they are known to provide food and support for a substantial number of wildlife species. Moreover, the structure created by dominance of oak and hickory in the forest community provides an environment for a highly diverse herbaceous understory. Data from oak-hickory stands with a maple-beech understory of saplings and small trees show a 90 percent drop in photosynthetically active radiation (PAR) at ground level accompanied by a 35 percent increase in litter weight compared to stands without an understory. The result is over a 90 percent drop in species richness and cover. This drastic loss of biodiversity, foliage, and fruit has serious implications for insect and bird populations and also suggests a potential for increased soil erosion and loss of nutrients. Extensive research into the loss of biodiversity is advised.

INTRODUCTION

Various oak (*Quercus*) and hickory (*Carya*) species have been the dominant components of the central hardwood forest for the past several millennia. Although the last glacial advance (Wisconsin Stage) did not extend much beyond Wisconsin and Michigan, it had a major influence on forest vegetation. Delcourt and Delcourt (1991) and Franklin (1994) have summarized the research on vegetation change since glacier degradation. Analysis of pollen profiles from bogs and information from geology, archeology, and anthropology indicate that the central states forest went through a progression of vegetation types. When the glacier was still advancing about 16,500 years BP, spruce (*Picea*) and pine (*Pinus*) dominated much of Wisconsin, Illinois, Indiana, and Ohio. From about 13,500 to 11,500 years BP, the forest was a mixture of hemlock (*Tsuga*), pine, spruce, fir (*Abies*), oak, birch (*Betula*), elm (*Ulmus*), ash (*Fraxinus*), maple (*Acer*), and beech (*Fagus*). By 10,000 years BP, mixed hardwoods were dominant within the forest because of the effects of the northward movement of the warm humid tropical airmass.

As the glacier melted between 10-11,000 and 9,000 years BP, a variety of oak species became the dominant forest species. The climate continued to warm and become drier between about 8,700 and 5,000 years BP. This period is known as the Hypsithermal. Concurrent with the warming of the climate was an increase in the occurrence of fire that probably was accentuated by the increased movement and activity of the Early American peoples. During this period, prairie expanded eastward well into Ohio and possibly farther east, and oak and hickory probably were the dominant woodland species. Transeau (1935) noted the existence of the prairie peninsula during the late 1700s and early 1800s. The present plant communities of the Tennessee Barrens are considered by Anderson and Bowles (2000) to be an extension of tall grass prairie. During the Hypsithermal, mixed oak and mesophytic hardwoods were restricted to coves and ravines.

After 5,000 years BP, precipitation levels increased so that oak expanded on uplands while mesophytic hardwoods, such as sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), American Beech (*Fagus grandifolia* Ehrh.), basswood (*Tilia americana* L.), and ash (*Fraxinus*), replaced oak in ravines and stream terraces. At that time, mesophytic species may also have been important on upland sites.

Later, succession to mesophytic species on upland slopes and hills was slowed due to the use of fire and clearing of land by the Woodland (2,500-1,000 years BP), Mississippian (1,000-500 years BP), and Native American Indians (<500 years BP). The Woodland culture depended largely on gathering of nuts, berries, and other wild plant foods such as roots. Southern pines (shortleaf, *Pinus echinata* Miller; Virginia, *Pinus virginiana* Miller) appeared in the forest during this period probably due to increased levels of fire. The Mississippian culture introduced agriculture into the central states; growing of foods such as corn, beans, squash, and pumpkin supplemented fishing and gathering of nuts and berries. Permanent villages often were constructed along major rivers and tributaries. Slash and burn agriculture and sedentary farming were common practices (Franklin 1994). The Native American Indians continued these practices and used fire to clear forest around their camps. Their reasons for use of fire included clearing of brush for improved hunting with bow and arrow, and better visibility for protection against enemy sneak attacks.

At the time of the original land survey in 1806-10, oak and hickory dominated the upland communities of most of southern Illinois including many north slopes and stream terraces (Fralish and others 1991, Fralish and others 2002, Sauer 2002). Forest ecologists universally agree that an active presettlement fire cycle (before ca. 1810) maintained the oak-hickory ecosystem. Abrams (1992) makes a strong case for the relationship between fire and development of oak dominated forests. The writings of early travelers reported relatively open woods and the frequency of fire.

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RECENT DISTURBANCE REGIMES AND OAK HICKORY

A new disturbance regime in the Central Hardwood Forest Region began at the time of settlement around 1810 to 1820. Fralish (1997) reported that the level of forest disturbance was reduced with settlement, and in some of the more eastern populated areas, this reduction probably was necessary to protect farms, towns, and other property including woodlots. However, during the period of European settlement and development in southern Illinois (1810-1930) and probably surrounding areas and states, the general level of disturbance was high as large land areas were cleared for agricultural crops. Fire used to clear land escaped in the woods so that the level of disturbance remained about that of presettlement time or was greater in some areas (e.g., Illinois Ozark Hills) as landowners and farmers continued to disturb the forest by various activities associated with settlement including heavy timber harvesting for buildings, railroad ties, and other construction, and grazing by free roaming cattle and pigs. In 1920, Miller reported that from the top of Bald Knob (a high point in the Illinois Ozark Hills), he could not see the Mississippi River because of smoke from six different wild fires. This level of disturbance maintained the oak-hickory component of the present forest at about that of the presettlement forest. Based on an analysis of presettlement witness tree records of the Land Office survey, McArdle (1991), and more recently, Fralish and others (2002) found that the amount of oak, hickory, and yellow-poplar in the present (Illinois Ozark Hills) forest was somewhat greater than in presettlement time suggesting a slightly greater level of disturbance during the period the present mature forest community was established as seedlings.

This disturbance regime abruptly ended and a new one began when fire protection laws were instituted in the late 1920s, and further, after large land areas were purchased for state and federal forests and parks developed in the 1930s and later. Grazing on private property and timber harvesting on national and state forest land continued but the beneficial effect of fire was absent. Since the passage of fire control laws and the cessation of wild fire, and the general protection of the ecosystem beginning in the late 1920s and early 1930s, oak and hickory trees have continued to grow while few seedlings reached sapling size before dying. Because large forested areas have remained undisturbed for the past 70+ years, scattered stems of fire-intolerant but shade tolerant species such as sugar maple, red maple, and American beech have grown to tree size and become major seed source. Now forest communities are rapidly converting from mid-successional oak and hickory species to shade tolerant climax mesophytes with a concurrent loss of biodiversity.

There is little doubt that near total absence of fire has permitted the development of this classical secondary successional process, particularly on mesic sites in large areas of the central hardwood forest (Interior Low Plateaus, Central Lowlands, and Ozark Plateaus). Replacement of high quality stands of oak and hickory by mesophytes has been reported for stands in Pennsylvania (Downs and Abrams 1991), Ohio (McCarthy and Wistendahl 1988, McCarthy and others 1987, Cho and Boerner 1991,1995),

Indiana (Myers and others 1983, Parker and others 1985, Parker and Sherwood 1986, Ward and Parker 1989), Kentucky and Tennessee (Fralish and Crooks 1988, 1989, Kettler 1990, Fralish and others 1993, Franklin and others 1993), Michigan (Host and others 1987, Hammett and Barnes 1989), Wisconsin (Menges and Loucks 1984), Missouri (Kucera and McDermott 1955, Anonymous 1983, Nigh and others 1985a, 1985b, Pallardy and others 1991), Iowa (Countryman and Miller 1989) and as far west as Kansas (Abrams 1986). In the center of the central hardwood region, a similar pattern has been reported for forest communities in northern Illinois (Wilhelm 1991), central Illinois (Boggess 1964, Boggess and Bailey 1964, McClain and Ebinger 1968, Anderson and Adams 1978, Adams and Anderson 1980, Ebinger and Newman 1984, Lehnen and Ebinger 1984, Ebinger 1986, Landes and Ebinger 1991, Edgington 1991), and in southern Illinois (Harty 1978, Schlesinger 1976, 1989, Fralish 1988, 1997, Fralish and others 1991, McArdle 1991, Shotola and others 1992, Schildt 1995, Helmig 1996). For the whole of Illinois, Iverson (1989) reported a 4,119 percent increase in the maple-beech forest type from 24,800 acres to 1,046,400 acres between 1962 and 1985.

Given time, the dense shade created by a closed canopy of shade tolerant mesophytic species will eliminate the oak and hickory by preventing seeding establishment and survival. Because oak and hickory have dominated the forest for thousands of years, the life cycle and ecological requirements of numerous other plant and animal species have become entwined with the existence of oak and hickory. Thus, oak, and to a lesser extent hickory, have become keystone species.

THE KEYSTONE SPECIES CONCEPT

A keystone species has been defined as a species (or group of species) that should be conserved because it makes an unusually strong contribution to community structure, maintains critical or key ecosystem processes, or has a disproportionately large effect on other species (Meffe and Carroll 1991) or on the persistence of other species in the community. A "key process" is a critical ecosystem function that controls ecosystem characteristics (Meffe and Carroll 1991). A keystone species may be of several types, such as a major producer, predator, prey, or mobile link species (e.g., pollinators). Either a single species or a group of species may function as a keystone species. It follows, therefore, that keystone species management is management directed toward ecologically important species as a surrogate for managing for all species in a [forest community or] ecosystem (Meffe and Carroll 1991). One function of a keystone species may be to support other forest species and maintain high biodiversity (species richness). High species diversity may promote stability at the ecosystem level because species usually vary in their tolerance to natural perturbation (e.g., fire) and anthropogenic stressors. Stressors may be single or multiple. As the number of independent stressors with different modes of action increases, there will be fewer resistant species with the potential to survive or increase under the influence of an altered environment (Breitburg and others 1998, Bond 1994). An altered environment includes the absence of fire in the fire-dependent oak-hickory forest.

However, depending on the type of ecosystem, it may be difficult to identify a keystone species in some ecosystems. In the central hardwood forest, there is sufficient evidence to classify oak and hickory species as keystones. A substantial number of wildlife species are not the only biota dependent on these species, but as will be shown later. Although large in number, oak and hickory species are relatively similar in their tolerance to natural and anthropogenic stressors, and thus, as keystone species, the absence of fire combined with invasion by mesophytic species become major stressors for oak-hickory forest both as a community and ecosystem. These two stressors (no fire, succession to mesophytes) are combining to eliminate the once strongly dominant keystone oak and hickory.

KEYSTONE CHARACTERISTICS OF OAK AND HICKORY

In the central hardwood forest, it is apparent that oak and hickory, when viewed in the light of changes that are occurring with invasion of maple, beech and other mesophytes, create a community structure and environment that maintains critical ecosystem processes, and has a disproportionately large effect on other species, particular on the persistence of other species in the community. It is well known that the production of mast (nuts from trees) is important to a substantial number of wildlife species, but for other living organisms, such as the highly diverse herb layer and oak and hickory seedlings and saplings, crown density and canopy structure are important.

Keystone species functions may deal with factors limiting production such as water, light, and nutrients (Vogt and others 1997). In the absence of a canopy created by an invasion by sugar maple, American beech, and other mesophytes, the structure of a mature or nearly mature (age >115 years) oak-hickory forest is typically even-aged with a single high, relatively thin overstory canopy easily penetrated by photosynthetically active radiation (PAR). However, level of PAR (photosynthetic photon flux density) varies with overstory structural characteristics that in turn vary with soil and topographic conditions. Photosynthetic photon flux density decreases rapidly with increasing depth of tree crowns (Kozlowski and Pallardy 1997).

On xeric sites (south, southwest, and west rocky slopes), post oak (*Quercus stellata* Wang.), blackjack oak (*Quercus marilandica* Muench.), southern red (*Quercus falcata* Michx.), scarlet oak (*Quercus coccinea* Muench.), white oak (*Quercus alba* L.), and black oak (*Quercus velutina* Lam.) trees are generally deformed as well as short (maximum height about 45 feet), have large openings in the individual crowns, and are widely spaced so that canopy closure may be only 35-50 percent in these woodlands or barrens (Fralish and others 1999); basal area (25-40 sq.ft. per A.; Fralish 1994), site index (35-50), and total biomass are extremely low. The overall result is that in a xeric post oak-blackjack oak forest, PAR at ground level is, on average, 15 to 20 percent (about 200-250 $\mu\text{mol}/\text{m}^2/\text{sec.}$) of full sunlight (about 1200 $\mu\text{mol}/\text{m}^2/\text{sec.}$) with many near full-sun flecks scattered across the forest floor. These sunflecks are essential for survival of many understory plants (Chazdon and Pearcy 1991). In the midcanopy, scattered

arborescents such as sparkleberry (*Vaccinium arboreum* Marsh.) and Juneberry [*Amelanchier arborea* (Michx. f.) Fern.] usually are present but typically there is no oak and hickory sapling stratum; but seedlings may be numerous and a herbaceous layer usually is present (Jones 1974, O'Dell 1978).

On xeric-mesic sites (south, southwest, and west slopes with relatively deep soil), the trees are tall (70-80 feet), relatively straight with more well developed crowns (higher leaf density), and have a higher site index (50-65) and basal area (75-120 sq.ft. per A.; Fralish 1994) compared to oak on xeric sites. The stands on these sites may be dominated by either pure white oak, white oak with several species of the "black oak" group (black, scarlet, southern red), or by species of only the black oak group. There generally is more light penetration in stands dominated by black oak. Because species of the black oak group are more shade intolerant than white oak, they tend to have thinner crown density and a greater distance between crowns to let more light through to the lower leaves. "Black oak" species not only have fewer leaves but leaves in the upper portion of the crowns have large sinuses to permit passage of light. The lower leaves tend to have more green leaf area to capture light with the extreme condition found in the large misshapen black oak seeding leaves that essentially have no sinuses. The sunflecks in these stands are smaller but may comprise up to 80 percent of total light reaching the forest floor (Chazdon and Pearcy 1991). The PAR in black oak stands is about 10-15 percent of full sunlight (Fralish 1997). Scattered arborescents such as Juneberry [*Amelanchier arborea* (Michx. f.) Fern.] and flowering dogwood (*Cornus florida* L.) may be present but typically there is no oak and hickory sapling stratum; seedlings may be numerous and a herbaceous layer usually is present (Jones 1976, O'Dell 1978).

Form and crown density are further developed in trees on mesic sites (north, northeast and east slopes and stream terraces). These stands generally are dominated by nearly pure white oak or northern red oak (*Quercus rubra* L.); black oak seldom is more than a scattered tree. At maturity, the trees are tall (100-120 feet) and stands have a high site index (96-75) and basal area (130-160 sq. ft. per A.; Fralish 1994). White and northern red oak are shade intermediate and slightly more shade tolerant than other upland oak species. White oak crowns usually are more dense than those of black oak although the crowns seldom touch or overlap in the forest overstory canopy. However, even in a forest of white or northern red oak, crown depth seldom exceeds 1/2 of total tree height. Here PAR probably is 5 to 10 percent of full sun; sunflecks are smaller and more scattered. Flowering dogwood is the most common mid-canopy arborescent and usually is scattered but pawpaw (*Asimina triloba* (L.) Dunal) may form dense thickets.

In contrast to oak and hickory species, the crowns of the shade tolerant species have leaves with small sinuses (sugar and red maple), leaves without sinuses (American beech), densely packed crowns, and a deep crown as shade tolerance permits survival of leaves and branches on the lower half of the trunk (sugar maple and beech). The green cells in the leaves of these shade tolerant species have a special light capturing mechanism that allows them

to photosynthesize under extremely low light conditions where PAR may be only one percent of full sunlight. The mechanism may be visualized as a large molecule in which antennae or spokes composed of chlorophyll A, carotenoids, and xanthophyll funnel light energy to chlorophyll B to the hub at the center of the spokes. Oak and hickory do not have this mechanism and are inefficient at photosynthesizing at low light levels.

Light levels are lowest in upland oak-hickory dominated stands where there also is a dense midcanopy of maple and beech. These multi-layered canopies reduce PAR to its lowest levels of less than 0.01 percent. Not only is there a total absence of sunflecks and indirect radiation but the light transmitted through the leaves is highly filtered. These stands also have a high leaf area index (area of leaves/area of ground), thus the litter layer may be several inches thick and create a smothering effect well into the summer and fall. Oak seedling and herbaceous layers and even sugar maple and beech seedlings usually are absent in this environment (Fralish and others 1991).

FOREST SUCCESSION AND LOSS OF BIOTA

The elimination of natural disturbance such as fire initiated the process of succession which has had and is having several distinctly negative impacts on the forest ecosystem. Succession usually has been viewed as a single lengthy event but in the central hardwood forest some events are distinct, relatively short, and independent and disjunct from other events or processes.

Loss of the Black Oak Species

In the central hardwood forest, the first stage of succession is the loss of "black oak" species (black, blackjack, southern red, scarlet) from post oak dominated stands on xeric sites, or from stands of mixed white oak, "black oak," and northern red oak on xeric-mesic and mesic sites. On xeric sites where mesophytes seldom invade, the loss of black oak may be considered as part of a compositional change as opposed to the process of succession. The death of "black oak" trees in post and white oak stands has been documented at LBL (Kentucky and Tennessee) and in Illinois. At LBL, data from the 1976 and 1986 remeasurement of permanent plots indicated that high mortality occurred in the black oak group while species of the "white oak" group (white oak, post oak and chestnut oak (*Quercus prinus* L.) and hickory had relatively low mortality (Groton and others 1988). Approximately 70 percent of the stems alive in 1988 were oak with only 20 percent of these in the black oak group, but approximately 45 percent of total mortality was black oak (Wellbaum 1989). On permanent plots at Kaskaskia Experimental Forest in southern Illinois, mortality of scarlet, black and northern red oak was higher than that of white oak with the mortality level of scarlet twice that of black oak (Schlesinger 1989).

However, loss of trees of black oak species on xeric and xeric-mesic sites may only be temporary because mesophytic species usually are not a problem and opening of the canopy may permit the establishment of black oak seedlings. A comparison of 10-12 year old clearcut oak stands at Land Between The Lakes indicates that species of the black oak group have a collective average relative density

of 20 to 30 percent (Snyder 1995); however, in many stands, the density was double or triple that of the white oak group or hickory suggesting that there could be a substantial recovery over time.

On mesic sites in the central hardwood forest region, death of black oak species is the only beginning of a more extensive loss of biodiversity as species richness (number) decreases concurrently with purification (reduced equability) as white oak temporarily assumes greater dominance. Small trees {< 8 inches in diameter at breast height (d.b.h.)} with poorly developed crowns and the largest trees (70-100 cm in d.b.h.) of the shorter lived (150-175 years) "black oak" species have been or are being phased out while trees of the longer lived (300-350 years) white oak and hickory remain. Individuals of "black oak" reach physiological maturity and the end of their life span at about 150-170 years. At 125-150 years or earlier for some species such as scarlet oak, trees begin to show the typical signs of old age: heart rot, presence of large dead branches, patches of dead bark, large broken branches and/or tops, reduced number of leaves (thin crown) and a weak root system (frequent wind thrown trees). The relatively high density and increased competition in forest stands in addition to the drought and insect attacks of the 1980s may have reduced tree vigor which subsequently resulted in increased mortality due to secondary causal agents such as Hypoxylon canker.

Loss of White Oak and Hickory

The loss of white oak and hickory is probably the last event to occur as mesophytes totally occupy the site. On mesic sites, white oak (specifically *Quercus alba*) and hickory (extreme life expectancy = 300-400 years) will be replaced by the more long lived (450-500 years) sugar maple and American beech. Because of the extensiveness of mesic sites, the effect of succession will be to create "islands" of remaining white oak and post oak stands on xeric and xeric-mesic sites in some regions (e.g., Shawnee Hills; LBL) or to completely blanket the landscape with a near monoculture of sugar maple or American beech in others (e.g., Illinois Ozark Hills, Illinois Coastal Plain, Tipton Till Plain).

Reduced Productivity/Mast

Forest productivity will decrease as oak and hickory trees are systematically eliminated from the forest. In a high light environment (direct sunlight on the upper crowns), they grow faster than maple and beech. In a shaded environment, maple and beech seedlings, saplings, and midcanopy trees survive better and grow faster. The physiological basis for the growth differential between these two groups is reviewed by Hale and Orcutt (1987), Kozłowski and others (1991), and Kozłowski and Pallardy (1997).

There is an interesting paradox regarding the rate of oak growth and rate of succession. It would be reasonable to expect that slow-growing oak and hickory stands on xeric and xeric-mesic sites should be easily replaced by invading species, while their high growth rate on mesic sites would permit them to dominate indefinitely. The reverse situation actually occurs. The lack of soil moisture which results in slow oak growth on xeric sites also prevents succession to

mesophytic (moisture requiring) species. High soil moisture on mesic sites permits a rapid oak growth rate but creates an environment suitable for invasion and development of a community dominated by shade tolerant mesophytes. In terms of resource management, the most productive oak and hickory stands are being replaced by slower growing mesophytic species while the least productive stands remain intact. The amount of mast produced for wildlife parallels that of tree growth.

Loss of Animals

The importance of oak and hickory nuts to wildlife is well known and documented. Nationwide, oak is used by 96 animals (Martin and others 1951); however, for eastern United States (land west of the prairie zone), the number is considerably lower (table 1). Of the 44 animals listed, the majority are birds (28) and of these only seven are considered game animals; the remainder (21) are small birds.

Succession impacts stand productivity by reducing the amount of mast (nuts, buds, twigs) produced for wildlife as oak and hickory are replaced by mesophytes. Thus, loss of animals will start to occur as the black oak are lost but the major impact will come decades or more latter when white oak trees die. While beech is a mast producer, the soft tissues of maple seed quickly decompose if the seed does not germinate.

However, the impact of succession on wildlife populations is going to be greater than that suggested by the number of species listed in table 1. The somewhat more indirect influence will be on herbaceous plants which support various neotropical migrant birds and insect populations.

Loss of Herbaceous Plants

The present high density of seedlings, saplings and small trees of mesophytic species within the central states oak-hickory forest is having a major deleterious effect on the herbaceous layer. This loss is the most important unreported impact resulting from forest succession. The loss in herb richness can be considerable as Jones (1974) and Harty (1978) reported between 50 and 75 herbaceous plants for both spring and summer/fall guilds.

Data collected from Trail of Tears State Forest in the Illinois Ozark Hills region indicates that as photosynthetically active radiation decreases and the amount of ground litter increases, there is a major decrease in the number of herbaceous species (table 2). Species richness increased 200 percent from an average of 10 species/10 m² sample in a forest composed of black and white oak and hickory with a closed canopy of smaller sugar maple trees (d.b.h. of 10-20 cm) to an average of 31.5 species/10 m² in open stands dominated by black oak, white oak, and hickory without maple. There is little difference in species richness between the open black/white and post oak stands although post oak occurs on drier sites and has considerably higher PAR levels. In dense sugar maple dominated forest of the Ozark Hills region, few seedlings or herbs can be observed.

Wilhelm (1991) also reported a decrease in the number of summer and fall flowering species between 1980 and 1988 and related this decrease to the increase in sugar maple

importance in the tree canopy. At Land Between The Lakes (LBL) in Kentucky and Tennessee, Close (1996) recorded cover for herbaceous in uncut post oak, black oak, and white oak dominated stands. By comparison, Glickauf (1998) found about twice the number and double the cover of species in shelterwood cut stands at LBL, suggesting that even in oak dominated stands, the light resource prevents full development of understory herbs. Therefore, it should be of no surprise that the added layers of branches and leaves, due to a midcanopy of mesophytic species, impoverishes the herbaceous stratum.

In a related experiment on a common oak-hickory forest herb, pots containing dittany [*Cunila origanoides* (L.) Britt.] plants were placed in the open and in the same four community/structural types as listed in table 2: post oak, black oak/white oak without a sugar maple understory, black oak/white oak with a thin maple understory, and black oak/white oak with a dense maple understory. The amount of light decreased with increasing overstory and understory density. The plants in the two open areas (no shade) were healthy and robust (high dry weight) and produced copious flowers in the fall. The plants in the post oak and black oak/white oak stands (minimum shade) without maple grew well, were slightly taller than the open grown plants, and flowered in the fall, but were less robust (smaller dry weight). One-half of the dittany plants in the black oak/white oak forests with a thin maple midcanopy (moderate shade) and all but one plant under the dense maple midcanopy (heavy shade) were dead by July or August. The one plant that survived under heavy shade did not flower. Across the light levels (table 2), plants grown in shade were taller and thinner than those grown in the open, and the heavier the shade, the taller and thinner the stem such that under the two lowest light levels, the plants were unable to maintain an upright orientation, fell over and died.

As described earlier, the amount of PAR on the forest floor is a function of crown and stand density (structure). The adaptive geometry of oak trees (Horn 1971) permits light penetration through the canopy and increases photosynthesis not only in lower leaves but permits survival of herbaceous plants on the forest floor. Because of oak species have thin crowns and there is space around each crown, the relatively low amount of leaf biomass produces only a thin leaf litter layer in the fall, and this layer is decomposed by early summer.

Conversely, extremely shade tolerant species such as sugar maple and American beech have a high stem density, overlapping crowns and thick crowns of multiple leaf layers as lower branches remain alive. These characteristics produce a high leaf biomass. In autumn, the leaves create a thick (3-5 cm deep) litter layer that often remains throughout the growing season and smothers the new growth of herbaceous plants. The litter appears to be of sufficient thickness that new seedlings will not survive because the extending radical cannot reach mineral soil and water before desiccation occurs. Bazzaz (1979, 1996) describes these and additional relationships.

Although the invasion of mesophytes reduces the number of oak forest herbs, the herbaceous layer of maple/beech

Table 1—Amount of oak (*Quercus*) species used as food by bird and animal species in eastern United States

Type of animal	Percent of diet	Region
Upland game birds (<i>acorns, buds</i>)		
Grouse, ruffed	**	E
Pheasant, ringed-necked	*	NE
Prairie chicken, greater	*	Wisc
Prairie chicken, lesser	*	Okla
Quail, bobwhite	**	NE
Songbirds (<i>acorns</i>)		
Blackbird, rusty	+	NE
Crow, common	*	E
Flicker, yellow-shafted	+	E
Grackle, purple	***	E
Grosbeak, rose-breasted	+	E
Jay, blue	****	E
Meadowlark	+	SE
Nuthatch, white-breasted	***	E
Sapsucker, yellow-bellied	+	E
Starling	+	NE
Thrasher, brown	**	E
Titmouse, tufted	**	E
Towhee, red-eyed	**	NE
Woodpecker, downy	+	E
Woodpecker, red-bellied	***	E
Woodpecker, red-cockaded	+	SE
Woodpecker, red-headed	***	E
Wren, Carolina	+	E
Waterfowl (<i>acorns</i>)		
Mallard duck	*	E
Pintail duck	+	SE
Wood duck	*****	NE
Wood duck	***	SE
Marsh birds (<i>acorns</i>)		
Rail, clapper	+	SE
Fur and game animals (<i>acorns, buds, bark</i>)		
Bear, black	****	NE
Beaver	+	NE
Fox, gray	+	S
Fox, red	+	NE
Muskrat	+	NE
Opossum	*	E
Rabbit, cottontail	*	NE
Rabbit, mearns	+	NE
Raccoon	++++	E
Squirrel, flying	**	NE
Squirrel, fox	****	E
Squirrel, gray	****	E
Squirrel, red	**	E
Small mammals (<i>acorns</i>)		
Chipmunk, eastern	**	NE
Mouse, meadow	+	E
Rat, wood	++	S
Hoofed browser (<i>twigs, foliage, acorns</i>)		
Deer, white-tailed	****	E

Data summarized from Martin and others (1951). The star ranking system for percent of diet is: + = 0.5–5 percent; * = 2–5 percent; ** = 5–10 percent; *** = 10–25 percent; **** = 25–50 percent; ***** = > 50 percent. Location is designated by region: E = eastern United States; NE = central hardwood forest region including most of the Appalachian Mountains and the northern hardwood-conifer forest of the Lake States and New England; SE = southern pine-hardwood forest.

Table 2—The relationship between number of species, photosynthetically active radiation, and litter weight under four forest canopy/community types on southeast, south, and southwest slopes in the Illinois Ozark Hills region

	Canopy/community type			
	Open		Closed	
	Post oak	Black oak	Black oak	Oak/maple
PAR (umol m ⁻¹ s ⁻¹)	233.8	138.4	51.7	8.85
Litter weight (kg/m ²)	0.75	0.66	0.97	1.10
Species/10 m ²	31.5	31.5	25.0	10.0

PAR = photosynthetically active radiation.

Unpublished data collected in 1996. All the oak communities include some white oak, southern red oak, and scarlet oak.

dominated communities has high species richness in some regions (Curtis 1959) and some mesic sites in the central hardwood forest (Jones 1974, Harty 1979, Close 1996). Small stems of sugar maple, American beech and other mesophytes indicate the advance of this forest, but the gap between time of elimination of oak-hickory forest herbs and time of invasion of mesophytic forest herbs may be 50 to 100 years or longer and may not occur on more xeric sites. During this gap, insect populations are likely to be reduced and soil surface erosion increased depending on seedling density. These aspects of herb importance should be the thrust of future research.

A dense herbaceous layer is important for production of flowers and seeds and of leaf material for insects, all of which are used by various neotropical bird species. The above ground herbaceous layer also protects the soil from erosion by heavy rains as roots assist in holding soil in place. Herbaceous plants also store nutrients and reduce the loss of nutrients from the site and ecosystem.

OAK MANAGEMENT

It would appear that near complete loss of the oak-hickory forest component is eminent. Given another 75-100 years, there will be few stands dominated by oak and hickory species although a few scattered trees may remain. Moderate disturbances that would regenerate oak and hickory remain absent or restricted, and at this time, there appears to be limited opportunity to reintroduce fire into the ecosystem. Non-scientists have suggested that oak regeneration will appear when large individual trees die as is occurring with the black oak component. These large individuals may be standing dead or on the ground as windfalls. Standing dead typically lose progressively larger branches over a period of five to ten years and then fall as a single pole-like structure. A windfall, where the entire tree tips and falls, will typically leave intact the midcanopy of mesophytic species where it was standing but may disrupt the midcanopy under adjacent large trees. In either case of individual tree death, or under a silvicultural program of individual tree selection where sugar maple and American beech have formed a sufficiently mid-canopy, no canopy gap for light penetration is formed, or if formed, it is rapidly closed by the crowns of mesophytes. The death of or removal of individual trees works strongly to the advantage of sugar maple and beech

and to the detriment of oak and hickory seedlings and saplings which need direct solar radiation throughout their entire life.

Conversely, data from 80 permanent plots in the Illinois Ozark Hills have shown that clearcutting is not the answer to regenerating oak on moist sites. This case study by Presmyk (1987) examined four contiguous areas: 1981 clearcut, 1975 clearcut burned (wildfire) in 1981, mature forest burned (wildfire) in 1981, unburned forest. The original overstory on these areas was black, white, and northern red oak with yellow-poplar and beech as secondary species. The plots were resampled in mid 1990. In the 1981 clearcut (no fire), the north slopes converted immediately to beech, red maple, yellow-poplar, black gum and sassafras; a small amount of oak was present. In the 1975 clearcut that burned in 1981, the beech, maple, and other tree species on north slopes were killed and the area reverted into a tangle of brush [devil's walking stick, *Aralia spinosa* L.; sassafras, *Sassafras albidum* (Nutt.) Nees; mulberry, *Morus rubra* L.; grape, *Vitis* spp.]. Few stems of oak were present. However, on the drier south slopes, white and black oak were major regenerating species along with red maple, yellow-poplar (*Liriodendron tulipifera* L.), black gum (*Nyssa sylvatica* Marsh.), and sassafras. The burned mature forest had a similar understory as did the unburned forest but the burned forest had larger amounts of sassafras, white oak, yellow-poplar, and black gum. The conclusion is that clearcutting alone does not regenerate oak, post harvest fire may reduce a forest to non-productive status for a lengthy period, and that fire in mature forest increases the amount of oak regeneration. It would appear that on moist sites in particular, fire prior to harvesting is necessary to establish oak regeneration. In the absence of fire after cutting, the forest will immediately convert to mesophytic hardwoods if they are the major understory component. In the clearcuts of these watersheds, erosion of tributaries to the main intermittent stream was evident and substantial.

Based on research, it would appear that in stands where stems of the invading mesophytes are still relatively small (saplings), several prescribed fires followed by partial harvesting using an even-aged approach such as shelterwood would permit the establishment of oak and hickory seedlings, maintain mast production at a reasonable level, and develop the herbaceous layer while protecting the site.

CONCLUDING REMARKS

For many years, mast production for wildlife has been considered one of the most important attributes of oak and hickory dominated communities. However, due to the length of time (centuries) oak and hickory have dominated the central hardwood forest region, and because of the low density of their crowns and overstory canopy, they have become of major importance to the herbaceous stratum and the wildlife that depend on herb foliage and seed for survival. In terms of supporting mammals, birds, herbs, and insects, oak and hickory have become keystone species. In the central hardwood forest, loss of these dominant keystone species through succession will result in loss of biota ecologically and evolutionarily associated with oak-hickory forest.

In recent years, new attitudes developed jointly with new available scientific information have directed forest management away from timber production and toward other forest ecosystem values such as preservation of rare or endangered species, development of old growth characteristics, and maintenance of species diversity to the level thought to be present in presettlement communities (before ca. 1810). Unfortunately, it is too often believed that total protection will permit the forest to maintain or restore these values. This belief is in error because oak and hickory are shade intolerant keystone species subject to successional replacement, and thus, their response is similar to other communities composed of disturbance dependent, pioneer species of the southwest (e.g., longleaf pine, *Pinus palustris*), the north (quaking aspen, *Populus tremuloides*), and west (lodgepole pine, *Pinus contorta*).

Disturbance plays an important role in ecosystem development. Fire in particular reduces invasion of mesophytes in oak stands, and with a less dense overstory, white and black oak stands can be maintained to old growth with a full complement of understory herbs. Conversely, the extremely dense, multi-layered mesophytic forest is viewed by many as the epitome of old growth (primeval forest), yet according to early land survey records, it was rare to nonexistent in most areas of the central hardwood forest (Crooks 1988; Fralish and others 1991, 2002).

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A PILOT TEST OF INDICATOR SPECIES TO ASSESS UNIQUENESS OF OAK-DOMINATED ECOREGIONS IN CENTRAL TENNESSEE

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Abstract—We used tree indicator species occurring on 438 plots in the Plateau counties of Tennessee to test the uniqueness of four conterminous ecoregions. Multinomial logistic regression indicated that the presence of 14 tree species allowed classification of sample plots according to ecoregion with an average overall accuracy of 75 percent (range 45 to 94 percent). Additional analysis revealed that the largest ecoregion could be subdivided into northern and southern zones based on frequency of occurrence of five other indicator species. Under the premise that tree assemblages of varying composition indicate areas of differing environmental conditions, results of our test suggest the delineated ecoregions are unique.

INTRODUCTION

Ecoregions are large areas of the Earth's surface that enclose smaller ecosystems having common characteristics (Bailey 1998). Ecoregions may be delineated using differing mapping criteria, but are largely integrations of physical, biological, and cultural components, including climate, geologic formations, soils, terrestrial and aquatic fauna and flora, and land use (Bailey 1983, Omernik and others 2000). Assessment, evaluation, analysis, and planning across sub-regional areas are increasingly being based on ecoregions (Bryce and others 1999) and particularly land management decisions dealing with water-quality issues (Griffith and others 1999). Ecoregion maps are typically delineated in a subjective, qualitative manner, but generally are not tested because independent datasets are not available. Untested ecoregion maps have been used for purposes such as resource assessments (Rudis 1998).

Tree species in the Southern Appalachian Mountains are distributed individualistically along temperature and moisture gradients (Whittaker 1956) that are likely associated with physiological requirements of vegetation for establishment, growth, and reproduction (Kramer and Kozlowski 1960). McNab and others (2002) found that Southern Appalachian tree species can be used as indicators of forest site productivity. Kuchler (1964) and others used overstory cover types, consisting largely of tree species, as a means of stratifying large, subregional geographic areas into smaller, more homogeneous ecological units. We reasoned that if adjacent mapped polygons are dissimilar environmentally, then the frequency of occurrence of one or more tree species should differ also and provide a means of testing ecoregion uniqueness. Also, tree species could provide a biological basis for subdivision of large ecoregions into more homogeneous smaller units.

We are not aware of tests of ecoregion mapping in the South. We have successfully used data from an extensive series of U.S. Department of Agriculture, Forest Service, Forest Inventory and Analysis (FIA) plots to identify tree

species that indicate site quality (McNab and others 2002). Our success suggests that FIA data could be used to test similarity of ecoregions, also using an indicator-species approach. The primary objective of our current study was to determine if species composition differed among ecoregions. We based our study on the premise that assemblages of tree species will vary among areas of differing environmental conditions. Our study should be considered a pilot test because it was made in a small geographical area that did not include the full extent of the mapped ecoregions.

METHODS

Our study was limited to FIA unit 4 of Tennessee (fig. 1), which consists mainly of the Cumberland Plateau physiographic province and smaller areas of three other provinces. Schweitzer (2000) describes forest statistics of this region, which extends over 4 million acres, includes 16 counties,

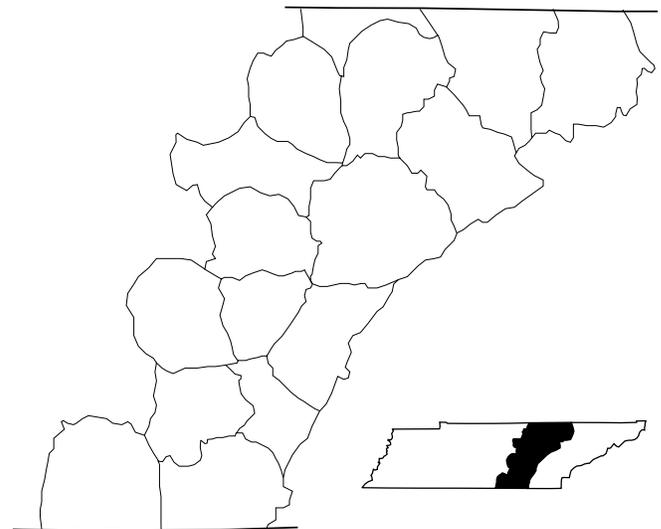


Figure 1—The study occurred in the plateau FIA survey unit of Tennessee.

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and is about 71 percent forested. Smalley (1982, 1983, 1984) developed a conventional forest site classification system for this region. In Hinkle's (1989) extensive vegetation study, oak and hickory assemblages dominate forest cover types.

We evaluated ecoregions mapped by Griffith and others (1998). Griffith and others (1997) described the mostly qualitative methods of their ecoregionalization process in Tennessee as "compiling and reviewing relevant materials, maps and data; outlining the regional characteristics; drafting the ecoregion boundaries; creating digital coverages and cartographic products; and revising as needed after review by national, state, and local experts." Essentially, the U.S. Environmental Protection Agency (EPA) ecoregions are areas of relatively uniform climate, geology, landform, natural disturbance, land use, terrestrial vegetation, and aquatic fauna. Other intermediate-scale ecoregion maps were available in digital format. However, we selected this one primarily because it delineated the escarpment as a sinuous but relatively large, distinctive, and detailed ecoregion that could be displayed relatively accurately on the base map. Also, the escarpment unit generally agreed with our field observations and knowledge of the area. Our study tested this ecoregion as a unique ecosystem, which apparently was an issue among reviewers of the final map product (Griffith and others 1997). Ecoregions were retained for analysis that included a minimum of 30 plots.

Using the FIA Eastwide database (Hansen and others 1992), tree- and plot-level data were available for 513 sample plots in the 1999 inventory that had been installed at intersection locations on a 3- by 3-mile grid. Arborescent vegetation ≥ 1 inch in diameter at breast height at each grid location was inventoried by species at four points with 1/24-acre and 1/300-acre nested plots. However, genera were used as inventory groups where species could not be determined accurately, such as for hawthorns (*Crataegus* spp.), serviceberries (*Amelanchier* spp.), and occasionally for hickories (*Carya* spp.). Schweitzer (2000) provides additional information on the vegetation sampling methods. In addition to a species list, available data for each plot included elevation (nearest 10 feet), aspect (nearest degree), slope gradient (nearest percent), and latitude and longitude. For tree species we recorded the inventory data on each sample plot as a binary variable: present or absent. To reduce the confounding influence of disturbance associated with regeneration of certain species, e.g., yellow-poplar, red maple, and sweet birch (Beck and Della-Bianca 1981, Golden 1974), we did not use a measure of abundance as independent variables, such as number of individuals of each species present or crown area by species. We excluded plots that were not forest land, or had been planted, or were not stocked with trees.

In the analysis, we included only those species present on 10 percent or more of the total plots to reduce the chance that uncommon species unique to this dataset could unduly influence the results. We excluded the hickory genus from the analysis because some species are highly site specific; e.g., bitternut, but were not identified. We used several types of analyses to investigate the distribution of tree species among and within ecoregions. We used chi-square to test

hypotheses that the frequency of occurrence of each species among ecoregions did not differ from its frequency of occurrence over the entire unsubdivided study area. We used calculated species richness, i.e., the number of species present on each plot, and available plot basal areas to characterize the tree stands among ecoregions.

We used logistic regression instead of discriminant analysis to develop classification functions because most of our independent variables were qualitative (Press and Wilson 1978). We used multinomial logistic regression to examine the relationship of the presence of multiple species with the four ecoregions. Our statistical software package, STATA v. 7 (StataCorp 2001), did not provide a fast and efficient stepwise procedure to determine a suitable model with this type of analysis. Therefore, we began initial trial formulations with influential species from the chi-square goodness-of-fit tests and our own field experience. We followed the rationale of Hosmer and Lemeshow (2000) to develop and interpret a significant and parsimonious multinomial model.

We used ordinary logistic regression to study the effect of latitude on tree distribution within the largest ecoregion, the Cumberland Plateau. We arbitrarily subdivided the Plateau into north and south zones at 36° latitude, near Crossville, TN, to provide about equal plot numbers for analysis. Species included in this analysis were limited to those occurring on ≥ 10 percent of the plots. This model used backward elimination of species insignificant at the $P = 0.05$ level of probability.

RESULTS AND DISCUSSION

Ecoregion Study Areas

For analysis we retained ecoregions that included a minimum of 30 plots, which included, from west to east: (1) eastern highland rim, 40 plots; (2) plateau escarpment, 115 plots; (3) Cumberland Plateau, 216 plots; and (4) Cumberland Mountains (67 plots) (table 1). For brevity, these ecoregions are hereafter called rim, escarpment, plateau, and mountains, respectively. We excluded smaller portions of two ecoregions (Sequatchie Valley and Nashville Basin) because of their small size and lack of sufficient plots for analysis. Over the study area, plot elevation averaged 1,568 feet (range 670 to 3,200 feet), slope gradient averaged 24 percent (range 0 to 84 percent), and all aspects were represented.

Mean Basal Area and Species Richness

Stand basal area averaged almost 105 square feet per acre throughout the study area (table 2). Average basal area was lowest in the rim and highest in the Cumberland Mountains. Except for one plot in the plateau, stand basal areas among ecoregions ranged from about 10 square feet per acre to > 150 square feet per acre. The plot of highest basal area was located in the northern portion of the plateau and consisted of an unusual species combination of red maple, three oak species (chestnut, scarlet, and chinkapin), black gum, sourwood, bigleaf magnolia, white pine, and hemlock. The latter three species suggested that the site was situated near a mesic environment, such as a stream ravine. High stocking levels were not unusual in the plateau, where nine stands had basal areas exceeding 170 square feet per acre.

Table 1—Characteristics of principal ecoregions in the study area of Tennessee

Characteristic	Ecoregions			
	Rim	Escarpment	Plateau	Mountains
Physiography	Weakly dissected plateau	Mountainsides	Rolling tableland	Low mountains
Elevation (ft.)	800 – 1,300	800 – 2,400	1200 – 2,000	1,200 – 3,500
Geologic age	Mississipp.	Pennsylvan.	Pennsylvan.	Pennsylvan.
Primary bedrock or mixture	Limestone, chert	Sandstone-limestone mix	Sandstone, siltstone	Sandstone, siltstone
Soil order	Ultisols	Ultisols	Ultisols	Inceptisols
Precipitation (in.)	52 – 56	52 – 60	48 – 60	50 – 55
Frost free (days)	190 – 210	180 – 200	180 – 200	180
Jan. Min/Max (F)	25 – 46	24 – 44	24 – 44	21 – 43
Jul. Min/Max (F)	65 – 88	63 – 85	63 – 85	61 – 85
Potential natural vegetation	Mixed oak	Mixed mesophytic, mixed oak	Mixed oak	Mixed mesophytic
Primary landuse	Agriculture	Forests	Forests	Forests

Table 2—Mean (SE) and range of stand basal area and species richness by ecoregion in the study area of Tennessee

Ecoregion	Plots <i>N</i>	Stand basal area (ft ² per ac)		Species richness	
		<i>Mean (SE)</i>	<i>Range</i>	<i>Mean (SE)</i>	<i>Range</i>
Rim	40	99.9 (5.4)	10 – 158	13.5 (0.6)	7 – 24
Escarpment	115	104.3 (3.0)	34 – 206	13.2 (0.2)	6 – 20
Plateau	216	105.3 (2.3)	4 – 224	11.9 (0.2)	6 – 18
Mountains	67	106.8 (4.2)	16 – 186	12.3 (0.4)	3 – 19
All	438	104.8 (1.6)	4 – 224	12.5 (0.1)	3 – 24

Species richness averaged 12.5 throughout the study area and ranged from about 3 in the mountains to almost 24 in the rim (table 2). The lowest species richness (3) occurred on a single plot on a mesic site in the mountains where a stand with basal area of 48 square feet per acre consisted only of red maple, yellow-poplar, and black locust. Generally, a minimum of 6 to 7 species and maximum of 19 to 20 species were present on plots of all ecoregions. In the plateau ecoregion, species richness was negatively correlated with elevation ($r = -0.24$, $P < 0.0004$) and positively correlated with slope percent ($r = 0.28$, $P < 0.0001$). In the rim, richness was correlated with slope gradient ($r = 0.38$, $P = 0.009$) and transformed aspect ($r = -0.37$, $P = 0.019$).

Species Composition of Ecoregions

A total of 87 species or species groups, e.g., *Amelanchier* spp., were identified in the study area, of which 35 species were present on ≥ 10 percent (43) of the total 438 plots (table 3). The nine most common species occurred on more than one-third of the sample plots in each of the four ecoregions. Red maple was the species of widest distribution, occurring on 83 percent of the total study area, followed by white oak and black gum. Some species were uniformly common in three of the four ecoregions, such as sugar

maple, chestnut oak, and American beech. Species such as shortleaf pine, hophornbeam, and southern red oak occurred with higher frequencies in two of four ecoregions. None of the common species occurred with obviously higher frequency in a single ecosystem, which alone could be used as an indicator species. Several of the less common species, including tree-of-heaven, bigleaf magnolia, and willow oak, occurred almost exclusively in a single ecoregion, but their scarcity makes them unsuitable as an indicator species. Chi-square tests of hypothesized proportional frequency ratios indicated that the frequency of occurrence (expressed as a percentage) of many species varied among ecoregions (table 3). Although the individual variation in occurrence of species suggests differences exist among ecoregions, a multispecies model should provide increased classification accuracy.

Classification Among Ecoregions

A multiple logistic model utilizing the 36 common species occurring on the field plots indicated that 14 were significantly associated with the four ecoregions (table 3). Overall classification accuracy was 75 percent. The model classified inventory plots in the plateau with greatest accuracy, 94 percent, and those in the rim with lowest accuracy, 42 percent.

Table 3—Arborescent taxa occurring on ≥ 10 percent of the total 438 sample plots occupying four ecoregions in the study area of Tennessee and their significance as potential indicator species

Arborescent taxa	Ecoregion ^a					Indicator	
	Rim	Esc.	Plt.	Mtn.	All	Ind. ^b	Mul. ^c
	-----percent of plots-----						
Red maple (<i>Acer rubrum</i>)	73	64	94	87	83	0.032	.
White oak (<i>Quercus alba</i>)	63	51	94	67	76	0.001	*
Black gum (<i>Nyssa sylvatica</i>)	78	57	82	69	73	0.085	*
Sourwood (<i>Oxydendrum arboreum</i>)	40	40	85	45	63	0.001	*
Yellow-poplar (<i>Liriodendron tulipifera</i>)	73	65	47	76	58	0.012	.
Black oak (<i>Quercus velutina</i>)	40	43	67	42	54	0.005	.
Sassafras (<i>Sassafras albidum</i>)	40	42	57	48	50	0.171	.
Pignut hickory (<i>Carya glabra</i>)	45	59	44	45	48	0.253	.
Dogwood (<i>Cornus florida</i>)	68	49	46	34	47	0.104	.
Chestnut oak (<i>Quercus prinus</i>)	13	46	47	63	46	0.003	.
Scarlet oak (<i>Quercus coccinea</i>)	30	24	61	31	44	0.001	.
Northern red oak (V: <i>Quercus rubra</i>)	43	57	27	54	40	0.001	.
Mockernut hickory (<i>Carya tomentosa</i>)	55	27	46	39	41	0.030	.
Virginia pine (<i>Pinus virginiana</i>)	18	21	53	30	38	0.001	.
Sugar maple (<i>Acer saccharum</i>)	55	71	6	55	35	0.001	*
Black cherry (<i>Prunus serotina</i>)	45	32	25	36	30	0.142	.
Shortleaf pine (<i>Pinus echinata</i>)	0	12	39	22	26	0.001	.
Shagbark hickory (<i>Carya ovata</i>)	35	49	9	13	23	0.001	*
American beech (<i>Fagus grandifolia</i>)	43	30	8	36	21	0.001	*
Post oak (<i>Quercus stellata</i>)	20	5	35	6	21	0.001	.
Green ash (<i>Fraxinus pennsylvanica</i>)	43	32	5	15	17	0.001	.
White ash (<i>Fraxinus americana</i>)	28	42	2	13	16	0.001	.
Eastern redbud (<i>Cercis canadensis</i>)	33	43	0	10	16	0.001	*
Eastern white pine (<i>Pinus strobus</i>)	0	3	28	9	16	0.001	*
Southern red oak (<i>Quercus falcata</i>)	33	2	24	6	16	0.001	*
Black locust (<i>Robinia pseudoacacia</i>)	3	26	5	33	14	0.001	*
Eastern hemlock (<i>Tsuga canadensis</i>)	0	9	20	15	14	0.005	.
American holly (<i>Ilex opaca</i>)	0	3	23	9	13	0.001	.
Cucumbertree (<i>Magnolia acuminata</i>)	5	18	3	34	12	0.001	*
Eastern hophornbeam (<i>Ostrya virginiana</i>)	28	28	2	6	12	0.001	.
Serviceberry (<i>Amelanchier sp.</i>)	3	3	19	9	12	0.001	.
Eastern redcedar (<i>Juniperus virginiana</i>)	43	25	4	0	12	0.001	*
Bitternut hickory (<i>Carya cordiformis</i>)	18	10	9	19	11	0.077	.
Sweetgum (<i>Liquidambar styraciflua</i>)	28	11	7	12	11	0.006	*
Winged elm (<i>Ulmus alata</i>)	33	25	1	3	11	0.001	*
Black walnut (<i>Juglans nigra</i>)	20	23	1	7	10	0.001	.

^a Abbreviations of ecoregions and number of plots: Rim = Eastern Highland Rim (40 plots); Esc. = Cumberland Plateau escarpment (115); Plt. = Cumberland Plateau (216); Mtn. = Cumberland Mountains (67).

^b Chi-square probability that the actual frequencies of occurrence of individual species among ecoregions are equal to the expected frequency determined for the area as a whole.

^c Multinomial logistic regression probability (* denotes $P \leq 0.05$) that the presence of certain combined species discriminate among ecoregions.

Source: Griffith and others (1998).

Inclusion of black gum as a significant indicator species was surprising and probably was simply an artifact of the dataset because it occurred in all ecoregions at a relatively high level.

Several contributing factors are possible explanations for the reduced classification accuracy of several ecoregions, particularly the mountains and escarpment. The most important factor is lack of precise map delineation of some ecoregion boundaries, particularly the upper elevation loca-

tion of the highly crenulated escarpment. Unlike boundaries of other ecoregions that have broad transition zones, the escarpment is generally sharply defined. Also, the small sample sizes for several ecoregions likely influenced model accuracy. In our test, the best results were obtained for the largest ecoregion, for which 233 plots were available for analysis. Finally, our biological indicator, tree species, may be an inexact integrator of environmental conditions. Inclusion of shrub and herbaceous species would likely increase classification accuracy.

Classification Within Ecoregions

Twenty-two species were present on >10 percent of the 216 plots in the plateau and were used to develop a logistic model for subdividing this ecoregion into northern and southern zones (table 4). Three of the 22 species, yellow-poplar, white pine, and shortleaf pine, occurred with unequal frequencies between the two zones, and two species, chestnut oak and American holly, were significant at a lower level ($P \leq 0.1$). An overall classification accuracy of 70 percent was achieved with a logistic model that included the three significant ($P \leq 0.05$) species. Two species, chestnut oak and American holly, which were not significantly associated with the two ecoregion zones, increased in importance ($P < 0.02$) in the presence of the other species. The presence of both these species increased the probability that a subject plot was situated in the southern zone of the plateau. The presence of two pine species, shortleaf and white, were strong indicators of plot classification membership in the northern zone. Individual classification accuracies were similar for the two zones: 70 percent for the south and 72 percent for the north.

These results suggest the plateau could be subdivided into northern and southern zones. If a latitude effect within the plateau ecoregion is real, perhaps resulting from climatic or physiographic differences, the boundary likely would not be at the location of our subdivision, 36° latitude, which we selected arbitrarily. Inclusion of shrubs and herbs has often increased classification accuracies of site-specific applications of indicator species, such as productivity evaluation (Hodgkins 1961); however, it is unclear if nontree species would be beneficial to classification over large geographic areas.

CONCLUSIONS

In this pilot study in the Cumberland Plateau region of Tennessee, we investigated the use of tree indicator species as a means of testing the delineation of ecoregions, which are ecologically dissimilar areas that likely respond differently to management. Using inventory data from > 400 permanent FIA plots established throughout the study area of > 4 million acres, we found that the relative frequency of occurrence of 14 tree species varied significantly in each of

Table 4—Arborescent taxa occurring on ≥ 10 percent of the total 216 sample plots occurring in two zones of the Cumberland Plateau ecoregion in Tennessee and their significance as potential indicator species

Arborescent taxa	Zone ^a			Indicator	
	South	North	All	Ind. ^b	Mul. ^c
	- percent of plots- -				
Red maple (<i>Acer rubrum</i>)	94	94	94	0.994	.
White oak (<i>Quercus alba</i>)	93	96	94	0.773	.
Sourwood (<i>Oxydendrum arboreum</i>)	86	84	85	0.900	.
Black gum (<i>Nyssa sylvatica</i>)	83	81	82	0.843	.
Black oak (<i>Quercus velutina</i>)	65	69	67	0.761	.
Scarlet oak (<i>Quercus coccinea</i>)	63	60	61	0.779	.
Sassafras (<i>Sassafras albidum</i>)	63	52	57	0.317	.
Virginia pine (<i>Pinus virginiana</i>)	51	55	53	0.714	.
Yellow-poplar (<i>Liriodendron tulipifera</i>)	36	57	47	0.028	N
Chestnut oak (<i>Quercus prinus</i>)	55	39	47	0.074	S
Dogwood (<i>Cornus florida</i>)	39	52	46	0.157	.
Mockernut hickory (<i>Carya tomentosa</i>)	46	47	46	0.914	.
Pignut hickory (<i>Carya glabra</i>)	50	37	44	0.125	.
Shortleaf pine (<i>Pinus echinata</i>)	28	50	39	0.011	N
Post oak (<i>Quercus stellata</i>)	41	29	35	0.145	.
Eastern white pine (<i>Pinus strobus</i>)	16	40	28	0.001	N
Northern red oak (<i>Quercus rubra</i>)	28	26	27	0.739	.
Black cherry (<i>Prunus serotina</i>)	24	26	25	0.838	.
Southern red oak (<i>Quercus falcata</i>)	24	23	24	0.837	.
American holly (<i>Ilex opaca</i>)	28	17	23	0.102	S
Eastern hemlock (<i>Tsuga canadensis</i>)	16	24	20	0.190	.
Serviceberry (<i>Amelanchier sp.</i>)	15	22	19	0.228	.

^aLatitude 36° arbitrarily divides the Cumberland Plateau ecoregion into southern (107 plots) and northern zones (109 plots), approximately at Crossville, Tennessee.

^bChi-square probability that the frequencies of occurrence of individual species between the two zones are not different from the expected frequency determined for the area as a whole.

^cMultiple logistic regression probability (letter denotes $P \leq 0.05$) that the presence of certain combined significant species discriminates between the southern (S) and northern (N) zones of the ecoregion.

Source: Griffith and others (1998).

4 adjacent ecoregions. In addition, five other indicator species provided evidence of latitudinal differences in the largest ecoregion. In conclusion, our study provides evidence suggesting that the delineated ecoregions are discrete ecological units that should not be combined. Also, we demonstrated the potential value of indicator species for purposes other than their conventional use for evaluation of forest site quality.

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OAK FOREST COMPOSITION, SITE QUALITY, AND DYNAMICS IN RELATION TO SITE FACTORS IN THE SOUTHEASTERN MISSOURI OZARKS

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Abstract—Physical site factors are known to affect forest species composition but the pattern and variation across forest landscapes has not been well quantified. We discuss relationships between site factors including soil parent materials, depth to dolomite bedrock, aspect, and landform position and the distribution of vegetation, site index, and short-term succession in oak forests in the southeastern Missouri Ozarks. Overall, we found few strong relationships between these site factors and tree species composition except black oak (*Quercus velutina* Lam.) was more abundant on summit and shoulder landform positions. On average, site index was three to five ft. greater on backslopes than on summits and four ft. greater on north-facing slopes than on south-facing slopes. In the absence of disturbance, white oak (*Q. alba* L.) was generally succeeding species in the red oak group, especially on upper landforms.

INTRODUCTION

In most parts of the Central Hardwood Region, physical site factors are important determinants of species composition, site quality, and successional trends (e.g., Johnson and others 2002, Nigh and others 2000, VanKley and others 1994). Although general trends in species composition related to aspect, landforms, and soil conditions are readily recognized by experienced resource managers, the magnitude of those differences and the variation in responses across similar sites has not been well quantified.

The Missouri Ozark Forest Ecosystem Project (MOFEP) is an on-going, centuries-long experiment that is evaluating the effects of even-aged, uneven-aged, and no-harvest management on a wide array of forest attributes, including overstory and understory vegetation, wildlife populations, mast production, insects, and fungi (Brookshire and Shifley 1997, Shifley and Brookshire 2000, Shifley and Kabrick 2002). An initial part of that experiment was the detailed mapping of soils and landforms and the detailed inventory of forest overstory and understory vegetation (Grabner 2000, Jensen 2000, Kabrick and others 2000, Shifley and others 2000). This has afforded a unique opportunity to examine the relationship of site factors to species composition across nearly 9,400 acres of mature, relatively undisturbed, second-growth Ozark forest.

Grabner (2002) found that depth to dolomite, geology and soil order (which together reflect major physical and chemical differences of soil parent materials in the study region), slope aspect, and landform position were important site factors for identifying and distinguishing different ecological landtypes and landtype phases in the MOFEP study region. These site factors affect the availability of light energy, nutrients, and water. In this paper, we evaluate the relative importance of each of these site factors for explaining differences in oak species composition and growth relative to other tree species and to forest site quality in Missouri

Ozark forests. Specific objectives were to (1) quantify the composition and growth of oaks and other overstory species in relation to the site factors of landform, aspect, depth to dolomite bedrock, and parent materials, and (2) relate those site factors to site index which has traditionally been used to evaluate site quality in the region.

METHODS

MOFEP Site Description

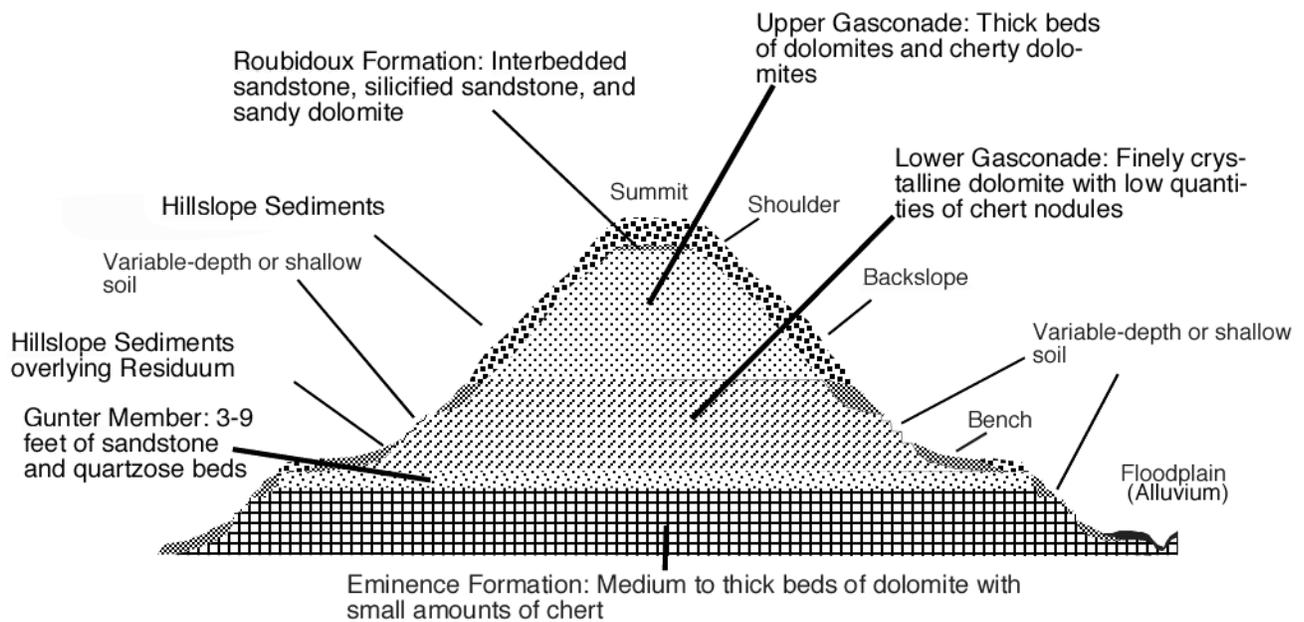
The MOFEP study and experimental design is described elsewhere in detail (Brookshire and Hauser 1993, Brookshire and Shifley 1997, Kurzejeski and others 1993, Sheriff 2002, Shifley and Brookshire 2000). The study consists of nine sites ranging in size from 772 ac to 1,271 ac, primarily within the Current River Oak Forest Breaks and the Current River Oak-Pine Woodland Hills landtype associations of the Ozark Highlands. The Current River Oak Forest Breaks has narrow ridges and steep sideslopes with relief of 300–450 ft, which exposes the Roubidoux, Gasconade, and Eminence formations. The Current River Oak-Pine Hills has broad ridges with relief <300 ft and exposes only the Roubidoux and Gasconade bedrock formations. Upland soils of these landtype associations are primarily Ultisols and Alfisols formed in highly weathered hillslope sediments or residuum; soils in upland waterways and bottomlands are primarily Ultisols and Alfisols formed in gravelly alluvium (Kabrick and others 2000; Meinert and others 1997).

Vegetation Sampling and Site Index Determinations

There are 648 permanent vegetation plots distributed roughly equally among the nine MOFEP sites. Since 1991, these permanent plots have been re-inventoried approximately every three years to document the condition of woody vegetation. Within permanent plots, live and dead trees ≥ 4.5 in. diameter at breast height (d.b.h.) are sampled in 0.5-ac circular plots; trees between 1.5 and 4.5 in. d.b.h.

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Landform	Description
Backslope	The landscape position that forms the steepest inclined surface and principle element of many hillslopes. Slopes > 20%. Contains sideslope, noseslope and headslope components.
Bench	A narrow, nearly level to slightly sloping platform breaking the slope continuity. Typically occurs on backslope positions in the Ozarks where underlying bedrock is more resistant to weathering than layers above or below. Slopes 0-20%.
Flood Plain	The nearly level plain that borders a stream and is subject to inundation under floodstage conditions. Slopes 0-4%.
Shoulder	The landscape position that forms the upper most inclined surface near the top of a hillslope. It is commonly convex in shape and comprises the transition from summit to backslope. Slopes 8-20%. Also includes shoulder ridges which are narrow, convex ridgetops.
Summit	The topographically highest hillslope position of a hillslope profile and exhibiting a nearly level surface. Slopes 0-8%.

Figure 1—Illustration of hill cross section showing typical locations of bedrock geology, landforms, soil parent material, and soil depth to bedrock. Definitions for landforms are included. See Methods for definitions of soil parent material, soil depth to bedrock, and aspect classes.

are sampled in four 0.05-ac circular subplots; trees at least 3.3 ft tall and less than 1.5 in. d.b.h. are sampled in four 0.01-ac circular subplots nested within the 0.05-ac subplots. Characteristics recorded for each tree include species, d.b.h. or size class for trees < 1.5 in. d.b.h., and status (e.g., live, dead, den, cut, blow-down). Plot and subplot data were combined to obtain plot averages by d.b.h. or size class and all values are converted to an acre basis for analysis.

From 1993 to 1996, site index was determined on suitable trees at MOFEP. Trees considered suitable were canopy codominants having good form with no indication that they had been suppressed and showing the best growth potential. One to five candidate trees selected for site index determination were sampled outside of the 0.5 ac permanent vegetation plots but within 330 ft of vegetation plots. Tree distance and azimuth from the geo-referenced vegetation plot center were recorded for each site index tree and later used to determine the latitude and longitude of each site

index tree. Trees were assigned a ranking of their perceived quality for indicating site index. Tree heights were measured with clinometer to the nearest ft. A single increment core was extracted at breast height and taken to the lab for age determination. Site index was determined using species, height, age at d.b.h., and published site index equations for species in the Missouri Ozarks (McQuilkin 1974, 1978; Nash 1963).

Soil and Site Characterization

A detailed landscape-scale soil mapping project was conducted on MOFEP in 1994-1995 (Kabrick and others 2000; Meinert and others 1997). This included characterizing geomorphology, geology, and soil characteristics of each permanent MOFEP vegetation plot. Laboratory data generated from 120 soil excavations was correlated to the soil-landscape map units. Detailed information about the soil-landscape mapping and soil characterization data can be found in Kabrick and others (2000), Meinert and others (1997), and data available through the Missouri Department of Conservation.

Site Factors and Variables Used in this Study

We considered four site factors: landform position, parent material, aspect, and depth to bedrock. Definitions of landforms follow those used for routine soil surveys and are defined in figure 1. Soil parent materials were alluvium, hillslope sediments (Daniels and Hammer 1992), and hillslope sediments overlying residuum. At MOFEP, alluvium contained 35 to 60 percent cherty gravel and/or cobbles, clays having mixed mineralogy, cation exchange capacities (CEC) of 2-22 cmol(+)kg⁻¹, and base saturations (BS) of 2-60 percent. Hillslope sediments generally had 15-60 percent cherty gravel, kaolinitic mineralogy, CEC <20 cmol(+)kg⁻¹, and BS of 5-55 percent. Residuum, primarily from dolomite, had < 15 percent gravel, mixed or smectitic mineralogy, CEC 5-40 cmol(+)kg⁻¹, and BS of 30-100 percent. Aspect classes were protected (316-135 degrees), and exposed (136-315 degrees). Site depths to bedrock were classified as deep (>48 in. throughout), variable depth (10-50 percent dolomite out crop; soil depth 0 to >48 in.), or shallow (glades with >50 percent dolomite outcrop and soil depth <48 in.).

To evaluate relationships between species composition and site factors, we selected a subset of 310 MOFEP vegetation plots that were each uniform with respect to site factors. Because harvest treatments on MOFEP that began in 1996 reduced the number of undisturbed plots available, we used data inventoried in 1994-1995, prior to implementing harvest treatments, for our analysis. Response variables included mean number of trees per acre and mean basal area per acre for white oak, post oak, scarlet oak, black oak, and for other oaks and tree species combined.

To evaluate site quality relationships, we used site index estimates made from 289 white oaks and 706 black oaks. These two species were selected because they were most abundant site index tree species at MOFEP. Because site index trees were located outside of the permanent vegetation plot boundaries, we identified site factors of each site index tree by projecting the geo-referenced tree locations

onto the soil-landscape map with GIS software. We then estimated individual site factors associated with each site index tree using the soil-landscape information database.

To evaluate dynamics, we selected a subset of 210 MOFEP vegetation plots that were each uniform in site factors and had not been harvested or thinned during the period from the first MOFEP inventory in 1991-1992 and the most recent inventory completed in 2001-2002. We then calculated the mean change in basal area of trees ≥ 4.5 in. d.b.h. from the first to the most recent inventory. This was done for white oak, post oak, scarlet oak, black oak, other oaks (combined), and all other tree species (combined).

RESULTS

Oaks are the dominant trees at MOFEP (table 1). The four most abundant oaks, black oak, scarlet oak, white oak, and post oak, together comprise nearly 71 percent of the total basal area. Chinkapin oak, blackjack oak, Shumard oak, and northern red oak also occur, but together they comprise 1 percent of the basal area. Shortleaf pine, pignut hickory, black hickory, mockernut hickory, blackgum, and flowering dogwood are also abundant and important species of Missouri Ozarks forests and woodlands.

We found few strong relationships between selected site factors and tree species composition. Black oak basal area was relatively greater on upper landforms than on lower landforms, and both black oak and scarlet oak basal area were greater on soils formed in hillslope sediments than on soils formed in other parent materials (fig. 2). White oak and post oak basal areas were slightly greater on benches than on other landforms. Post oak basal area was slightly greater on soils formed in alluvium than on soils in other parent materials and on soils variable in depth to dolomite than on deep soils or shallow soils. The basal area of "other oaks," of which chinkapin oak was most abundant, was greatest on shallow soils.

White oak site index was approximately three ft. less than black oak site index regardless of site factor (fig. 3), illustrating the well-documented height growth rate difference between these two species (Carmean and others 1989). White oak and black oak site index each were greater on backslopes and less on summits. We also found the site index for each species to be four ft. greater on protected (316-135 degrees) aspects than on exposed (136-315 degrees) aspects. Site index was considerably lower on shallow soils than on soils that were deep or variable in depth to dolomite.

During the past decade, white oak basal area increased considerably regardless of the site factors and increased the most on benches (fig. 4). Post oak basal area also increased, and relatively large net growth increases occurred on both upper and lower landforms, in alluvium, and in soils that were either variable in depth or shallow to dolomite bedrock. Most notably, both scarlet oak and black oak basal area decreased on summits and shoulders and black oak basal area also decreased on benches. The category "other oaks," which is mostly composed of chinkapin oak, increased primarily on sites having soils that were variable in depth or shallow to dolomite bedrock. The basal areas of "other

Table 1—The 48 tree species observed on 648 MOFEP vegetation plots

Scientific name	Common name	Basal area <i>ft²/ac</i>	Trees per acre <i>no.</i>
<i>Quercus velutina</i> Lam.	Black oak	23.2	58
<i>Q. coccinea</i> Muenchh.	Scarlet oak	20.3	49
<i>Quercus alba</i> L.	White oak	19.6	130
<i>Pinus echinata</i> Mill.	Shortleaf pine	8.0	21
<i>Quercus stellata</i> Wangenh.	Post oak	5.8	22
<i>Carya glabra</i> (Mill.) Sweet	Pignut hickory	3.8	49
<i>C. texana</i> Buckl.	Black hickory	3.6	44
<i>C. tomentosa</i> Poir. Nutt.	Mockernut hickory	3.4	56
<i>Cornus florida</i> L.	Flowering dogwood	3.2	349
<i>Nyssa sylvatica</i> Marsh.	Blackgum	2.3	86
<i>Quercus muehlenbergii</i> Engelm.	Chinkapin oak	0.6	5
<i>Q. marilandica</i> Muenchh.	Blackjack oak	0.5	3
<i>Acer rubrum</i> L.	Red maple	0.4	54
<i>Sassafras albidum</i> (Nutt.) Nees	Sassafras	0.4	104
<i>Juglans nigra</i> L.	Black walnut	0.3	1
<i>Ulmus rubra</i> Muhl.	Slippery elm	0.3	20
<i>U. alata</i> Michx.	Winged elm	0.3	19
<i>Fraxinus americana</i> L.	White ash	0.2	18
<i>Juniperus virginiana</i> L.	Red cedar	0.1	3
<i>Acer saccharum</i> Marsh.	Sugar maple	0.1	3
<i>Quercus shumardii</i> Buckl.	Shumard oak	0.1	1
<i>Q. rubra</i> L.	Northern red oak	0.1	< 1
<i>Carya cordiformis</i> (Wangenh.) K. Koch	Bitternut hickory	0.1	1
<i>Ulmus americana</i> L.	American elm	0.1	4
<i>Rhamnus caroliniana</i> Walt.	Carolina buckthorn	0.1	36
<i>Cercis canadensis</i> L.	Redbud	0.1	16
<i>Morus rubra</i> L.	Red mulberry	< 0.01	4
<i>Diospyros virginiana</i> L.	Persimmon	< 0.01	6
<i>Amelanchier arborea</i> (Michx. f.) Fern.	Serviceberry	< 0.01	7
<i>Crataegus</i> spp.	Hawthorn	< 0.01	4
<i>Prunus serotina</i> Ehrh.	Black cherry	< 0.01	5
<i>Bumelia lanuginosa</i> (Michx.) Pers.	Gum bumelia	< 0.01	3
<i>Carya ovata</i> (Mill.) K. Koch	Shagbark hickory	< 0.01	< 1
<i>Celtis occidentalis</i> L.	Hackberry	< 0.01	9
<i>Viburnum rufidulum</i> Raf.	Rusty black haw	< 0.01	7
<i>Fraxinus pennsylvanica</i> Marsh.	Green ash	< 0.01	2
<i>Carpinus caroliniana</i> Walt.	Hornbeam	< 0.01	3
<i>Gleditsia triacanthos</i> L.	Honey locust	< 0.01	< 1
<i>Prunus americana</i> Ehrh.	Wild plum	< 0.01	1
<i>Ostrya virginiana</i> (Mill.) K. Koch	Ironwood	< 0.01	< 1
<i>Asimina triloba</i> (L.) Dunal	Pawpaw	< 0.01	8
<i>Rhus copallina</i> L.	Winged sumac	< 0.01	1
<i>Celtis laevigata</i> Willd.	Sugarberry	< 0.01	1
<i>C. tenuifolia</i> Nutt.	Dwarf hackberry	< 0.01	2
<i>Rhus glabra</i> L.	Smooth sumac	< 0.01	1
<i>Elaeagnus umbellata</i> Thunb.	Autumn olive	< 0.01	< 1
<i>Robinia pseudoacacia</i> L.	Black locust	< 0.01	< 1
<i>Staphylea trifolia</i> L.	Bladdernut	< 0.01	< 1

species,” mostly comprised of shortleaf pine, and the three most common hickories, increased regardless of site factors.

DISCUSSION

Oaks are the most dominant genera of trees in our study area and comprise most of the basal area regardless of

landform, soil parent materials, aspect classes, and depths to and extent of dolomite bedrock. This differs from meso-phytic forests of the Central Hardwood Region found north and east of the Missouri Ozarks where oaks are components of more diverse forests and where oaks are often restricted to drier sites such as on ridge tops and south-facing slopes (Johnson and others 2002). This suggests that the condi-

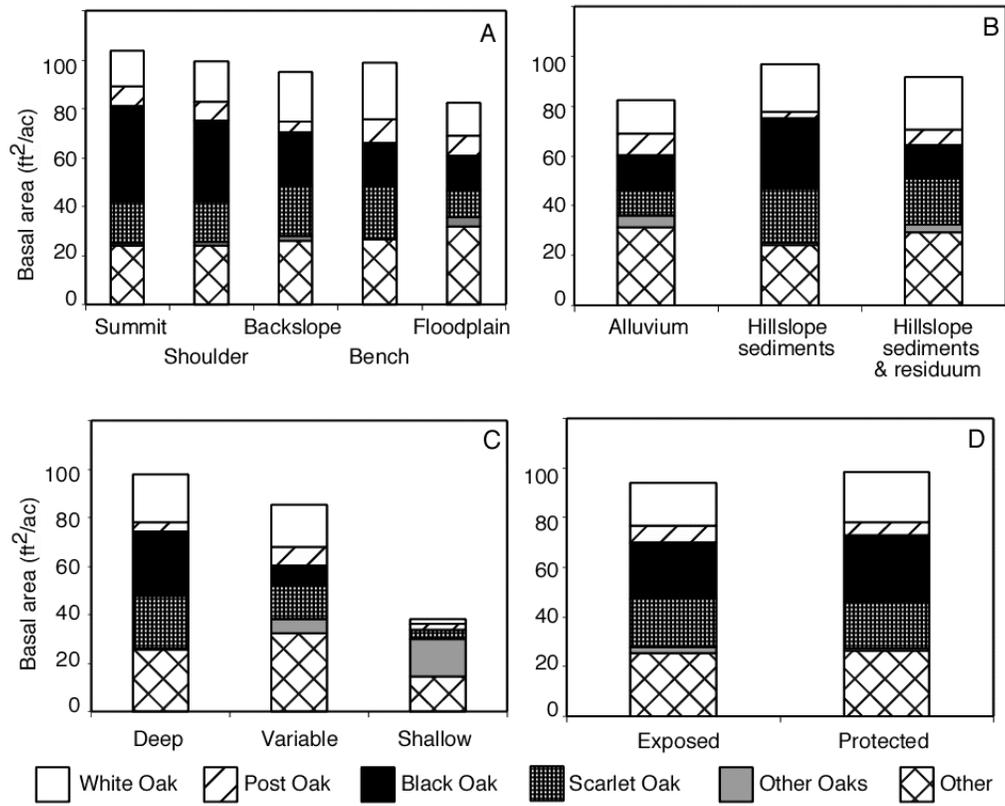


Figure 2—Proportion of mean basal area by species group and (A) landform, (B) soil parent material, (C) soil depth to bedrock, and (D) aspect.

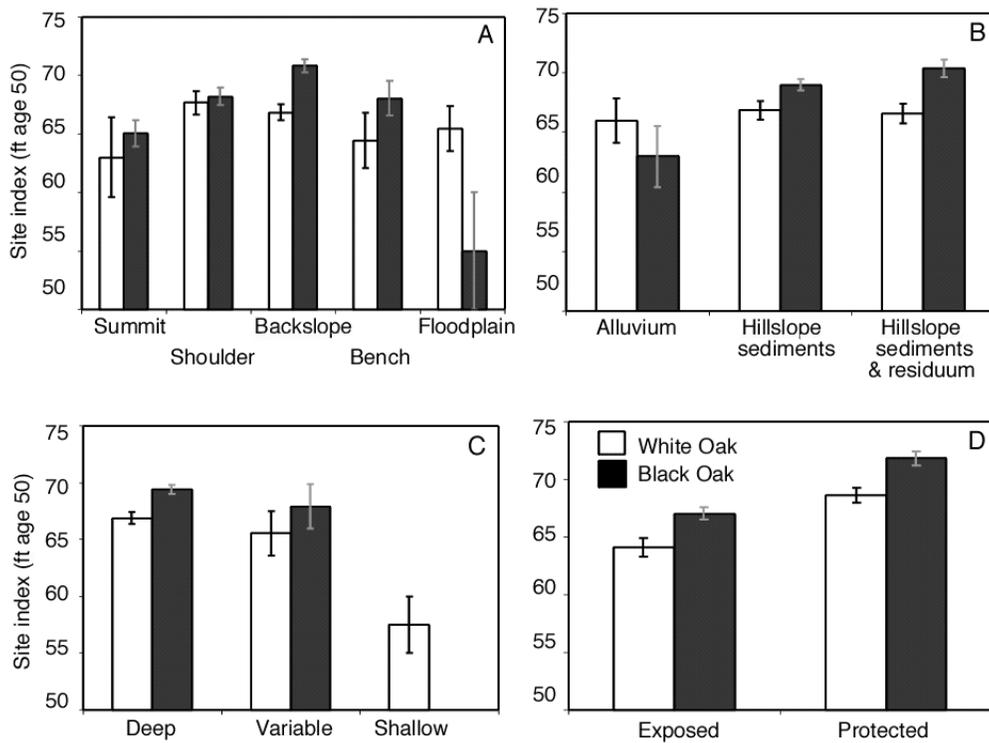


Figure 3—Mean site index (age 50) for white oak and black oak by (A) landform, (B) soil parent material, (C) soil depth to bedrock, and (D) aspect. There were no black oak site index trees on shallow soils, panel (C).

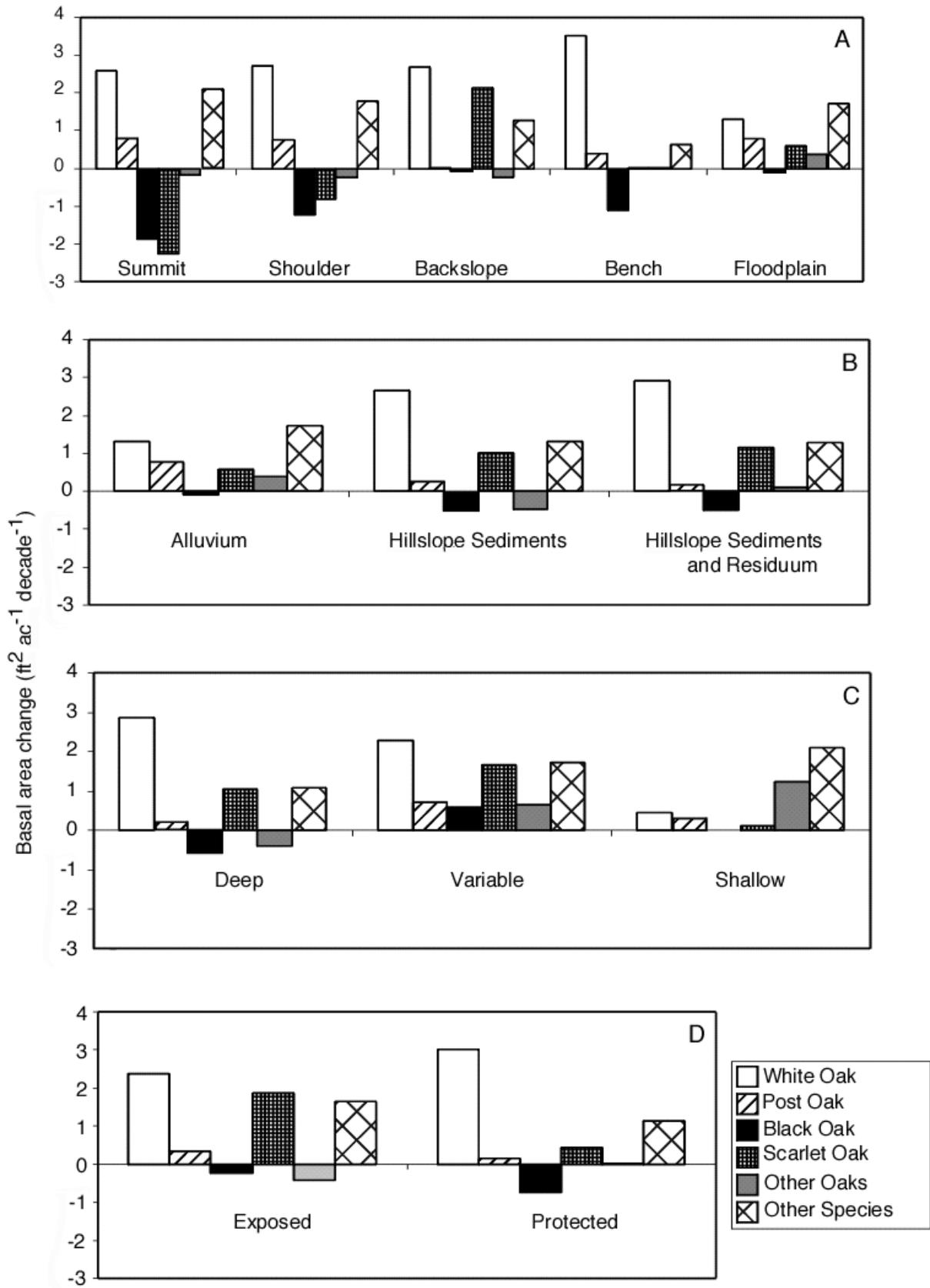


Figure 4—Mean net basal area growth (ft² ac⁻¹ decade⁻¹) by species group and (A) landform, (B) soil parent material, (C) soil depth to bedrock, and (D) aspect for trees ≥ 4.5 in. diameter at breast height.

tions of our study area are generally drier, and therefore they restrict development of many of the mesic species that are abundant elsewhere in the Central Hardwoods Region. Moreover, oaks are adapted to fire (Guyette and Dey, 1997; Johnson and others 2001), an important disturbance throughout the Ozarks for hundreds of years prior to extensive fire suppression efforts beginning around 1940 (Batek and others 1999, Guyette and Dey 1997). Most evidence suggests that fire in the pre-European landscape also maintained a more open woodland structure in our study region rather than the closed-canopy forests present today (Batek and others 1999).

In our analysis, the species composition differences related to site factors were subtle. The most prominent relationships were that black oaks were more abundant on drier landforms such as summits and shoulders than on other landforms and both black oaks and scarlet oaks were more abundant in soil parent materials having a low water holding capacity and low nutrient supply than in other soil parent materials. Evidence from remnant stumps indicates that in the pre-European landscape, shortleaf pines were once much more prominent on these drier and nutrient-poor sites than they are today (Guyette and Dey 1997). Guyette and Dey (1997) attribute relatively low abundance of shortleaf pine in these sites today to the extensive pine harvesting during the late 1800's and early 1900's followed by frequent burning. It appears that black oaks, and to some degree scarlet oaks are now most abundant in sites that historically supported more shortleaf pines.

Both black oaks and scarlet oaks are susceptible to decline as they mature, particularly on droughty, nutrient-poor sites (Johnson and others 2002). At MOFEP, most of the black oak and scarlet oak basal area is from older, large-diameter trees. Our data show that black oaks on all sites had a net growth loss due to high mortality and both black oak and scarlet oak net growth losses were particularly great on summits and shoulders. On undisturbed sites, white oaks appear to be replacing black oaks and scarlet oaks and are increasing in basal area regardless of the site factors. Compared to black oaks and scarlet oaks, white oaks are more shade tolerant, live longer, and are less susceptible to oak decline. Consequently, white oaks had a greater in-growth rate and lower mortality rate than either black oaks or scarlet oaks. Post oaks are also increasing in dominance, but at a much slower rate because of their slow growth rate and because their shade intolerance limits their regeneration in the absence of disturbances. Much like white oaks, post oaks are long lived and not considered very susceptible to decline. Relatively large net growth increases by post oaks occurred where post oaks were particularly abundant such as on both upper and lower landform positions, in alluvium, and in variable depth and shallow soils. Of the common, "other species," shortleaf pine, pignut hickory, black hickory, and mockernut hickory had the greatest net basal area increases, largely due to moderate growth rates of residual trees and low mortality rates during the sampling period (data not shown).

Site quality, as determined by site index, was more closely related to site factors than was species composition. Landform position and aspect were the two most important factors

followed by depth to or extent of dolomite bedrock and soil parent materials. Specifically, our data suggest that the highest site indices for both white oaks and black oaks occurred on protected backslopes where soils were deep and were formed in hillslope sediments overlying residuum. These particular site factors thus indicate where water and nutrients are more available and where rooting volume is greater.

It is important to recognize that the four site factors evaluated in our study are not completely independent of one another. For example, soils that are shallow to bedrock occur more frequently on exposed aspects, and alluvium is found nearly exclusively in floodplains. Clearly, these site factors must be used in combination as is the practice in ecological classification schemes such as the one that Grabner (2002) developed for the MOFEP study area. Our analysis quantified relationships among the composition, site quality, and growth of oaks and other trees species, and site factors most important for identifying and distinguishing ecological land types and phases in the southeastern Missouri Ozarks.

ACKNOWLEDGMENTS

We thank the dozens of technicians who sampled woody vegetation on MOFEP during the past decade as well as all of the scientists and Missouri Department of Conservation staff who have made conducting MOFEP possible. We also thank Doyle Henken of the Mark Twain National Forest and Dr. Eric Zenner of the University of Minnesota for reviewing an earlier draft of this manuscript.

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A DENDROCHRONOLOGICAL ANALYSIS OF RED OAK BORER ABUNDANCE

Rose-Marie Muzika and Richard P. Guyette¹

Abstract—Unprecedented outbreaks of red oak borer (*Enaphalodes rufulus* Haldemann) have occurred in the lower Midwestern United States. Although generally not a mortality agent, red oak borer appears to contribute to general oak decline and mortality. The objective of this project was to explore dendrochronology as a means of determining the role of tree age, tree growth and climate in long-term red oak borer activity and to quantify the historic importance of red oak borer. In a *Quercus* (oak) dominated forest in Missouri, 31 oak trees were sampled and dendrochronological methods used to develop a red oak borer chronology. Borer activity in the stand has increased over the past 70 years with large increases occurring over the last 25 years. The abundance of wounds was related to tree age, ring width, annual mean temperature, and annual mean minimum temperature. Red oak borer wound abundance was not related to tree basal area increment, mean maximum temperature nor precipitation.

INTRODUCTION

Enaphalodes rufulus (Haldeman) Coleoptera: Cerambycidae, (red oak borer) is a wood boring insect that occurs throughout a wide range of deciduous forests in North America (Donley and Acciavatti 1980). In the past, damage associated with this insect has resulted in log degrade and overall decrease in wood quality. Recently very high population levels of the red oak borer have coincided with oak decline sites, and although not a primary mortality agent, it is clear that an abundance of red oak borer damage occurs in oak dominated forests with high tree mortality. Many explanations have been invoked to explain recent and unprecedented outbreaks of *E. rufulus* in the Ozark Highlands of Missouri and Arkansas. Among these, the abundance and age of host tree species, principally *Quercus* species (oaks), may provide an explanation. It is more likely, however, that the outbreaks are a result of host abundance coupled with the potential effect of climate on the development of *E. rufulus*. Historically, borer populations may have been limited by the sporadic occurrence and mixed age distribution of host tree species in the Missouri Ozarks. Forest harvesting regimes (ca. 1900), however, have resulted in extensive tracts of even-aged forests consisting predominantly of host species, namely *Quercus* sect. *Lobatae* (red or black oaks). On many sites these tree species have replaced shortleaf pine (*Pinus echinata*). A complete understanding of oak decline and specifically red oak borer abundance is lacking; in particular the relationship of red oak borer and site, climate, stand history has yet to be clarified. There is a need to understand tree, forest, and environmental conditions that influence such outbreaks.

Dendrochronology has been used often in entomology research to evaluate the frequency and timing of defoliator outbreaks (e.g., Fritts and Swetnam 1989, Swetnam and Lynch 1993), or the influence of defoliators on growth loss (Muzika and Liebhold 1999). The use of dendrochronology to examine wood boring insects, however, is relatively uncommon. Notable exceptions include a study by McManus and Giese (1968) that revealed that precipitation, temperature and flooding, were positively related to population fluctuations of the Columbian timber beetle (*Corthylus*

columbianus Hopkins). Cambium mining insects (Diptera: Agromyzidae) create scars, sometimes referred to as pitch flecks, and have been used to evaluate population dynamics over a period of several decades (Schimitschek 1935, Ylloja and others 1999).

For this study, our primary goal was to document historic red oak borer occurrences as a way to examine the presence and abundance of red oak borer relative to a variety of abiotic factors. The intent is to begin to decipher the components of oak decline. Specifically, we examined the response of oak borers to climate, tree growth, tree age and stand age. We used dendrochronologically-dated xylem wounds made by oak borer larvae to construct borer activity chronologies at an oak decline site in the Missouri Ozarks.

METHODS

The study area was located in the Mark Twain National Forest, approximately 5 km east of Bixby, Missouri. The stand was a designated salvage site where most of the trees were to be removed soon after our study was complete. The 70-year old stand was dominated by scarlet oak and black oak. We established two 20 m belt transects and sampled each scarlet and black oak that fell within the transects. Thirty-one trees were sampled. Each sampled tree was felled and cut into one meter intervals, beginning at 1 m.

In the lab cross sections were prepared by sanding. Annual tree growth increments were cross-dated (Stokes and Smiley 1986) and tree stem initiation dates determined. Injuries were identified as borer damage by the wound configuration and characteristics (size, xylem wound shape, holes in bark, excelsior fibers), the presence of borer tunnels and tunnel stain traces, and infrequently, the occurrence of live larvae in tunnels. Although all borer wounds can be dated, not all borer tunnels on a cross-section are datable. The dimensions of each dated wound were measured and used as confirmation and stratification of wounds. These include: tangential extent of callus tissue and cambial death, the radial extent of callus tissue, presence/absence of tunnels, tunnel width and length. Borer wounds from all thirty-one

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trees were then compiled into a frequency distribution with annual resolution. Specifically, this oak borer chronology represents a time series of oak borer activity as preserved in the tree-ring record by the larval scarring of the cambium.

Radial growth chronologies of sampled trees were constructed in order to examine the relationships between borer activity and tree growth. Growth chronologies were calculated as raw ring-width (mm) and annual basal area increment (cm²) was constructed. Basal area chronologies were used to assess tree growth and vigor while ring-width chronologies were used as an indirect estimate of change in wood density. Correlation analysis was used to determine the strength of relationship between red oak borer abundance and several stand and climate variables.

RESULTS

We tree-ring dated a total of 743 oak borer wounds on the 31 trees that grew in a declining oak forest in southeastern Missouri. From these data we developed a red oak borer chronology that described the levels of larval activity for a period extending more than 60 years (fig. 1). The red oak borer has a synchronized two-year life cycle (Solomon 1995). The predominance of wounds (89 percent) occurred biennially, supporting our supposition that red oak borer caused most cambial injuries.

Borer wounds increased abruptly during the late 1970's and remained at high levels to such an extent that red oak borer abundance was consistently greater than at any time since stand initiation in 1935 (fig. 1). The dramatic increase in red oak borer wounds occurred at a stand age of approximately 50 years.

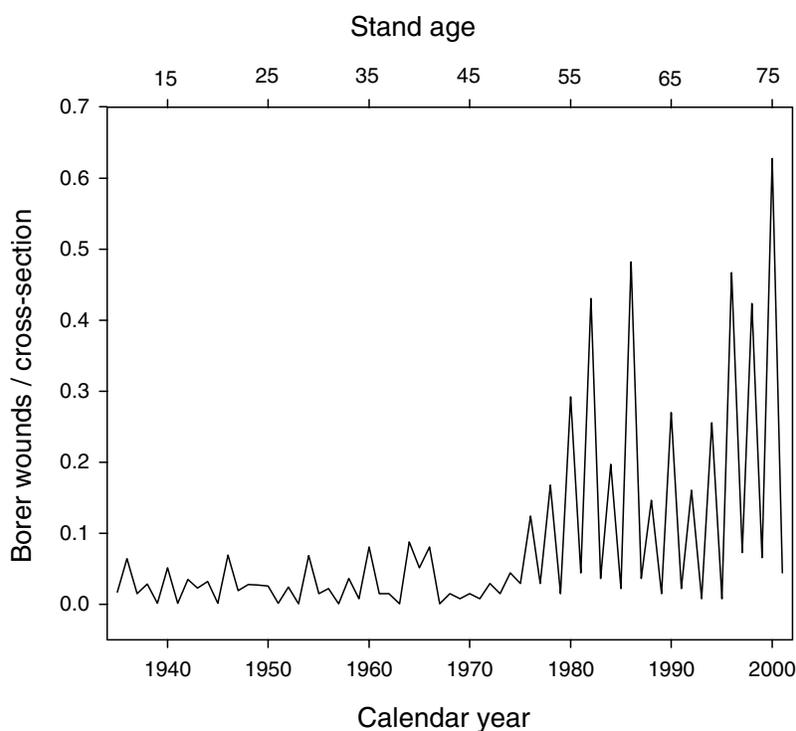


Figure 1—An annual frequency distribution of larval borer wounds dated on 137 cross sections from 31 oak trees near Bixby, MO.

Table 1—Correlation coefficients for the relationship between growth variables and tree-ring dated borer wounds

Growth variables	All dated wounds	Dated wounds/tunnels
Mean ring-width	-0.47**	-0.43**
[ln] ring-width	-0.51**	-0.47**
Basal area increment	0.17	0.15
Forest stand age	0.50**	0.46**

* = $p < 0.05$; ** = $p < 0.01$.

Dated wounds/tunnels are wounds that were associated with characteristic red oak borer tunnels. Mean ring-width is the raw nonstandardized width of the rings. Analysis includes all years of record (1920–2000).

Table 2—Correlation coefficients for the relationship between climate variables and tree-ring dated borer wounds

Climate variables	All dated wounds	Dated wounds/tunnels
Annual mean temperature	0.49*	0.56**
Annual mean max temperature	-0.22	-0.12
Annual mean min temperature	0.54*	0.59**
Annual total precipitation	0.18	0.06

** = $p < 0.05$; * = $p < 0.01$.

Dated wounds/tunnels are wounds that were associated with characteristic red oak borer tunnels. Analysis is for even calendar years only during the period of recent red oak borer abundance (1956–2000). Even years are the years of synchronous red oak borer larval injury to the cambium.

We examined the correlations between growth variables and red oak borer activity. Correlations were performed on all dated wounds, as well as only those wounds that co-occurred with tunnels. The latter category of wounds represents a more conservative estimate of red oak borer activity. Basal area increment was not significantly related to the frequency of borer wounds (table 1), but mean ring-width and logarithmic transformed ring-width were both inversely related to red oak borer abundance, and forest stand age was positively related to red oak borer abundance.

Annual mean temperature and annual mean minimum temperature were positively related to red oak borer activity (table 2). Neither annual mean maximum temperature nor annual total precipitation was significantly related to red oak borer activity. Results were similar whether all dated wounds were used or dated wound with tunnels only.

DISCUSSION

These data indicate that the large increases in the frequency of borer wounds occurred in the mid to late 1970s (fig.1) despite the fact that this wood boring beetle has gained attention only during the late 1990's. Furthermore, red oak borer wounds did not correlate with basal area increment, an index that quantifies the amount of basal area that accrues on a tree or in a forest, i.e. the cross sectional area of wood produced by the tree annually. The lack of a relationship indicates that red oak borer outbreaks are not simply related to decreases in tree vigor. There was an inverse association between mean ring-width and increases in wound frequency (table 1). This association may be related to several direct and indirect factors such as reductions in wood density. Although outbreaks of red oak borer are associated with stressed trees that eventually succumb, these data suggest that individual trees and entire stands can support substantial populations of red oak borer for decades before the stand exhibits signs of decline.

Correlation analyses indicate that temperature, ring width, and stand age were most strongly related to the frequency of borer attacks. Minimum temperature was most strongly related to the frequency of red oak borer wounds (table 2). The effect of temperature on red oak borers is corroborated by previous laboratory experiments that found increases in

temperature (21.1 to 32.2 °C) were positively related to the survival and fecundity of laboratory reared red oak borer (Galford 1974). We found no significant relationships between precipitation (table 2) and borer activity, despite the purported influence of drought on reduction in tree resistance.

Climatic factors can strongly influence insect populations, and substantial evidence exists to demonstrate how fecundity, survival, and dispersal are affected by temperature, precipitation, wind or humidity. Over long time periods, rainfall has been the most consistent predictor of insect populations, at least defoliators (Swetnam and Lynch 1993). Our data suggests that although drought may play a role in general oak decline, there seems to be no relation between precipitation at our study sites and red oak borer abundance.

Considering the potential implication of climate change and red oak borer, among other insects (Williams and Liebhold 2002), it is critical to examine trends in temperature in order to develop predictions. Although the magnitude of increase in mean temperatures has been modest, change in mean minimum temperature has been much larger. In the region of the case study, minimum temperatures have increased about 2.8 °F since the 1960s. Minimum temperatures could be most limiting to borer development, growth, reproduction, and fecundity (Galford 1974).

Whole wood density and ring-width have been shown to be strongly related in ring-porous angiosperms (Panshin and Zeeuw 1970). Large-diameter vessel elements that occur only in earlywood have large empty lumens that make the earlywood less dense. Since earlywood width tends to be consistent among rings, irrespective of total width; proportionally, more earlywood (low-density) occurs in narrow rings. Since ring width size is negatively related to red oak borer wounds, wood density could be a direct and important variable concerning the temporal, spatial, and stem distribution of larval wounds. Wood density might reflect host quality from both a physical and chemical perspective. As density decreases the proportion of early wood within rings increases as does the proportion of readily hydrolyzed hemicellulose (Wu and McGinnes 1974). Further research may explain the significance of this factor.

CONCLUSIONS

Our research has provided insight into the evaluation of historical abundance of red oak borer and of factors controlling its activity. Oak borer wound chronologies offer us a new tool. The sectioning of trees and dating of wounds provides data on insect larval populations in an exact location for from 50 to 150 years. The data compiled is high resolution (tree wounds dated to the year), relatively long-term (many generations of insects), and abundant (many single trees have over one hundred borer wounds). This type of research will greatly improve our ability to sample and interpret both short and long-term changes in the abundance of wood boring insects and decipher basic biological limitations on insects.

This research represents a case study providing some indication about the factors that influence red oak borer activity and consequently oak decline. Further research will provide greater information about these and other factors that may ultimately assist in developing predictive models and influence management activity.

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WILDLIFE AND UPLAND OAK FORESTS

James G. Dickson¹

Abstract—The oak forests of the eastern U.S. have always been diverse as well as dynamic; continually molded and influenced by a variety of natural and anthropogenic forces. These forests support thousands of species of plants, untold numbers of insects and other invertebrates, and hundreds of species of vertebrate wildlife. Because of the large number of species, I focus on species and communities of special interest or concern. Acorns are a primary fall and winter diet item of many vertebrate species. Acorns build energy reserves, which are very important for winter survival and successful reproduction for a number of species. The wild turkey, white-tailed deer, and American black bear, which suffered and were very limited a century ago, have been restored and now flourish. There are a wide variety of bird species associated with upland oak forests; most associated with specific habitat attributes. Generally, there is concern for two categories of birds: nearctic-neotropical migratory birds, and early successional, grass-forb associated birds. Bats are important ecological components of oak forests; several species of cave bats are endangered and there is concern for others. Even though upland oak ecosystems are mostly xeric, the forests support a high diversity of reptile and amphibian species, and provide important habitat for many species.

HISTORY

Around 10,000 BC or even earlier, the first humans arrived in North America. Here they found several species of megafauna and beech-maple forests. By about 5,000 BC the megafauna had disappeared and the climate had become warmer and drier. Oak-Hickory forests dominated the lower eastern United States on upland sites, with Pine-Hardwood forests prominent in the deep South. The influence of the natives in North America grew, and accounts of early French explorers in the 1500s chronicled substantial populations and influence on the land by natives. But later accounts by Spanish explorers in the 1700s painted quite a different picture. Apparently there had been widespread demise of the natives, attributed to diseases contracted from the earlier explorers. A substantially reduced human population had lessened effect on the forest and there was widespread development of old-growth forests.

Accounts of the earliest naturalists in the 1700s such as William Bartram (Van Doren 1928) tell of vast old-growth forests with large trees, snags, and down material. But he also describes prairies and grass-forb habitat with associated species, such as indigo buntings and yellow-breasted chats, and game species such as the wild turkey, white-tailed deer, and elk; each of which depend on early successional habitat during some stage of their life cycle. A forest savannah condition with sparse overstory and grassy ground cover probably was widespread in the lower South, but also apparently prevalent in some mountain systems, such as the Ouachitas as recounted by Bukenhofer and Hedrick (1997).

But the old growth forests of the 1700s and its associated wildlife would soon face the onslaught of European colonizers who rapidly changed the landscape. As natives were overcome or evicted, new settlers colonized the eastern North American hardwood forests. They cleared new ground to make way for their crops, and felled trees for wood to heat their homes and build their houses and barns. The vast forests of the East fell to the axe and saw.

In the late 1800s and early 1900s the wholesale clearing of the forest and the direct harvest of many species of animals were profound. There was little thought of or provision for the future, nor concept of conservation. Game animals were taken at will to feed the settlers' burgeoning families, and predators were regarded as competitors or threats and shot. A few species, such as the Carolina parakeet and passenger pigeon, were lost forever and other species suffered. The relatively remote eastern mountains functioned somewhat as refuges for a few impacted species, such as black bears and wild turkeys.

Recovery of the forests in some fashion began in early 1900s. Southeastern mountains were less fertile than prairies or bottomland, and were less populated by humans. Consequently, a higher portion of these mountainous regions was included in the National Forests. Later, cutover forest land and crop land were abandoned and regenerated to forest. And even later, wildlife management had its beginnings. The first efforts were directed toward game species whose populations were precariously low.

In recent years, oak forests of the U.S. have aged and increased in extent. The broad category of upland hardwood forests of the South increased from 65 to 75 million acres from 1952 to 1996 (Sheffield and Dickson 1998). And many stands are even-aged, having regenerated at about the same time.

DYNAMIC NATURE

The oak forests of the eastern U.S. have always been diverse as well as dynamic; having been continually molded and influenced by a variety of natural and anthropogenic forces. Fire, windstorms, diseases, and insects have played a major role in what the forests were and how they functioned. The natives, and even more so the early settlers, added to these forces, compounding the effects. One wholesale change illustrates. The American chestnut was once a dominant tree of eastern Appalachian hardwood

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forests. But the chestnut blight in the early 1900s eliminated mature forms of American chestnut from the landscape. So what once was an oak-chestnut forest became an oak-hickory forest.

Today, the dynamic nature and changes continue. For example, demise of older oak stands is being wrought by the gypsy moth in the Appalachians and the red oak borer in the Ozarks. Influences on the forests are exacerbated by the increased number of humans and their associated technology. Large scale damming of rivers, wholesale land use changes, and pesticides serve as examples.

WILDLIFE

Upland oak forests of the U.S. support thousands of species of plants, untold numbers of insects and other invertebrates, and hundreds of species of vertebrate wildlife. Wildlife communities have evolved over thousands of years with the forests and have been molded by the dynamic nature of the forests. A few species, such as the Carolina parakeet, have been lost. Premier game species, such as the white-tailed deer and wild turkey, have been restored. While the status of others, such as the myriad reptiles and amphibians, remain generally unknown.

Acorns

Obviously, one of the most prominent characteristics of oak forests in relation to wildlife is the acorns they produce. Acorns are a primary fall and winter diet item of many vertebrate species, as well as insects. Some examples of the variety of species which consume acorns include: passerine birds- such as blue jays, woodpeckers- red-headed and red-bellied, waterfowl-wood ducks (even on upland sites), squirrels- gray, fox, and southern flying, small terrestrial rodents- such as wood rats and *Peromyscus*, raccoons, wild hogs, and high profile species: black bear, white-tailed deer, wild turkey, and northern bobwhite.

Oak acorns have relatively low levels of protein and phosphorus (Short and Epps 1976), but with a high lipid content they provide an important energy source to animals. Acorns build energy reserves, which are very important for winter survival and successful reproduction for a number of species.

An important feature of oak mast production in regard to the ecology of the forest and its wildlife communities is the extreme variability in annual production. For example, in a 19-year study in the Ozark Mountains of Arkansas, annual acorn production fluctuated drastically in all four vegetation types (Dickson 1990). In each forest type there was very little or no production in 5 of the 19 years. There was no production in the cedar glades or streambottom oak type, less than 10 kg/ha in the pine-oak type, and less than 22 kg/ha in the upland oak type. Conversely, mast production was profuse (>120 kg/ha) in 7 of the 19 years in the upland oak type and 9 of 19 years in the pine-oak type.

In that myriad species consume acorns, this phenomenon of erratic acorn production helps insure regeneration of oak forests during years when the ample acorn supply surpasses the collective demands of species that consume acorns. But this extreme variability in annual production is tough on the wildlife that depends on mast.

The importance of acorns to species and its' effects on their population viability is demonstrated by data from studies of several different species. During boom years life is good; but in bust years there is extreme competition for acorns and wildlife suffers. For example in an oak dominated Ozark forest, annual acorn production was critical to deer herd health and productivity (Rogers and others 1990). During years of low acorn production, winter survival of deer was lower and fawn survival the subsequent spring also was lower than that of years of moderate to high production.

Mast from oaks also is very important to black bears. In the southern Appalachians, oak mast, primarily white oak, has a significant impact on bears in terms of natality, mortality, and movements (Pelton 1991). The birth and survival of young bears were directly associated with oak mast crops.

Acorns are also very important to some species of rodents. For example, populations of white-footed mice declined with acorn failures and increased with acorn supplementation (Jones and others 1998).

Oak forests are important habitat for wild hogs (Dickson and others 2001). For example, in the Appalachians Eurasian wild hogs used mixed oak stands more than expected during years of high mast production, but not when little mast was available (Singer and others 1981); and a similar habitat use pattern was observed in bottomland hardwoods in South Carolina (Kurz and Marchinton 1972). Acorns are a preferred food item and hogs are efficient foragers. During years of minimal acorn production, wild hog consumption of acorns probably negatively affects native mast-consuming species.

Turkeys, deer, and bear

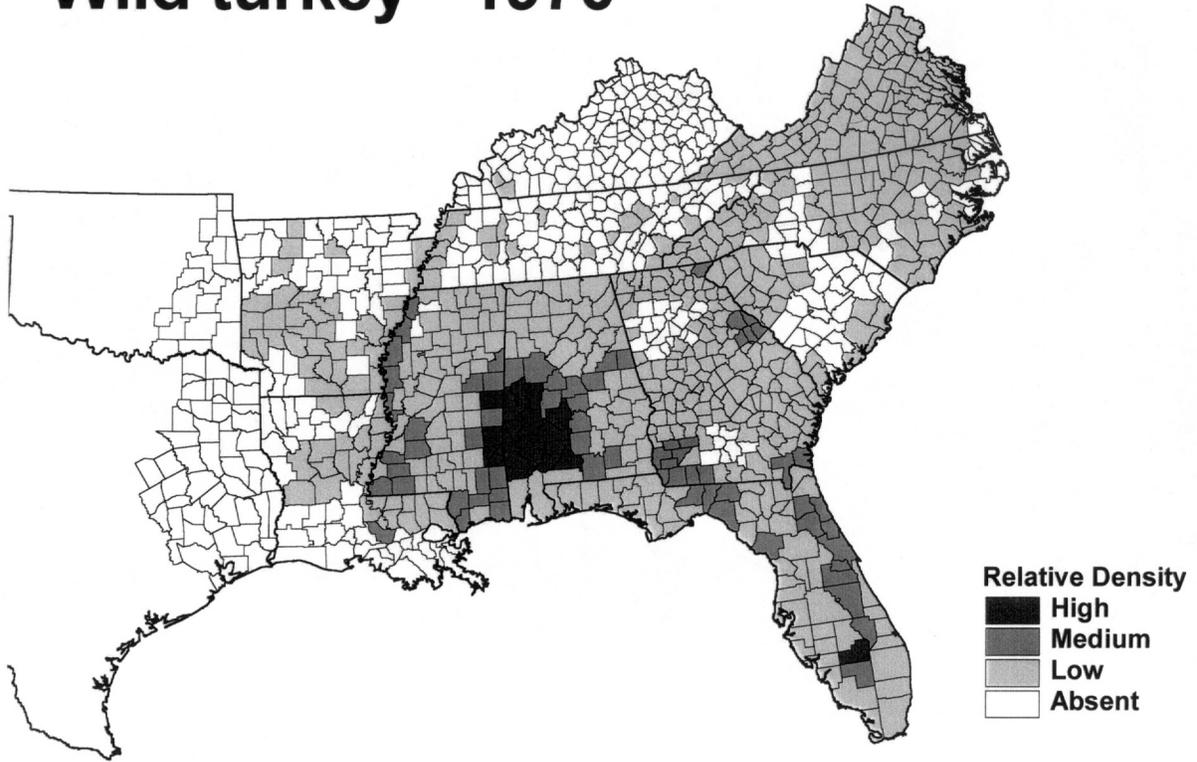
The wild turkey, white-tailed deer, and American black bear suffered, and experienced population lows during the era of exploitation in the 1800s and early 1900s. But they have been restored, and populations have increased dramatically in recent decades (fig. 1).

Traditional and optimum habitat for the wild turkey is oak forests in conjunction with other associated land uses (see Dickson 1992). These forests and the mast they produce provide optimum fall and winter habitat, and are used extensively. Associated forest ground and shrub vegetation, openings, and agriculture pastures and crop land provide strutting grounds, nesting sites, and appropriate brood habitat.

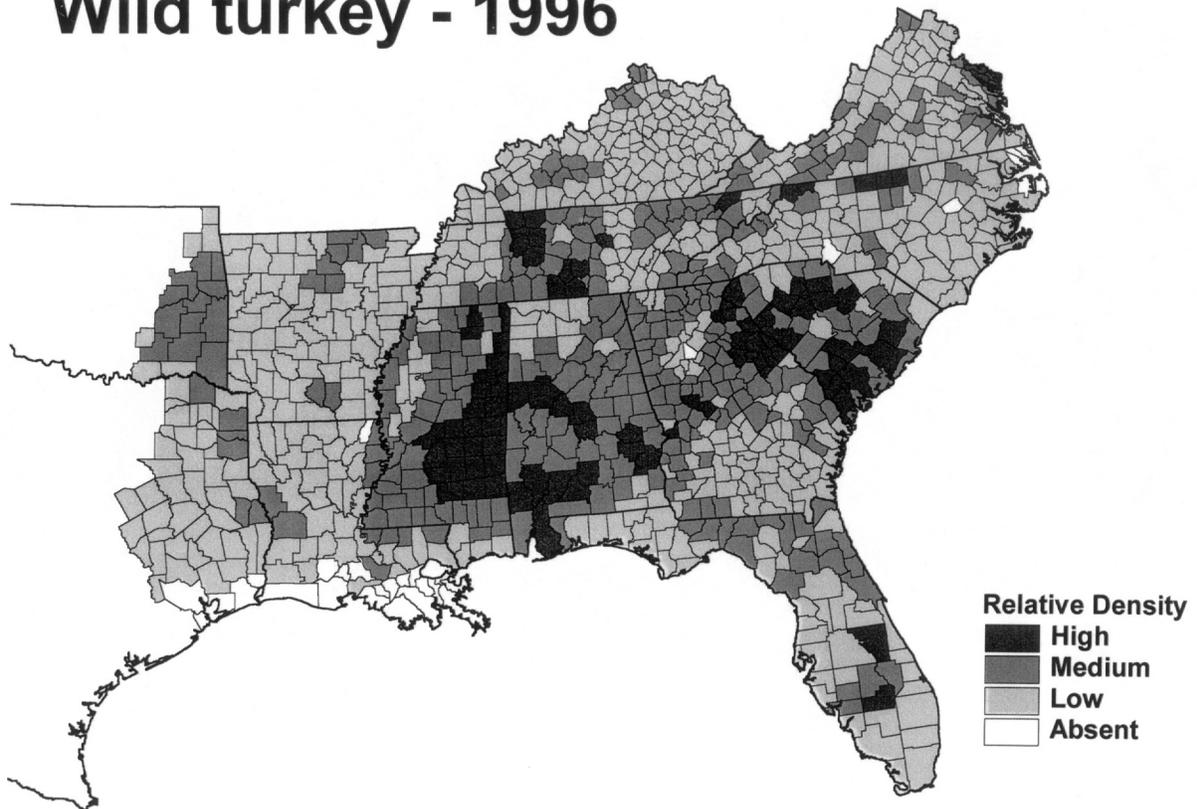
Wild turkeys have persisted in oak forests historically. Recently, due to maturing of the forests, better protection, and trapping and transplanting, populations have prospered, and now thrive throughout southern oak forests (fig. 1) and elsewhere. Population estimates nationwide now surpass 5 million.

White-tailed deer are distributed throughout and thrive today in upland oak forests where their dietary needs of browse, forbs, fungi, and soft and hard mast are met. Populations today are found in every county in the Southeast (fig. 1). Although soils are not as productive in mountainous oak forests as in some other types and they are not optimum

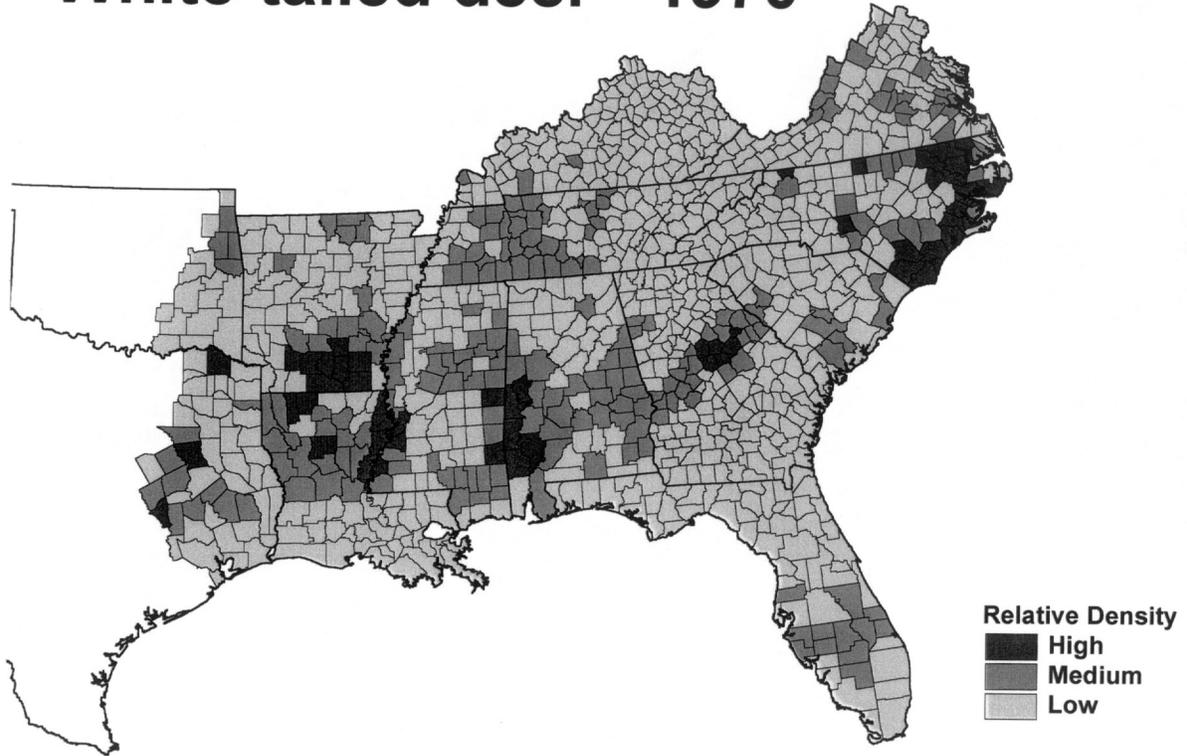
Wild turkey - 1970



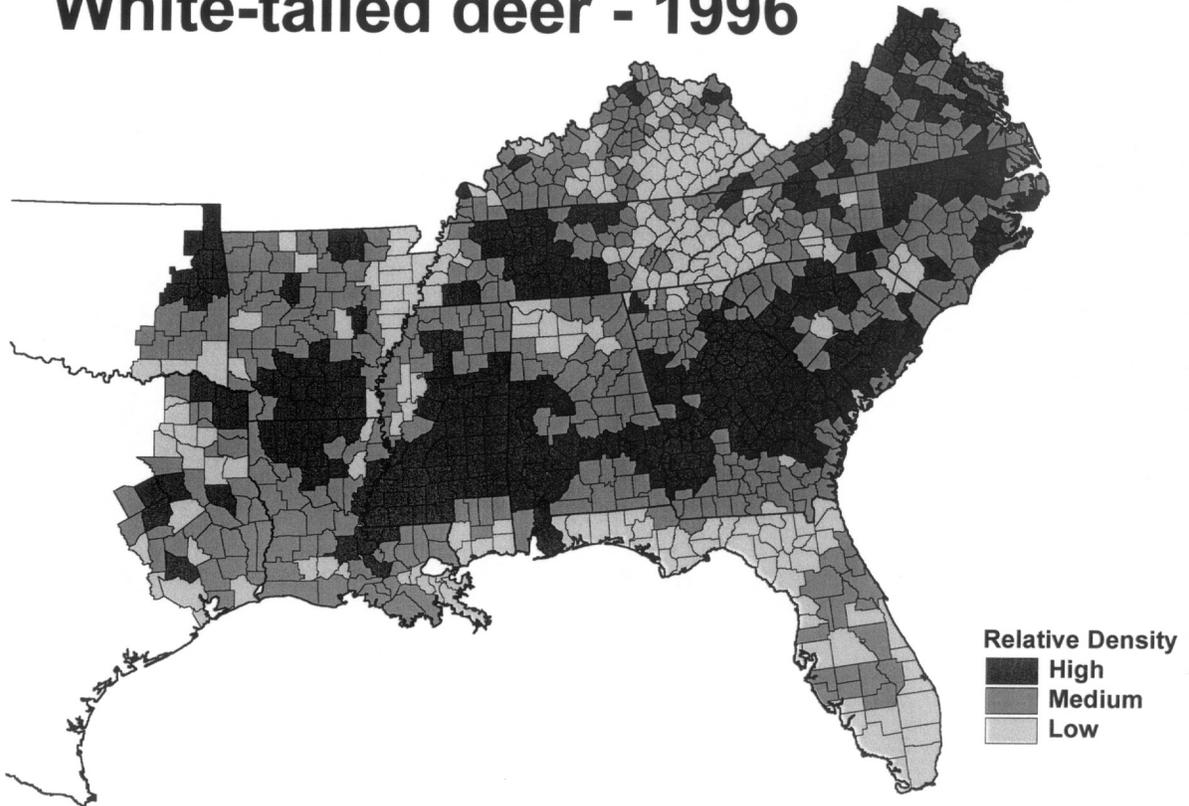
Wild turkey - 1996



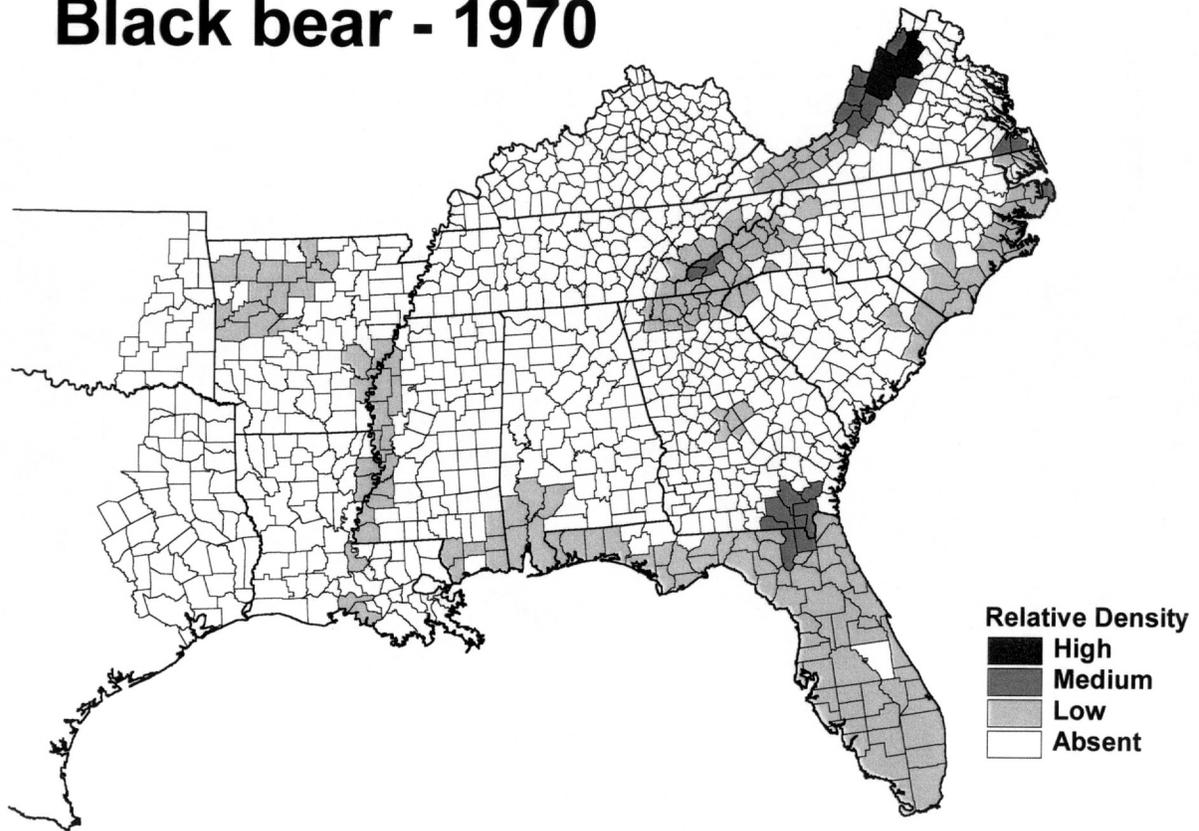
White-tailed deer - 1970



White-tailed deer - 1996



Black bear - 1970



Black bear - 1996

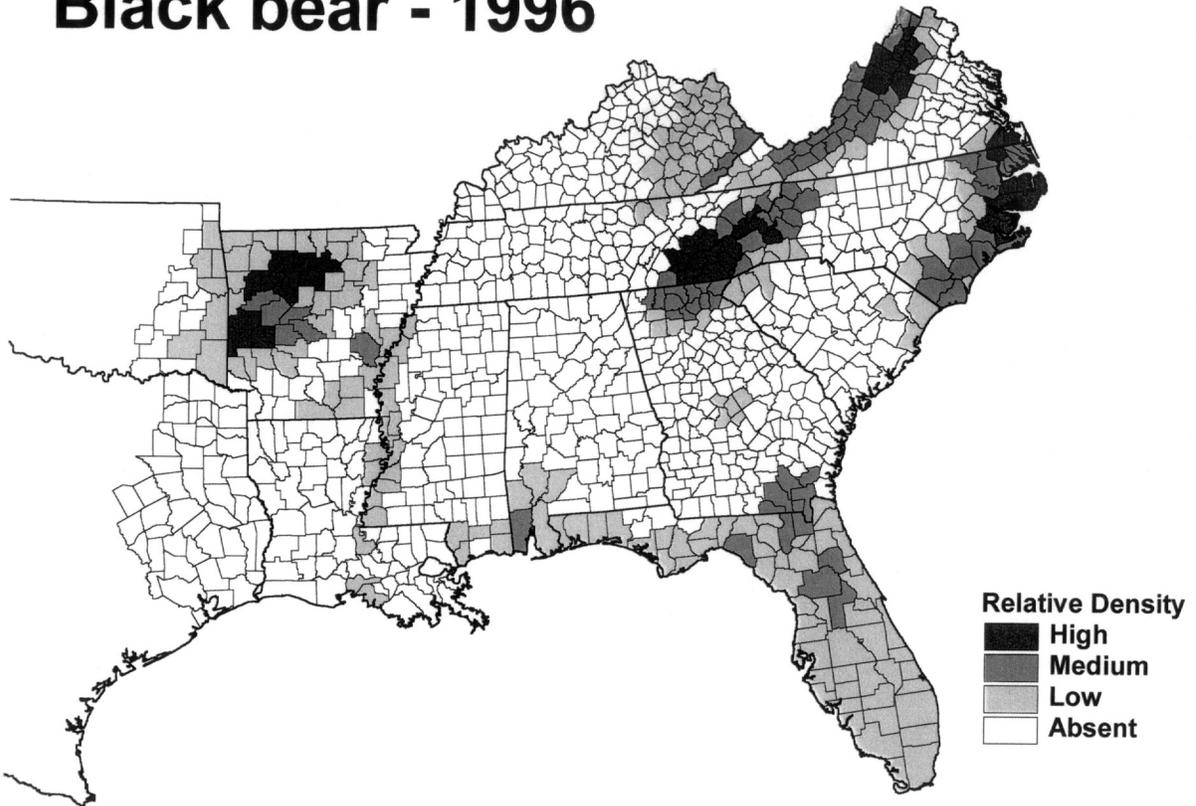


Figure 1—Relative densities of wild turkeys, white-tailed deer, and American black bear for 1970 and 1996 by county in the Southeast. Density categories are: turkey-low <6, med 6-15, high >15 per sq mi; deer- low <15, med 15-30, high >30 per sq mi; bear-low <1 per 1,500 ac, med- 1 per 1,500-1 per 1,000 ac, high >1 per 1,000 ac (from Dickson 2001).

deer habitat, they still remain heavily forested and white-tailed deer fare well there. Also, the white-tailed deer has proven highly adaptable, and thrives where oak forests are interspersed with agriculture crops or even suburbs.

Black bears require large areas of suitable habitat with little human interaction, secure corridors for movements, some very thick understory habitat, and rocky outcrops or large hollow trees for denning (Pelton 2001). As with the wild turkey and white-tailed deer, the American black bear suffered substantially earlier from habitat loss and direct

harvest. The last refuges were remote areas, such as swamps and mountains. Populations persisted and recently, numbers have increased and populations are viable in mountainous eastern oak forests- the Appalachians and Ozark/Ouachitas (fig. 1).

Birds

Some upland oak forests, such as the southern Ridge and Valley and Interior Low Plateau are heavily fragmented. Conversely the oak forests of the Ozarks and southern Appalachians are substantial in distribution and remain

Table 1—Abundance of nearctic-neotropical migratory birds in central hardwood forests

Species	Stand age					
	R	S	P	M	G	T
Whip-poor-will	U	U	U	U	U	U
Ruby-throated hummingbird	C	N	N	N	?	N
Acadian flycatcher	N	N	C	A	N	A
Eastern wood-pewee	N	N	U	A	N	A
Eastern phoebe	N	N	U	U	N	U
Great-crested flycatcher	C	C	C	C	C	C
Blue jay	C	C	C	C	C	C
American crow	U	U	U	U	U	U
Carolina wren	C	C	U	N	?	?
Blue-gray gnatcatcher	A	C	C	C	C	C
Eastern bluebird	C	N	N	N	N	N
Wood thrush	U	C	C	C	U	C
Gray catbird	C	C	N	N	?	N
White-eyed vireo	C	C	N	N	?	N
Yellow-throated vireo	N	N	N	U	N	U
Red-eyed vireo	U	U	A	A	U	A
Blue-winged warbler	A	C	N	N	?	N
Golden-winged warbler	C	U	N	N	?	N
Northern parula	N	N	U	C	N	C
Chestnut-sided warbler	C	C	N	N	?	N
Yellow-throated warbler	N	N	U	U	N	U
Pine warbler	N	N	C	C	N	C
Prairie warbler	A	C	N	N	?	N
Black-and-white-warbler	C	C	C	C	C	C
Worm-eating warbler	U	C	C	C	C	C
Ovenbird	U	C	C	C	U	U
Louisiana waterthrush	N	U	C	C	C	C
Common yellowthroat	A	U	N	N	?	N
Kentucky warbler	A	C	U	U	A	C
Hooded warbler	C	C	U	U	C	C
Yellow-breasted chat	A	C	N	N	?	N
Orchard oriole	U	N	N	N	N	N
Summer tanager	C	C	C	A	C	C
Scarlet tanager	U	U	C	A	U	A
Indigo bunting	A	C	U	U	A	C
Eastern towhee	A	U	N	N	C	N
Field sparrow	A	N	N	N	?	N
Brown-headed cowbird	A	C	C	C	C	C
American goldfinch	U	N	N	N	N	N

R = regeneration; S = sapling; P = poletimber; M = mature; G = group selection; T = single tree selection; A = abundant; C = common or regular; U = uncommon; N = not present.

Source: Dickson and others (1993).

mostly intact. These widespread hardwood forests may serve as source populations for some species, contributing to landscape-scale population viability.

There is a wide variety of bird species associated with upland oak forests. Some are habitat generalists, but most are associated with specific habitat attributes. Forest structure, among other factors, determines bird species distribution (table 1). Some species, such as the field sparrow and northern bobwhite, are associated with grass-forb habitat. Others, such as the prairie warbler and white-eyed vireo,

inhabit shrub level vegetation. Some, such as the Kentucky and hooded warblers inhabit shaded forest understories. And some, such as the red-eyed vireo and summer and scarlet tanagers, are found in tree canopies.

Based on Partners in Flight assessments, generally there is concern for two categories of birds: nearctic-neotropical migratory birds, and early successional, grass-forb associated birds (Hunter and others 2001). Migratory species considered of high priority and associated with mature oak forests are presented in table 2. Causes for the decline are

Table 2—Primary habitat associations and seasonal status among high priority landbird species within upland hardwood-dominated forested landscapes of the Southeastern U.S.

Regional high priority species	Hardwood-dominated forests		
	Hardwood pine mix	Central hardwoods	Appalachian forests
American Woodcock	B,W		B
Yellow-billed Cuckoo	B	B	B
Northern Saw-whet Owl S. Appalachian pop.			b
Chuck-will's-widow	B		
Red-headed Woodpecker		B,W	
Yellow-bellied Sapsucker S. Appalachian pop.			B
Eastern Wood-Pewee	B	B	B
Acadian Flycatcher	B	B	B
Black-capped Chickadee S. Appalachian pop.			b
Red-breasted Nuthatch S. Appalachian pop.			b
Brown Creeper S. Appalachian pop.			b
Winter Wren S. Appalachian pop.			b
Golden-crowned Kinglet S. Appalachian pop.			b
Wood Thrush	B	B	B
Yellow-throated Vireo		B	B
Northern Parula	B	B	B
Black-throated Blue Warbler			B
Black-throated Green Warbler Atlantic Coastal pop.	B		
Blackburnian Warbler			B
Cerulean Warbler	B	B	B
Worm-eating Warbler	B	B	B
Swainson's Warbler	B		B
Louisiana Waterthrush		B	B
Kentucky Warbler	B	B	B
Hooded Warbler	B	B	B
Canada Warbler			B

Appalachian forests = Appalachian forests include here mature to old-growth northern hardwoods, hemlock-white pine-hardwoods, mixed mesophytic (cove) hardwoods, with various gradations into Appalachian oak (central hardwoods) types on drier more exposed sites and into spruce-fir at the highest elevations; B = breeding; W = wintering; B,W = refers to species using similar habitat but in different areas between seasons (i.e., highly migratory); lower case (b) = refers to habitats where species occurs in very low densities but may still prove to be important to that species.

Source: Hamel (1992); Hunter and others (2001).

unclear. Perhaps wintering habitat is important; populations of some mature forest associated species have declined while upland hardwood forests in the U.S. have aged. Some of these are isolated populations of otherwise widespread species, such as the southern Appalachian population of the Bewick's wren (Hunter and others 2001).

Another group that has experienced declines in recent decades is the early successional associated species. Populations of resident game species, such as northern bobwhites, ruffed grouse, and American woodcock, have suffered substantial declines in recent decades as upland forests have aged (Dickson 2001). Because of habitat changes and/or population declines, several species in both groups, nearctic-neotropical migrants associated with early successional habitat, such as prairie, chestnut-sided, and golden-winged warblers are often listed as species of concern (Hunter and others 2001).

So forest structure, and natural and anthropogenic forces that affect that structure, to a large extent determine bird communities. One example is the effects of the ecosystem management practices on the Ouachita National Forest (Bukenhofer and Hedrick 1997). In response to thinning and prescribed burning, Wilson and others (1995) found 10 ground/shrub foraging and shrub nesting species of breeding birds were favored, and 2 ground nesters, the ovenbird and black-and-white warbler were disfavored.

The effects of tree harvesting on habitat structure and bird communities have been amply demonstrated (Dickson and others 1993). Two studies serve as examples and illustrate the relationships. In an oak-hickory forest in northwestern Arkansas, heavy cutting of understory and selective cutting of overstory disfavored the understory nesting bird guild, but favored some early successional species such as the indigo bunting, edge species such as the eastern wood pewee, and canopy nesters in the short term (Rodewald and Smith 1998). In a central hardwood forest in Missouri (Annand and Thompson 1997), five migrant songbirds, the blue-winged warbler, prairie warbler, northern towhee, white-eyed vireo, and yellow-breasted chat were more abundant in clearcut treatments. Indigo buntings and field sparrows were more abundant in clearcut and shelterwood treatments. Hooded warblers and northern parulas were more abundant in selection treatments. Ovenbirds and wood thrushes were more abundant in mature sites. And Acadian flycatchers and red-eyed vireos were more abundant in group and single-tree selection treatments and mature stands. A nest parasite, the brown-headed cowbird, was more abundant in clearcuts, and abundance of the two avian nest predators, the blue jay and American crow, did not differ among the five treatments.

Bats

Bats are important ecological components of oak forests. Several species are endangered, and there is concern for other species. Bats are long-lived and have a low reproductive rate; usually one offspring each year. Bat species can be grouped into two categories: cave bats, which inhabit caves at some time, and non-cave bats, which seldom enter caves. Three species of cave bats in the southern oak forests are endangered: the gray bat, the Indiana bat, and

the eastern populations of Townsend's big-eared bat (Ozark and Virginia big-eared bats) (Harvey and Saugey 2001). And three other species of forest cave bats, the southeastern bat, the eastern small-footed bat, and the Rafinesque's big-eared bat are of special concern.

Disturbance of cave bats by humans can be a problem. Cave bats in hibernating or maternity colonies expend precious energy when disturbed, and are vulnerable to disturbance. Protection of cave sites is important to the conservation of these species.

Habitat features and management activities near bat caves and even forest wide may affect bats (Harvey and Saugey 2001). For example, a group of Rafinesque's big-eared bats always foraged less than 2.5 km from their hibernaculum and maternity cave along ridgelines in an upland oak-hickory forest (Hurst and Lacki 1999). Forest structure obviously is important to bats during some time in their life cycle. Bats use tree leaves, loose bark, cavities, snags, and other structure, such as spanish moss for roosting and sometimes maternity sites. Trees with these features are used by and benefit bats. Streamside zones contain many tree and stand features positive for bats; so retention of mature trees in streamside zones when harvesting adjacent stands is beneficial. Bats are insectivorous, and silvicultural practices which promote flying insects can be positive. Tree harvesting or prescribed burning may open foraging areas and enhance insect prey. Bats often forage over water, such as ponds and lakes, so appropriate habitat near water probably benefits bats.

Reptiles and amphibians

Even though upland oak ecosystems are mostly xeric, the forests support a high diversity of reptile and amphibian species, and provide important habitat for many species. Some species are not associated with water, and spend their entire life in forested habitat, often in small areas. The greatest diversity of salamanders in the United States occurs in the oak-dominated southern Appalachian region (Gibbons and Buhlmann 2001). Species of the genus *Plethodon* are common and several are endemic, with relict populations inhabiting isolated mountains (Pough and others 1998). Examples include the Peaks of Otter salamander on a 5-mile stretch of ridge in Virginia, the Cow Knob salamander at high elevations on the George Washington National Forest along the Virginia-West Virginia boundary, and the Weller's salamander in the high elevation remnant spruce forests on mountain tops in North Carolina and Virginia.

Other species are dependant on non-forest habitat for critical stages of their life cycle. Salamanders, such as *Ambystoma*, and frogs, such as narrow mouthed toads, inhabit forests as adults but lay their eggs in water and their larvae are aquatic. For these species, stream structure and water quality in conjunction with moist forest habitat are important habitat features. Streamside zones or strips of mature trees along permanent or intermittent streams can provide important habitat for a number of species (e.g., Rudolph and Dickson 1990).

Other species are dependant on different and often limited habitat. Examples include the Tennessee cave salamander,

which inhabits caves, and the green salamander that inhabits shaded, moist, sandstone cliffs. For species or populations that inhabit limited and often isolated habitat, moist upland forests may function very importantly as connective or linkage habitat. Also, other forest structures, such as snags and down material, afford protection and provide habitat for a variety of reptiles and amphibians.

CONCLUSIONS

Upland oak forests have always been dynamic, subjected to and developed by a variety of natural and anthropogenic forces. Wildlife communities of these forests have evolved with and are adapted to these forests and their dynamic nature. To accommodate the full complement of native wildlife a wide variety of different habitats, such as grass-forb, shrub, woodland savannah, and mature stands should be maintained in sufficient quantity and size.

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APPENDIX A

Common and Scientific Names of Animals in Text

Common name	Scientific name	Common name	Scientific name
Mammals		Birds (cont.)	
Small-footed bat	<i>Myotis leibii</i>	Bewick's wren	<i>Thryomanes bewickii</i>
Indiana bat	<i>M. sodalis</i>	Blue-winged warbler	<i>Vermivora pinus</i>
Southeastern bat	<i>M. austroriparius</i>	Golden-winged warbler	<i>V. chrysoptera</i>
Gray bat	<i>M. grisescens</i>	Northern parula	<i>Parula americana</i>
Rafinesque's big-eared bat	<i>Plecotus rafinesquii</i>	Chestnut-sided warbler	<i>Dendroica pennsylvanica</i>
Townsend's big-eared bat	<i>P. townsendii</i>	Prairie warbler	<i>D. discolor</i>
Gray squirrel	<i>Sciurus carolinensis</i>	Black-and-white warbler	<i>Mniotilta varia</i>
Fox squirrel	<i>S. niger</i>	Ovenbird	<i>Seiurus aurocapillus</i>
Southern flying squirrel	<i>Glaucomys volans</i>	Kentucky warbler	<i>Oporornis formosus</i>
White-footed mouse	<i>Peromyscus leucopus</i>	Hooded warbler	<i>Wilsonia citrina</i>
Eastern woodrat	<i>Neotoma floridana</i>	Yellow-breasted chat	<i>Icteria virens</i>
Black bear	<i>Ursus americanus</i>	Summer tanager	<i>Piranga rubra</i>
Raccoon	<i>Procyon lotor</i>	Scarlet tanager	<i>P. olivacea</i>
Wild hog	<i>Sus scrofa</i>	Eastern towhee	<i>Pipilo erythrophthalmus</i>
Elk	<i>Cervus elaphus</i>	Field sparrow	<i>Spizella pusilla</i>
White-tailed deer	<i>Odocoileus virginianus</i>	Indigo bunting	<i>Passerina cyanea</i>
Birds		Brown-headed cowbird	<i>Molothrus ater</i>
Wood duck	<i>Aix sponsa</i>	Reptiles and Amphibians	
Ruffed grouse	<i>Bonasa umbellus</i>	Eastern narrow-mouthed toad	<i>Gastrophryne carolinensis</i>
Wild turkey	<i>Meleagris gallopavo</i>	Green salamander	<i>Aneides aeneus</i>
Northern bobwhite	<i>Colinus virginianus</i>	Tennessee cave salamander	<i>Gyrinophilus palleucus</i>
American woodcock	<i>Scolopax minor</i>	Peaks of Otter salamander	<i>Plethodon hubrichti</i>
Carolina parakeet	<i>Conuropsis carolinensis</i>	Cow knob salamander	<i>P. punctatus</i>
Red-headed woodpecker	<i>Melanerpes erythrocephalus</i>	Weller's salamander	<i>P. welleri</i>
Red-bellied woodpecker	<i>M. carolinus</i>	Invertebrates	
Eastern wood-pewee	<i>Contopus virens</i>	Gypsy moth	<i>Lymantria dispar</i>
Acadian flycatcher	<i>Empidonax vireescens</i>	Red oak borer	<i>Enaphalodes rufulus</i>
White-eyed vireo	<i>Vireo griseus</i>	Plants	
Red-eyed vireo	<i>V. olivaceus</i>	American chestnut	<i>Castanea dentata</i>
Blue jay	<i>Cyanocitta cristata</i>	White oak	<i>Quercus alba</i>
American crow	<i>Corvus brachyrhynchos</i>	Spanish moss	<i>Tillandsia usneoides</i>

OAK-BLACK BEAR RELATIONSHIPS IN SOUTHEASTERN UPLANDS

Joseph D. Clark¹

Abstract—Bears (*Ursus americanus*) primarily occur in upland habitats in the Southeast because uplands were the last to be developed for agriculture and were more likely to become publicly owned. National parks and forests created in the early to mid-1900s served as sources to supply surrounding uplands with bears. Bears could not survive in southeastern uplands without oak mast. Bear reproductive and mortality rates in the region have been shown to be directly linked with acorn production. Masting is thought to be an adaptation by oaks to satiate predators during good acorn years, thus ensuring that the remainder will germinate. Acorn predator populations, however, cannot respond numerically to increased acorn production because the masting is episodic and synchronous. Consequently, bears have developed physiological, behavioral, and ecological adaptations to cope with such food shortages. Despite such adaptations, upland hardwood forests in the Southeast are of lower quality than they once were. The loss of the American chestnut (*Castanea dentata*), higrading, and soil degradation have markedly decreased the carrying capacity for bears and other wildlife. Other changes such as recent forest management practices, forest fragmentation, invasion by the gypsy moth (*Lymantria dispar*), and oak decline threaten to further degrade the capability of southeastern uplands to support bears.

UPLANDS BY DEFAULT

Although we tend to equate bear habitat in the Southeast with mountainous upland hardwood forests, bear occurrence in the mountains is probably by default rather than preference. Historically, bears were common in the bottomland hardwoods of the Southeast (Gerstacker 1854, Bartram 1955). Remnant bottomland forests in Louisiana and Arkansas continue to support some of the highest bear densities in North America (Beausoleil 1999, R. Eastridge, Arkansas Game and Fish Commission, unpublished data). Those fertile bottomlands, however, were among the first to be developed for agriculture and other uses and now comprise only about 15 percent of their historic acreage (Gosselink and others 1989). Bears rapidly disappeared from those developed areas and, today, black bear populations in fragmented bottomlands are at greatest risk of extinction (Neal 1992, Bentzien 1998).

As the conversion of bottomland forests to farmland occurred, the less fertile, rugged land in the mountains remained relatively undeveloped. During the early to mid-1900s, many such upland areas came into public ownership, primarily as national forests and parks. Bears managed to persist in inaccessible reaches of many of these areas and later served to repopulate adjacent uplands where bear densities had been severely reduced (Clark and Pelton 1998). Today, many consider bears to be overabundant in portions of the region's uplands. Although bears were extirpated in the Cumberland Plateau of Tennessee and Kentucky, and in the Interior Highlands of Arkansas and Missouri, bear reintroduction programs in these areas have been successful (Smith and Clark 1994, Eastridge and Clark 2001).

OAKS, THE DRIVING FORCE

Simply put, bears could not survive in southeastern uplands today without oak mast. Acorns have been found to be the major fall food item of bears in virtually every study conducted in southeastern uplands (Vaughan 2002). Pelton (1989)

describes acorns as the “driving force for bear population dynamics” in the southern Appalachians; the same is probably true in the Interior Highlands of Arkansas (Clapp 1990, Clark 1991).

Acorns are an important energy source for bears because they are relatively high in fat and carbohydrates (Inman 1997). High-energy fall diets enable bears to withstand the rigors of winter denning, production of young, lactation, and food scarcity in early spring (Poelker and Hartwell 1973, Eagle and Pelton 1983). During good acorn years, bears are capable of fulfilling their energy requirements for 4 to 6 months of hibernation during a 2- or 3-month period of intense foraging in the fall. Bears have been known to consume >20,000 calories in a 24-hr period while feeding on acorns (Nelson and others 1983). Additionally, acorns are sometimes eaten in spring following years of mast abundance. In the Interior Highlands, hard mast comprised up to 45 percent volume and 75 percent frequency of spring diets of bears during some years (Clapp 1990).

Bear movements increase dramatically in response to acorn abundance, known as the “fall shuffle.” Their activity patterns change from being primarily crepuscular, to nearly continuous activity to forage on acorns (Garshelis and Pelton 1980). Bears seasonally shift their home ranges and movement patterns to take advantage of localized mast (Garshelis and Pelton 1981) resulting in long-range movements during mast shortages. Acorn failures can have a marked effect on bear mortality rates, with increased highway deaths being associated with the extensive movements. Also, hunting mortality can be dramatically affected during poor acorn years (Kane 1989, McDonald and others 1994, Noyce and Garshelis 1997), with greater movements leading to higher success among hound hunters and localized mast resulting in increased effectiveness of archery hunters. With sequential years of mast failure, outright starvation can occur.

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The lack of acorns also can result in reproductive failure (Eiler and others 1989, Pelton 1989). Bears have delayed implantation, with breeding and fertilization occurring in summer, and implantation of the blastocyst into the uterine wall in fall. Failure to implant may occur in females in poor physical condition. If implantation does take place in such cases, the newborn cubs may not survive because of the inability of the female to lactate (Vaughan 2002). Following den emergence, cub mortality during mast failures has been shown to be >80 percent (Vaughan 2002). Reproductive rates may be particularly impacted when mast failures occur in 2 sequential years, as has occurred in the southern Appalachians (Pelton 1989). Such mast failures also delay age of first reproduction in females and can cause reproductive synchrony in this biennial breeder. In good mast years following poor ones, parturition occurs among nearly all adult females. This will result in a large cohort of dispersing 2-year-old subadults, an age class vulnerable to hunting and more prone to nuisance activity. Those 2-year-olds will likely breed the following year and subsequently contribute to another large cohort. Thus, acorn failures and, to a lesser extent, good acorn crops, have long-lasting ecological effects on bear population dynamics.

BEARS, OAKS, AND COEVOLUTION

Acorns are an important source of fats and carbohydrates in the diets of not only bears, but >180 other wildlife species as well. Reproduction and survivorship for many species are closely coupled with acorn production. Population fluctuations of white-footed mice (*Peromyscus leucopus*), gray squirrels (*Sciurus carolinensis*), white-tailed deer (*Odocoileus virginianus*), blue jays (*Cyanocitta cristata*), and red-headed woodpeckers (*Melanerpes erythrocephalus*) have all been linked with fluctuations in acorn mast crops (Pearson 1953, Smith 1986, Elkington and others 1996, McCracken and others 1999). Because of these many acorn predators, oaks have developed mechanisms which reduce such predation.

Masting is the intermittent production of large seed crops by a population of plants (Kelly 1994). One hypothesis to explain this phenomenon is predator satiation (Salisbury 1942; Janzen 1971, 1975; Silvertown 1980, 1982; Koenig and Knops 2002). Under that hypothesis, seed predator populations are kept low in non-masting years because of the scarcity of seeds whereas, during heavy mast years, overabundant fruit places foraging limitations on mast predators. Masting must be episodic so that populations of mast predators do not have enough time to respond reproductively. Masting must also be synchronous over broad areas so that acorn predation is not affected by immigration from poor to good mast areas. Although weather patterns (e.g., spring frosts, drought) can affect acorn production, recent evidence suggests a natural periodicity to acorn production consistent with the predator satiation hypothesis (Sork and others 1993).

Additionally, acorns have an anti-predator defense, tannin, which makes them less palatable and digestible. Red oaks have higher tannin content than do white oaks, but white oaks sprout soon after they fall to the ground and, thus, do not need as much protection from predation (Fox 1982). Red oak acorns, on the other hand, have about three times the fat content as white oaks. Both the fat and the tannin

are localized to certain portions of the acorns. White-footed mice, squirrels, and other animals prefer red oak acorns, perhaps because they can select the portion of the acorn with the highest fat and lowest tannin content for consumption (Fox 1982, Line 1999). Black bears consume acorns whole; consequently, they prefer white oak acorns. Thus, masting and tannin content in oaks appear to be adaptations to acorn predation by bears and other species.

Conversely, bears are well adapted to endure such acorn shortages and to take advantage of years of acorn abundance. Pelton (1989), in his review of the importance of oak mast to black bears, states that bears adjust physiologically, behaviorally, and ecologically in response to oak mast. Physiologically, bears are adapted systemically and hormonally to digest the fats and carbohydrates found in acorns (Brody and Pelton 1988). Once digested, bears have the ability to store large quantities of fat and to use that stored energy when needed. During hibernation, another adaptation to periods of food scarcity, that fat is converted to energy and urea and other byproducts are recycled (Nelson and others 1983). Weight loss during hibernation is from adipose tissue only; lean body mass is conserved.

Behaviorally, bears are able to scale trees to eat acorns from the canopy before the fruits fall. In acorn-rich areas, bears tend to partition themselves spatially and temporally, with minimal intraspecific conflicts, thus maximizing caloric intake while minimizing caloric expenditure. Rogers (1987) suggested that bears may first visit such food-rich areas as cubs and later return as adults. The high level of intelligence of these mammals undoubtedly helps them relocate areas where foods have been plentiful in the past.

Ecologically, bears are typical of a species adapted to fluctuating environmental conditions (Stearns 1977). The basic strategy for bears, in a teleological sense, is to produce young only when environmental (and, thus, physiological) conditions are favorable and, once born, invest a maximum amount of energy to ensure their survival. For example, bears have a long gestation period, delayed age of first reproduction, and a lengthy rearing period to maximize the chances that their progeny will survive. Litter sizes are small, enabling mothers to invest more energy to care for cubs. Also, bears may defer reproduction during periods of environmental stress (e.g., by implantation failure, fetal absorption). In years when food is scarce, bears enter dens earlier and avoid further energy expenditures. Thus, oaks and acorn predators such as bears are engaged in what has been called a "coevolutionary arms race."

A CHANGING LANDSCAPE

Although oaks are "the driving force" today, that may not have always been the case. The oak forests that we associate with southeastern uplands are essentially second- and third-growth replacements. Additionally, many important food-producing plants (e.g., American chestnut) have been lost within the past century. Consequently, upland habitat where most southeastern bears reside has been significantly degraded.

It is difficult to imagine how the southern Appalachians must have looked when the American chestnut was a dominant

tree; >40 percent of the overstory in the southern Blue Ridge Mountains once was chestnut (Keever 1953). The chestnut blight fungus (*Cryphonectria parasitica*), introduced around 1900, resulted in the nearly complete loss of American chestnut in the eastern U.S. (Keever 1953). Those oak-chestnut forests have since been replaced largely by oak-hickory forests (McCormick and Platt 1980). Besides being common, annual crops of chestnuts were more reliable, without the extreme fluctuations common to oaks. In North Carolina, mast production was estimated for 2 10-year periods; one before and one 35 years after the chestnut blight fungus had killed all mature chestnut trees (Diamond and others 2000). Total hard mast output was 34 percent less after the chestnut blight and annual pre-blight mast production was relatively stable, whereas annual post-blight production fluctuated substantially. These findings suggest that the loss of mature chestnuts markedly reduced the carrying capacity of southern Appalachian forests for certain wildlife species, which certainly included the black bear.

Bears have remarkable adaptability, and have flourished even with the loss of the American chestnut in the East. Nevertheless, changes are taking place in southeastern upland hardwood habitats that could negatively affect bears in the future. Past logging practices have resulted, not only in young forests in southeastern uplands, but in forest higrading and soil degradation as well. Another important consideration for bears is soft mast production, the importance of which may have been underestimated in the past (Inman 1997). Clapp (1990) found that soft mast [dominated by Carolina buckthorn (*Rhamnus caroliniana*), Virginia creeper (*Parthenocissus quinquefolia*), black cherries, (*Prunus serotina*), devil's walkingstick (*Aralia spinosa*), pokeweed berries (*Phytolacca americana*), blackgum (*Nyssa sylvatica*), and persimmon (*Diospyros virginiana*)] comprised a greater proportion of black bear diets in the Interior Highlands in 2 of 3 years than did hard mast. Blueberries (*Vaccinium* spp.), blackberries (*Rubus* spp.), cherries, and grapes (*Vitis* spp.) all respond favorably to light gaps and disturbance. Pokeweed, for example, requires soil disturbance to generate. Given the trend away from the creation of early successional stage habitats on national forests, such buffer foods may not be as abundant as in the past.

That is not to say that bears cannot thrive in mature hardwood forests. In Great Smoky Mountains National Park, for example, bear densities are high (Eason 2002). Forests in the Smokies, however, have a substantial old-growth component (>20 percent), and the large trees that fall create light gaps. It may be many years before such a dynamic is achieved in the second- and third-growth upland forests found on our national forests. Soft mast production may be low in the interim.

A change that has yet to fully strike the southeastern uplands is the invasion of the gypsy moth. These insects have defoliated oaks in much of Virginia, but bears there were able to make use of buffer foods (primarily soft mast including grapes and pokeweed) and shift their movement patterns to patches of oaks that were not affected by the moths (Kasbohm and others 1998). Again, changes in forest composition and a reduction in soft mast could greatly

affect the ability of bears to withstand chronic reductions in acorns.

Bears are a mobile, wide ranging species, and have developed the physical and intellectual ability to take advantage of patchy, sporadic food resources. Fragmentation through clearing of woodlands for other uses and the construction of roads through prime bear habitat will greatly diminish the ability of bears to exploit such food resources. Although bears have demonstrated the plasticity to adapt to historic and recent habitat changes (i.e., chestnut blight, gypsy moths, and forest fragmentation), the cumulative effects of these perturbations, along with future problems (i.e., climate change and oak decline), may have a more widespread and lasting effect on bears.

Bears are inextricably linked with oaks in southeastern uplands. Managers should strive for a landscape mosaic comprised of red and white oak species interspersed with a wide array of soft mast to serve as buffer foods during acorn shortages. It is important to monitor changes in food-producing plants within bear range and to evaluate the effects those changes may have on bear population dynamics. Only then will we be able to explore ways to mitigate their effects.

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USE OF TREE SPECIES BY SUMMER BIRDS IN OZARK UPLAND OAK-HICKORY FOREST

C. Joan Patterson and Douglas A. James¹

Abstract—Impacts of oak-boring beetles in the Ozark region could produce major changes in forest communities of northwestern Arkansas resulting in loss of oaks replaced by other tree species. Because the extensive Ozark forests are a major source of surplus birds, alterations of forest structure producing changes in foraging opportunities for birds could have serious consequences. This study compared tree species usage while foraging in summer by year-round resident and summer resident migratory forest bird species. Extent of usage was compared to relative abundance of different tree species at each of six study sites. The results show that oak species were used by forest birds in greater proportion than their abundance at the sites.

INTRODUCTION

When European settlers arrived, much of northwestern Arkansas was in oak-hickory forest, and many regions are still heavily wooded in this manner (James and Neal 1985). These extensive forests of the Ozarks in northwestern Arkansas are believed to be population sources for several species of birds (Robinson and others 1995). There is much concern in recent decades about population declines in forest breeding intercontinental migratory birds in many regions of eastern North America (Martin and Finch 1995, Sauer and Droege 1992, Sauer and others 1999). Due to these declines population sources are important in helping to maintain population numbers elsewhere (Pulliam 1988). In recent years the red oak borer, *Enaphalodes rufulus* (Haldane), has had considerable impact on oak trees, devastating large areas (Spencer 2001). The loss of these trees may have a negative impact on populations of bird species, some of which are already stressed by other factors.

The present study was designed to investigate the importance of oaks in summer foraging by species of both year-round resident and summer resident migratory bird species in closed canopy oak-hickory forests that were not infested with the oak borer. Relative abundance of different tree species was used to determine whether oaks are used in greater or lesser proportion than their abundance by various bird species and in what proportion are other tree species used compared to their abundance and compared to oaks.

SITES

Six sites, all in northwestern Arkansas, were used in this study. All were closed canopy oak-hickory forests in different stages of development with varying amounts of undergrowth. Tree composition differed between sites. The following sites were located in Washington County: (1) Mount Sequoyah in Fayetteville, Section 15, Township 16N, Range 29W; (2) Lake Fayetteville area, Section 19, Township 17N, Range 29W; (3) Wilson Lake area, southeast of Fayetteville, Section 2, Township 15N, Range 30W; and (4) Devil's Den, near West Fork, Section 26, Township 13N, Range 31W. The remaining sites are Hobbs State Management Area at

Beaver Lake near War Eagle in Benton County, Section 36, Township 19N, Range 29W; and Withrow Springs near Forum in Madison County, Section 10, Township 17N, Range 26W.

METHODS

During the months of May, June, and July 2002 foraging behavior was studied in birds occupying oak-hickory forests in areas appearing unaffected by the oak borer. Two investigators walking together found foraging birds as they were encountered. One identified the birds and the tree species they occupied, the other recorded the information. A bird was considered to use a tree if it was either seen or heard in the tree. Data was recorded sequentially (Robinson and Holmes 1982). No more than three sequential observations of the same bird in the same tree were made. Both year-round resident and intercontinental migratory species were investigated. The number of bird observations per study area were approximately the same, but did differ somewhat.

Relative abundance of different species of trees in the study areas was determined by establishing two perpendicular transects transversing each of the study areas. There were two investigators. One identified the species of each tree having a diameter at breast height (d.b.h.) greater than 7.5 cm that occurred within a meter each side of the transect line, the other recorded this information.

RESULTS AND DISCUSSION

Tree Species Composition

To summarize forest composition, oak species (*Quercus*) made up about 25 percent or more of the trees at Wilson Lake, the Hobbs State Management Area, and Withrow Springs, nearly 20 percent at Mount Sequoyah and Lake Fayetteville, and slightly more than 10 percent at Devil's Den. Hickory species (*Carya*) made up approximately 20 percent of the trees at Wilson Lake and the Hobbs State Management Area, somewhat less at Mount Sequoyah, between 5 and 10 percent at Lake Fayetteville and less than 5 percent at Devil's Den and Withrow Springs. Elm species (*Ulmus*) made up over 30 percent of the trees at

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Mount Sequoyah, over 20 percent at Wilson Lake, between 5 and 10 percent at Lake Fayetteville, Devil's Den and the Hobbs State Management Area, and < 2 percent at Withrow Springs. The proportion of black gum, *Nyssa sylvatica* Marsh, was around 20 percent at Withrow Springs, somewhat less at Devil's Den, around 5 percent at the Hobbs State Management Area, and low or not found at the three other sites. The proportion of flowering dogwood, *Cornus florida* Linnaeus, was > 25 percent of the trees at Devil's Den, nearly 20 percent at Lake Fayetteville and Withrow Springs, over 10 percent at the Hobbs State Management Area, and < 5 percent at Mount Sequoyah and Wilson Lake. Snags made up >10 percent but <20 percent of trees at all sites. Other tree species were present in smaller numbers.

Birds Found

To provide a summary of bird species involved, Tufted Titmice, *Baeolophus bicolor* (Linnaeus), were observed relatively frequently at all sites, with the most observations at Mount Sequoyah and Withrow Springs. Carolina Chickadees, *Poecile carolinensis* (Audubon), were observed frequently at Mount Sequoyah and Lake Fayetteville, less at Wilson Lake and Withrow Springs, and least often at Devil's Den and Hobbs State Management Area. White-breasted Nuthatches, *Sitta carolinensis* Latham, were observed with moderately high frequency at Withrow Springs and moderately low frequency at the other sites. Downy Woodpeckers, *Picoides pubescens* (Linnaeus), were observed with moderately high frequency at Mount Sequoyah and moderately low frequency at the other sites. The Red-bellied Woodpecker, *Melanerpes carolinus* (Linnaeus), was observed at moderate frequency at Hobbs State Management Area and at low frequency elsewhere. Blue Jays, *Cyanocitta cristata* (Linnaeus), were observed at moderate frequency at Devil's Den and at low frequency elsewhere. Of the summer resident migratory birds, Red-eyed Vireos, *Vireo olivaceus* (Linnaeus), were observed often at Wilson Lake and Hobbs State Management Area, somewhat less at Withrow Springs, less at Devil's Den, and at moderately low frequency at Mount Sequoyah and Lake Fayetteville. Blue-gray Gnatcatchers, *Poliptila caerulea* (Linnaeus), were observed very often at Wilson Lake, moderately often at Hobbs State Management Area and Devil's Den, less often at Lake Fayetteville and infrequently at Mount Sequoyah. Black-and-white Warblers, *Mniotilta varia* (Linnaeus), were observed rather often at Devil's Den, less at Lake Fayetteville, and rather infrequently at other sites. Twelve other species of birds were not abundant at the study sites but were included as part of the foraging data.

Trees used by birds

The focus of this study was use of tree species by foraging birds, not foraging differences between bird species, so all birds were combined in evaluation of bird use of various tree species, especially oak species compared to non-oaks. Bird observations were to some extent dependent. This problem was overcome by combining all bird species into a single data set totaling more than one thousand observations. At every site oaks were used in greater proportion than their abundance at the site and other tree species were used less than their abundance.

Table 1—Usage of oaks by birds compared to other tree species, whether used more or less frequently than tree species abundances in the forest

Taxa	Species events	Number used more	Number used less
Combined data less low frequencies			
Oaks	6	5	1
Non-oaks	24	5	19
Accumulated data less low frequencies			
Oaks	20	18	2
Non-oaks	59	23	36
Accumulated data including low frequencies			
Oaks	28	23	5
Non-oaks	110	35	75

The findings can be analyzed in three different ways (table 1). Firstly, data from all six study areas can be combined omitting the very low tree and usage frequencies. This produces the results in the top part of table 1. To elaborate, there were six species of oaks of which five were used by birds more frequently than their forest abundances, only one oak used less. There were 24 species of non-oaks and 19 were used less than their abundance in the forest, 5 were used more than their frequency. Chi-square analysis of this pattern (two-by-two contingency table) showed that the oaks were frequented by birds significantly more often than non-oaks relative to their respective frequencies in the forest (Chi-square = 8.44, 1 d.f., p<0.01, 2-tailed test).

Rather than combining across all study sites, the separate information of each site can be used and accumulated across all sites. Thus the information on relative tree species usage by birds can be inspected at one site, and the same usage of the same tree species at other sites can be added to that data, repeating and accumulating with the same tree species at each site. If the low frequencies of tree abundance and avian foraging usage are omitted, this produces the data in the middle of table 1. Thus, repeat species of oaks across all study sites totaled 20 species events, of which 18 were used more than expected, only 2 less than their frequency in the forest. The same information for non-oaks shows 59 species events of which 36 were used less than their proportion in the forest, 23 used by birds more than expected. Chi-square analysis of this pattern (two-by-two contingency table) showed that birds used oaks significantly more than their abundance in the forest, non-oaks significantly less (Chi-square = 17.15, 1 d.f., p<0.001, two-tailed test).

The same approach using information from each site accumulated across each site separately can include the low frequencies of tree presence and bird usage. These results are in the bottom part of table 1. Chi-square analysis of

these columns support the previous results (Chi-square = 20.41, 1 d.f. $p < 0.001$, 2-tailed test).

The study will be continued in upcoming years to confirm these preliminary findings and to obtain enough data to determine which birds rely most on oaks and to see which other tree species might also be preferred. This study raises serious cause for concern that indeed at least some of these forest birds will be negatively affected if oak species are devastated as predicted. It would also be valuable to study foraging behavior in forests already impacted by the oak borer to see which bird species are present and whether or not their foraging behavior has been modified in the presence of oak loss.

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SURVIVAL OF HARDWOOD REGENERATION DURING PRESCRIBED FIRES: THE IMPORTANCE OF ROOT DEVELOPMENT AND ROOT COLLAR LOCATION

Patrick Brose and David Van Lear¹

Abstract—Fire ecology studies in eastern hardwood forests usually use plot-based inventory methods and focus on sprouting stems to detect changes in vegetative composition and structure. Rarely are individual stems studied and stems that fail to sprout are usually ignored. In this study, an individual stem mortality approach was employed. Four hundred fifty stems of eight different species were tagged before prescribed burns. Top-killed stems later were analyzed to determine why some died and others did not. Root collar diameter and root collar location proved to be critical in rootstock survival. These findings indicate why oak and hickory, with their seed burial, hypogeal germination, and root-development strategies, are more likely to survive surface fires than many of their competitors.

INTRODUCTION

In the past 20 years, the perceived role of fire in mixed-oak forests has changed from a solely destructive force to be prevented, to acceptance of its historical role in perpetuating mixed-oak forests, to active research on the effects and potential uses of prescribed fire as a regeneration tool. This research has produced a wide variety of results: sometimes fire is beneficial (Brown 1960, Carvell and Maxey 1969, Ward and Stephens 1989); sometimes it is detrimental (Johnson 1974, Loftis 1990, Wendel and Smith 1986); and sometimes it has no noticeable effect on oak regeneration (Merritt and Pope 1991, Teuke and Van Lear 1982). The studies differed from each other in many important aspects. For example, they were conducted in different regions and at different times of the year. Some were post-wildfire assessments, while others dealt with prescribed fires. Some were burned – unburned comparisons, while others were preburn versus postburn evaluations. Some occurred in the dense shade of stands that had been undisturbed for decades, while others took place in the high-light conditions of new or recently disturbed stands. They did share some similarities: nearly all of the studies used plots to inventory vegetation, focused on sprouts, assumed fire intensity was equal throughout the burn, and ignored root development differences among hardwood species. Consequently, they produced widely disparate findings and resulted in no definitive silvicultural technique involving fire as a predictable regeneration tool.

In 1993, the Virginia Department of Game and Inland Fisheries conducted a 1-year pilot study of prescribed fire effects on hardwood regeneration in oak-dominated shelterwood stands (Keyser and others 1996). The study revealed that oak reproduction was more resistant to summer fire than were competing hardwood species. This study led to a 4-year comprehensive fire project, which was intended to address some of the shortcomings of previous studies. The goal was twofold: (1) confirm the pilot study's findings, and (2) elucidate why earlier fire/oak research had produced such different results. The fire project addressed some of the shortcomings of previous studies. For instance, responses

of regeneration of major hardwood species were compared among varying fire severities within differing seasons-of-burn (Brose and others 1999a, Brose and Van Lear 1998). The spatial relationship between fuel loading and its proximity to a residual tree and subsequent fire damage were studied (Brose and Van Lear 1999). Also, a fire – silvicultural technique was developed (Brose and others 1999b). Like previous fire studies, this one relied heavily on plots to inventory hardwood regeneration and focused on what sprouted after the fires.

However, the study did not use plot-based inventory methods exclusively. Data also were collected on the fate of individual stems of the major hardwood species groups. The purpose of this paper is to present the findings gleaned from using the individual-stem approach to study fire effects in mixed-oak forests.

METHODS

Site Description

The study took place from 1994 to 1998 in three central Virginia mixed-oak stands. The stands were similar to each other. All were situated on the top and upper side slopes of gently rolling hills at elevations of 500-600 feet above sea level. Soil series for all three stands was a Cecil sandy loam with a white oak site index of 75 feet (base age 50). The stands originated in the late 1890s, were even-aged, and had been partially harvested about 1990, reducing basal area from 120 to 60 ft² per ac. The resultant shelterwood had about 50 percent canopy closure. The most abundant canopy species were the upland oaks [black oak (*Quercus velutina*), chestnut oak (*Q. prinus*), northern red oak (*Q. rubra*), scarlet oak (*Q. coccinea*), and white oak (*Q. alba*)]. American beech (*Fagus grandifolia*), blackgum (*Nyssa sylvatica*), flowering dogwood (*Cornus florida*), mockernut hickory (*Carya tomentosa*), pignut hickory (*C. glabra*), red maple (*Acer rubrum*), and yellow-poplar (*Liriodendron tulipifera*) also were present, especially in the midstory. The heavy partial cut resulted in abundant advance regeneration (> 20,000 stems per ac) with all canopy species represented though yellow-poplar was the most abundant

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species. Hickory and oak regeneration height averaged less than 2 feet while red maple and yellow-poplar reproduction averaged more than 4 feet.

Study Design and Implementation

The basic design and implementation of the study are thoroughly described elsewhere (Brose and Van Lear 1998, Brose and Van Lear 1999, Brose and others 1999a), but are reviewed briefly here. The stands ranged from 15 to 50 acres; each was divided into four treatments (spring, summer, and winter burns, and an unburned control). In 1994, prior to the prescribed fires, fifteen 8-foot radius regeneration inventory plots were established systematically in each treatment to ensure uniform coverage. A linear transect to inventory fuels (Brown 1974) originated from each plot center and extended out 50 feet. Each plot/transect was photographed before the fires. Along each fuels transect, three to five advance regeneration stems, visually judged to represent the range in height of surrounding reproduction, were tagged for long-term study. Species, root collar diameter (RCD), and root collar location (RCL) were recorded for each tagged stem. Root collar is defined as the transition point between stem and root and is identifiable by a ring of callous tissue and dormant buds. A total of 150 stems per treatment were measured, for a total of 600 stems (450 in burn treatments, 150 in controls).

Virginia Department of Game and Inland Fisheries personnel conducted the prescribed burns in February (winter), April (spring), and August (summer) 1995. Fire behavior was typical for the seasons: spring fires burned more intensely than summer and winter fires. Plots, transects, and tagged stems were reinventoried for 3 years following the fires.

Statistical Analysis

In previous research (Brose and others 1999a, Brose and Van Lear 1998), fire severity (a continuous variable) was divided into discrete classes. This was accomplished by comparing the preburn photos to the appropriate plot immediately after the fire to visually assess fire effects. This evaluation subsequently was coupled with the initial postburn fuels inventory, leading to four severity classes (low, medium-low, medium-high, and high) within each season-of-burn (Brose and Van Lear 1998). The severity classes were defined as follows:

1. low - consumed only the most recently fallen leaf litter and 1-hour fuels, top-killed less than 75 percent of small reproduction (stems less than 4.5 feet tall) and small saplings [more than 4.5 feet tall but less than 2 in. in diameter at breast height (d.b.h.)]
2. medium-low - removed all leaf litter, 1-hour, and 10-hour fuels, top-killed more than 75 percent of small reproduction and small saplings but killed few, if any, stems greater than 2 in. in d.b.h.
3. medium-high – same as medium-low except stems 2-5 in. in d.b.h. were frequently top-killed
4. high – same as medium-high plus burned down into the duff layer, noticeably reduced 100-hour fuels, and top-killed stems greater than 5 in. in d.b.h.

Table 1—Impact of fire severity and season-of-burn interaction on mortality of hardwood regeneration^a

Fire severity classification	Season of burn		
	Spring	Summer	Winter
Low	Minor	Moderate	Minor
Medium-low	Moderate	Moderate	Minor
Medium-high	Major	Major	Minor
High	Major	Major	Moderate

^a Minor, moderate, and major signify that one, two, and more than two species groups were reduced in density, respectfully.

The 12 combinations of fire severity and season-of-burn could be reduced to three groups of distinct impact (table 1). Minor impact indicated that only one species group was significantly reduced in density (number of stems per acre) and this response was found in the low-, medium-low and medium-high severity winter burns and the low-severity spring burn. Moderate impact indicated that densities of two species groups were reduced and this effect was noted in the high severity winter burn, medium-low severity spring burn, and the low and medium-low severity summer burn. Major impact indicated that densities of more than two species groups decreased in response to the prescribed fires and this result occurred in the medium-high and high severity spring and summer fires.

The tagged stems were sorted into four categories based on RCL: in litter, at litter/duff interface, in duff, and at or below the duff/soil interface. Four RCD classes (<0.25 in. diameter, 0.25-0.50 in. diameter, 0.51-0.75 in. diameter, and >0.75 in. diameter) were defined based on an approximate minimum number of 20-tagged stems per RCD class. This created a 4x4 RCD/RCL grouping table for each impact level.

The null hypothesis was that the stem mortality rate (the proportion of stems failing to sprout after fire) would not differ by RCD/RCL grouping. To test this hypothesis, Chi-square analysis (Ott 1993) was used on each impact level. The mortality rate in each impact level was calculated by dividing the number of dead stems by the total number of stems. The number of stems in each cell of the RCD/RCL grouping table was then multiplied by the mortality rate to obtain the expected number of dead stems per cell. The number of tagged stems failing to sprout in each RCD/RCL grouping was the observed value.

Also tested by chi-square analysis was species distribution of all tagged stems by RCD/RCL grouping. For this test, the null hypothesis was that there were no differences among species by RCD/RCL grouping. The expected value for each species was its proportional contribution to the entire sample size. For both tests, alpha was set at 0.05 to detect significant differences between expected and observed values.

RESULTS

The 450 tagged stems in the burn treatments were distributed by species as follows: 228 oak, 55 hickory (combined with oak for analysis purposes), 80 red maple, and 87 yellow-poplar. All species were found in all RCD/RCL groupings, but definite species-specific trends were detected (table 2).

Table 2—Distribution of 450 hardwood stems in the burn treatments by RCD/RCL grouping^a

Root collar location	Root collar diameter			
	<0.25	0.25–0.50	0.51–0.75	>0.75
----- inches -----				
Litter	11, 8, 28	9, 8, 21	10, 3, 13	7, 6, 8
Litter/duff	35, 7, 6	16, 10, 6	12, 5, 0	12, 4, 1
Duff	32, 5, 2	22, 8, 0	17, 7, 1	14, 2, 0
Duff/soil	23, 3, 0	26, 1, 1	24, 2, 0	13, 1, 0

Chi-square: 181.65, Critical Value: 34.76 (alpha = 0.05, df = 47).
^a Each three-number sequence in each column represents, from left, numbers of hickory/mixed oak, red maple, and yellow-poplar, respectively.

Yellow-poplar dominated the smallest/shallowest RCD/RCL classes, while oak and hickory comprised the vast majority of the stems in the largest/deepest RCD/RCL classes, and red maple was predominated in the middle groupings.

Of the 450 tagged stems in the burn treatments, 37 were not top-killed by the fires and were dropped from the analysis. The remaining 413 were distributed among the three impact levels as follows: minor–121, moderate–135, and major–157. Within each impact level, the tagged stems were fairly evenly distributed among the 16 RCD/RCL groupings with about 5 to 15 stems per each combination. Of these, 183 failed to sprout by the end of the study and were distributed among the three impact levels as follows: minor–34, moderate–62, and major–87 (table 3).

Chi-square analysis rejected the null hypothesis, dead stems were not evenly distributed in any the three impact categories (table 3). The distribution of the 183 dead stems by RCD/RCL class was skewed toward the smallest/shallowest classes, regardless of impact level. At minor impact, 34 of the 121 (28.1 percent) tagged stems never sprouted and two-thirds of these dead stems were found in the two smallest RCD/RCL classes (<0.25/litter and <0.25/litter-duff). However, neither of these had 100 percent mortality of all stems.

Table 3—Distribution of total and dead stems by RCD/RCL grouping within each impact level^a

Root collar location	Root collar diameter			
	<0.25 in.	0.25–0.50 in.	0.51–0.75 in.	>0.75 in.
Minor impact (121 total stems, 34 dead, 28.1%)				
Litter	14, 12, 86%	9, 4, 44%	8, 1, 13%	4, 0, 0%
Litter/duff	15, 11, 73%	7, 3, 43%	5, 0, 0%	3, 0, 0%
Duff	9, 3, 33%	8, 0, 0%	7, 0, 0%	5, 0, 0%
Duff/soil	8, 0, 0%	10, 0, 0%	5, 0, 0%	4, 0, 0%
Moderate impact (135 total stems, 62 dead, 45.9%)				
Litter	17, 15, 88%	11, 7, 64%	6, 4, 67%	6, 2, 33%
Litter/duff	15, 13, 87%	8, 5, 63%	3, 1, 33%	4, 0, 0%
Duff	13, 9, 69%	10, 3, 30%	7, 0, 0%	4, 0, 0%
Duff/soil	8, 2, 25%	8, 1, 13%	9, 0, 0%	6, 0, 0%
Major impact (157 total stems, 87 dead, 55.4%)				
Litter	16, 13, 81%	14, 13, 93%	12, 5, 42%	5, 2, 40%
Litter/duff	18, 16, 89%	11, 8, 73%	9, 5, 56%	7, 1, 14%
Duff	14, 11, 79%	7, 5, 71%	5, 2, 40%	5, 0, 0%
Duff/soil	8, 4, 50%	10, 2, 20%	12, 0, 0%	4, 0, 0%

Chi-square: 46.23, critical value: 7.26 (alpha = 0.05, df = 15).

Chi-square: 32.74, critical value: 7.26 (alpha = 0.05, df = 15).

Chi-square: 26.72, critical value: 7.26 (alpha = 0.05, df = 15).

^a The first number in each column is the total number of stems before the prescribed fires, the second number is the number of dead stems after the prescribed fires, and the third is the proportion of stems killed.

Four other classes, occupying the upper-middle range of RCD/RCL classes, also contained some dead stems, but not to the same extent of the two smallest classes. The lower-middle and largest/deepest RCD/RCL classes contained no dead stems. Also, the dead stems were primarily yellow-poplar. Only a few red maple, hickory, and oak seedlings failed to sprout.

In the moderate-impact level, 62 of the 135 (45.9 percent) tagged stems never sprouted (table 3). Again, these were concentrated in the two smallest/shallowest RCD/RCL cells (<0.25/litter and <0.25/litter-duff) which had nearly 100 percent mortality, and the three adjacent intermediate RCD/RCL classes, which had mortality greater than 50 percent. As RCD and RCL increased, mortality decreased and no mortality occurred to stems in the largest/deepest RCD/RCL classes. Yellow-poplar and red maple constituted the majority of dead stems, but oak and hickory also were killed, especially in the smallest/shallowest RCD/RCL classes.

In the major impact group, 87 of the 157 (55.4 percent) tagged stems never sprouted (table 3). Only the largest/deepest RCD/RCL groups (0.51-0.75/duff-soil, >0.75/duff, and >0.75/duff-soil) had no mortality, while the smallest/shallowest groupings (<0.25/litter, <0.25/litter-duff, <0.25/duff, 0.25-0.50/litter, and 0.25-0.50/litter-duff) had almost 100 percent mortality. The remaining eight groups were split between four having greater than 50 percent mortality and four with less than 50 percent mortality. Nearly all yellow-poplar died in this impact grouping as did approximately 50 percent of hickory, oak, and red maple.

DISCUSSION

Previous research has shown the importance of season-of-burn and fire severity as factors influencing the response of hardwood regeneration to fire (Brose and others 1999a, Brose and Van Lear 1998). This study adds root collar diameter and root collar location as significant explanatory factors. The stems with the shallowest and smallest roots sprouted in far fewer numbers after the fires than stems with deeper and larger roots (table 3). Species seemed inconsequential as hickory and oak seedlings with shallow and small roots were as susceptible to fires as comparable red maple and yellow-poplar. The reverse also was true as large, deep-rooted maples and poplars sprouted after the fires, as well as similar oaks and hickories.

Species differed in distribution among the RCD/RCL classes (table 2). While generally all species were found in all cells, yellow-poplar dominated the smallest/shallowest ones, while oak and hickory dominated the largest/deepest classes. Red maples occurred most often in the intermediate RCD/RCL cells. Consequently, there were differing species responses to the fires and this was a function of at least four factors: season-of-burn, fire severity, root collar diameter, and root collar location.

This study also provides insight into the disparate results among many of the early fire/hardwood studies. Root collar location and diameter of the regeneration usually were not determined and fire severity often was ignored or considered equal throughout the burn area. Without knowing

these factors, predicting or understanding the outcome of a fire is virtually impossible. One can imagine a high-severity, growing-season fire annihilating a newly established cohort of oak seedlings arising from unburied acorns (shallow/small roots) while older, well-established red maple regeneration (somewhat deep/large roots) is able to sprout. A comparable fire in well-established oak reproduction (deep/large roots) and new red maple seedlings (shallow/small roots) would probably produce opposite results. Thus, fire studies that do not account for these important root characteristics could reach opposite conclusions about fire effects on oak and red maple regeneration.

The root collar diameter and location differences between oak/hickory and red maple/yellow-poplar (table 2) are a result of their silvics. Hickory nuts and acorns have hypogeal germination, i.e., cotyledons remain in the shell and serve as a belowground energy source for seedling development. Red maple and yellow-poplar seeds have epigeal germination, i.e., cotyledons emerge and rise above the shell to form the first photosynthetic leaves. This difference in germination strategy places hickory and oak seedlings' root collar, and the accompanying dormant buds, lower than that of red maple and yellow-poplar.

This basic difference in germination strategy is accentuated by wildlife. Hickory nuts and acorns are routinely buried an inch or more into the forest floor by birds and small mammals while seeds from red maple and yellow-poplar typically are not cached. Thus, a hickory or oak seedling generally will have a deeper root collar than a red maple or yellow-poplar seedling because of seed burial and hypogeal germination.

Another important silvical difference between hickory/oak and red maple/yellow-poplar reproduction is the developmental rate of the root system. Upon germinating, oaks and hickories send a strong radicle deep into the soil to establish a taproot and emphasize root development over stem growth (Kelty 1988, Kolb and others 1990). Red maple and yellow-poplar take the opposite approach; root development is sacrificed to promote rapid stem growth. Thus, hickory and oak regeneration usually are shorter than their competitors, but have larger root systems. It is these two silvical characteristics, hypogeal germination and emphasis on root development, and seed burial by wildlife that allows hickory and oak regeneration to be favored over reproduction of their competitors in a periodic fire regime.

An important management consideration evident from this study is the need to withhold fire, and possibly harvesting, too, when advanced reproduction is relatively small. Seedlings with root collars less than 0.25 in. diameter exhibit significantly greater mortality after a prescribed fire than reproduction with larger root collars. Treatment should be delayed a couple of years to allow newly established oak seedlings to grow large enough roots to survive a fire or other forest-floor disturbance.

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THE EFFECTS OF HUMANS AND TOPOGRAPHY ON WILDLAND FIRE, FORESTS, AND SPECIES ABUNDANCE

Richard P. Guyette and Daniel C. Dey¹

Abstract—Ignitions, fuels, topography, and climate interact through time to create temporal and spatial differences in the frequency of fire, which, in turn, affects ecosystem structure and function. In many ecosystems non-human ignitions are overwhelmed by anthropogenic ignitions. Human population density, culture, and topographic factors are quantitatively related to fire regimes and the long-term pattern in fire frequency and species composition. These factors can be quantitatively related and used to reconstruct and predict the frequency of fire in ecosystems and to identify changing factors involved in anthropogenic fire regimes. Quantitative fire histories from oak-pine sites in Arkansas, Indiana, Missouri, and Ontario are used to examine patterns of interaction in fuels, ignitions, and topography over a period of 300 years. Fire regimes and fire frequencies are associated with the abundance of many species of reptiles, birds, fungi, and plants. Human population density and topographic roughness are master variables in understanding temporal and spatial differences in fire regimes and their effects on ecosystems.

INTRODUCTION

Temporal and spatial differences in the frequency of fire effect ecosystem structure and function. In many fire regimes non-human ignitions are overwhelmed by anthropogenic ignitions. Consequently, human population density, culture, and topography control ignition in these fire regimes affect the long-term disturbance frequency and species composition. These factors can be quantitatively used to predict the frequency of fire in ecosystems. The interactions of fuels, ignitions, and topography as they affect the fire regime over a period of 300 years can be derived from analyses of fire history data.

The scale, frequency, and legacy of disturbance regimes and their effects on the distribution of forest species also have important management, policy, and political implications. Debates about even-aged versus uneven-aged management, or no timber harvesting often hinge on what is natural, or what was the pre-European disturbance regime. Managers and policy makers are often interested in mimicking natural disturbance regimes with silvicultural prescriptions to foster native plant and animal species diversity (Loucks 1970). The species composition of Ozark forest ecosystems is a legacy of their long-term disturbance regimes. Thus, fire regimes and fire frequencies are associated with the abundance of many species of reptiles, birds, fungi, and plants in the Ozarks. Knowledge of these regimes and their effects is valuable for understanding present-day forest species composition and structure. We show the long-term effects of anthropogenic disturbance and topographic roughness on forests, flora, and fauna using data from the Missouri Ozark Forest Ecosystem Project (MOFEP), a long-term study initiated to quantify forest management effects on flora and fauna (Brookshire and others 1997; Brookshire and Hauser, 1993). The goal of this paper is to illustrate how anthropogenic disturbance and topography have been major factors affecting disturbance frequency at the MOFEP sites and that historic disturbance regimes have a legacy that continues to affect contemporary plant and animal distributions today.

FIRE HISTORY SUMMARY

The three important factors that determine fire regimes in oak-dominated ecosystems are topographic roughness, human population density, and culture. Specifically, the roughness of the topography around a site mitigates the propagation of disturbance related factors, such as fire, logging, and human travel into a site. Topographic roughness is positively correlated with the length of mean fire intervals. Consequently, fires are less frequent in rough than in flat terrain, especially during periods of limited anthropogenic ignitions (fig. 1). The strength and direction of the topographic effect diminishes as the spatial and temporal frequency of anthropogenic ignitions increases to a point of pyro-saturation (ignitions occur throughout the landscape and fuels are burned as soon as they are able to support the spread of a fire). Since topography generally changes through time very slowly, its influence on fire regimes is not only long-term but dates to long before the first effects of human ignitions.

Fire has been an integral tool in the lives of humans for many thousands of years. Thus, humans are a potential and dynamic source of ignition, when and wherever they are present and irrespective of whether landscape burning is promoted (Pyne 1982, 1995) or suppressed (Westin 1992). The early records of fire history support the idea that fire frequency is a function of potential human ignitions. Fire frequency has been correlated with human population in a number of studies (Dey and Guyette 2000, Guyette and Dey 1997, Guyette and others 2002). The positive relationship between population density and fire frequency diminishes as ignitions become more frequent and fuels fail to accumulate. As population density increases further, fire frequency lessens due to change in land use and fire suppression.

Cultural values have influenced wildland fire use and suppression in different ways through time. Historically fire was used to improve travel, for hunting wild game, to

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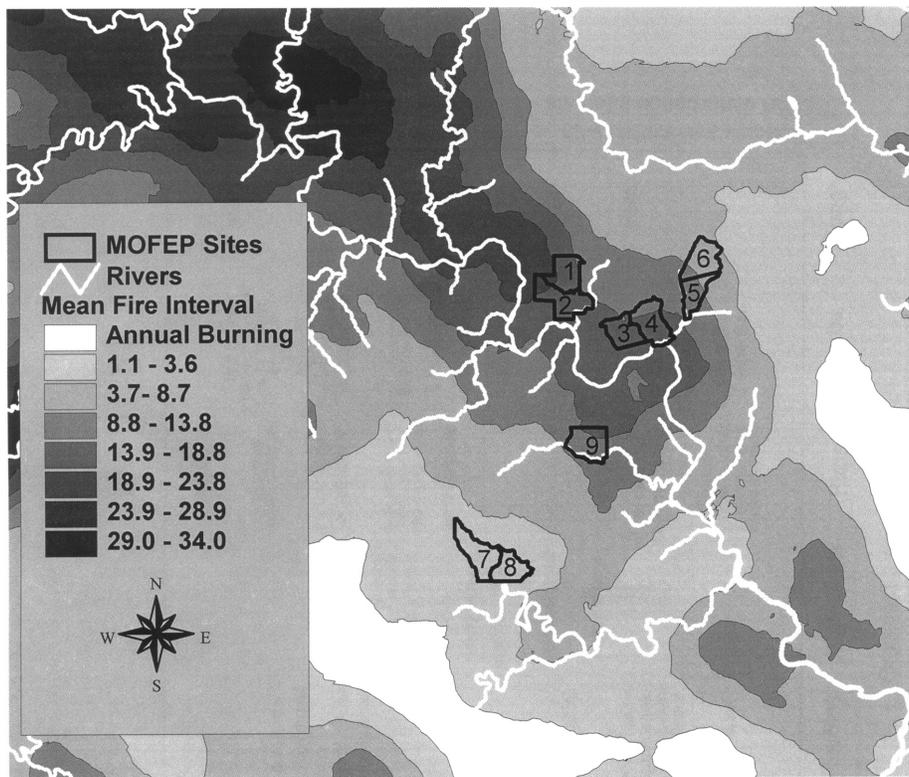


Figure 1—Landscape roughness and human population are major factors in disturbance regimes. Here, mean fire intervals are mapped for the period 1700-1780 in the MOFEP study region. Fire intervals are based on the model: $MFI = -442.1 + (449.9 \times topo) - (0.001 \times pop)$, where MFI is the mean fire interval, topo is an Index of topographic roughness, pop is the natural log of human population density times the square of river mile (Guyette and Dey 2000). Numbers are site designations and locations for the nine MOFEP sites.

promote nut and berry production, to prepare sites for agriculture, to improve browsing and grazing conditions, etc. But as a timber economy developed, and people built homes in the hinterlands, suppressing fire became a necessity. In the modern era, cultural values have become the most important factors controlling fire frequency as increasing population density increases the risk of wild fire to human safety and economics. Good pasture may require burning while defect free timber may require fire suppression. Unlike incidental anthropogenic ignitions (proxy: human population density), which stem directly from basic human requirements for cooking, transport, warmth and safety, value oriented cultural constraints on wildland fire originate from our societies economic system. This includes fire suppression for perceived and real safety as well as prescribed fire for ecosystem diversity, safety, and silvicultural purposes. The artifact of fire suppression (the human separation of ignition and fuels) creates its own dangers especially since fuel and economic conditions can be highly variable through time.

LONG-TERM LEGACY OF FIRE, DISTURBANCE, AND SPECIES GROUPS

Landscape level fire histories and species population data allow for the study of species abundance, distribution, and *beta* diversity within a region. Species groups are sensitive to the long-term effects of fire and forest disturbance as shown by the data collected on a wide array of species as

part of the Missouri Ozarks Forest Ecosystem Project (Brookshire and Shifley 1997). Data on plant and animal abundances (Kabrick and others 1997, Bruhn and others 1997, Clawson and others 1997, Grabner and others 1997, Renkin 1997, Fantz and Renken 1997) at nine sites in the Ozarks are associated with regional differences in the historic fire and disturbance regimes as quantified by an index of disturbance (Guyette and Kabrick, 2002). Disturbance interval indices are correlated with the abundance of tree species, small mammals, reptiles, amphibians, birds, herbaceous plants, fungi, oak species in the overstory, and ground flora (fig. 2). Trees, reptiles, birds, herbaceous plants, and *Armillaria* species, as groups, all show sensitivity to long-term disturbance regimes. This may be a positive or negative association with fire and disturbance. Amphibians show a lower sensitivity to disturbance. The low sensitivity of amphibians to disturbance may be explained by their subterranean habitat (e.g., salamanders), which may buffer them from aboveground disturbances and by the limiting effects on populations of scarce breeding habitat (water bodies) in the MOFEP study area.

Fire and disturbance result in changes in the distribution of light and spatial structure of forests that, in turn, regulates microclimate (i.e., light, temperature, humidity and moisture). Species have adapted to niches created by varying frequencies of disturbance. In the southeastern Ozarks,

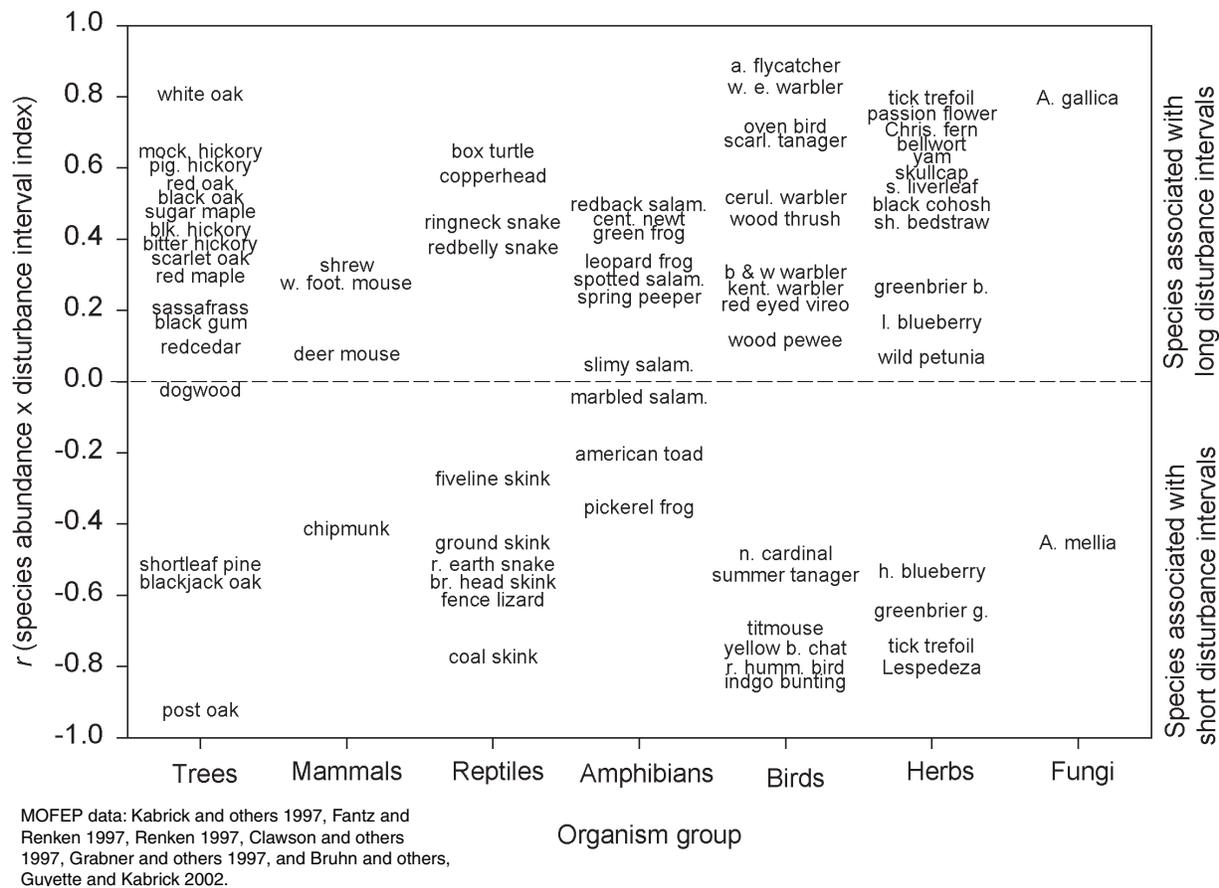


Figure 2—The association between fire and disturbance and the abundance of 75 species by group. Species near a correlation of 1 on the y-axis are strongly and negatively associated with frequent disturbances. Species near a correlation of -1 on the y-axis are strongly and positively associated with the frequent disturbances. Species near a correlation of 0 on the y-axis are not strongly associated with the frequency of disturbance. Significant ($p < 0.05$) correlations for a single species-disturbance test are greater than 0.60 or less than -0.60. While the power of an individual species test is low (only 9 sites), differences in the sensitivity of species groups to disturbance are evident.

several closely related species (fig. 2) are associated with very different frequencies of disturbance in the same region. The abundances of some closely related (in the same genus) trees, birds, and fungi (*Armillaria* spp.) have contrasting correlations with the frequency of disturbance (table 1).

Post oak (*Quercus stellata*), summer tanagers (*Piranga rubra*), and *Armillaria mellea* are found at sites with frequent disturbance while white oak (*Quercus alba*), scarlet tanagers (*Piranga olivacea*), and *Armillaria gallica* are found in forests with less frequent canopy disturbance.

Table 1—Correlation coefficients among genus pairs and disturbance illustrate how closely related species at the Missouri Ozark Forest Ecosystem Project sites are often very different in their association with long-term disturbance frequency^a

Genus	LS species, r	ES species, r	Difference ^b , r
<i>Quercus</i>	<i>alba</i> , +0.92	<i>stellata</i> , -0.96	<i>alba-stellata</i> , +0.97
<i>Armillaria</i>	<i>gallica</i> , +0.88	<i>mellea</i> , -0.49	<i>gallica-mellea</i> , +0.84
<i>Piranga</i>	<i>olivacea</i> , +0.68	<i>rubra</i> , -0.55	<i>olivacea-rubra</i> , +0.79

^a Correlation coefficients are for the disturbance interval index (Guyette and Kabrick 2002) and species abundances at the nine sites. Note the opposite signs of correlation coefficients by different species within the same genus.

^b Difference is the abundances of early successional (ES) species subtracted from late successional (LS) species. Significant ($P < 0.05$) correlations are shown in bold.

Source: Bruhn and others (1997); Clawson and others (1997); Guyette and others, in press; Kabrick and others (1997).

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FIRE HISTORY OF A FOREST, SAVANNA, AND FEN MOSAIC AT WHITE RANCH STATE FOREST

Daniel C. Dey, Richard P. Guyette, and Michael C. Stambaugh¹

Abstract—We present the fire history of a 1-km² area that is a mosaic of oak forest, savanna, and fen on the White Ranch State Forest, Howell County, Missouri. We dated 135 fire scars on 35 cross-sections of post oak (*Quercus stellata*) trees and constructed a fire chronology dating from 1705 to 1997. Mean fire return intervals by periods were 3.7 years (1705 to 1830), 7.6 years (1831 to 1960), and 3.6 years (1961 to 1997). Fire frequency was positively correlated ($r = 0.53$, $p < 0.01$) with the expansion and migration of the Osage Tribe from 1710 to 1830. Later, between 1831 and 1900, exponential increases in Euro-American population density were negatively correlated ($r = -0.64$, $p < 0.05$) with fire frequency. Fires were more likely to have occurred in drought years before 1830 than after 1830. Droughts after 1830 were related to the percent of trees scarred during years with evidence of fire.

INTRODUCTION

Wildfires have influenced Ozark forests, prairies, and wild-life for centuries (Chandler and others 1983). Speculation on the fire history of many areas in the southwestern Ozarks has been difficult because of the anthropogenic influence (Westin 1992) on these fire regimes and the highly variable nature of fuels and vegetation. Knowledge of fire history provides an ecological basis for restoring fire disturbance and developing silvicultural prescriptions that use fire to favor native communities. The objective of this study is to document a fire regime in a landscape with the potential for diverse vegetative assemblages, both in time and space, which includes closed canopy oak forests, savannas, prairies, and fens. We present a 292-year fire history based on dendrochronological analyses of fire scars for a site near the West Fork of the Spring River on the White Ranch State Forest, Howell County, Missouri.

METHODS

The study area is located (36° 32' N, 91° 52' W) along the northeastern slopes of the West Fork of the Spring River in the White Ranch State Forest, which is managed by the Missouri Department of Conservation. The landscape in the area is gently rolling with about 37 m of elevation change per km. The study site is about 1 km² in area and is presently covered by a complex mosaic of oak forests in the uplands and slopes, savannas and glades along slopes, and grassy fens in low lands.

Cross-sections were cut within 20 cm of ground level from 44 post oaks in the study area. Trees with solid boles were selected for cutting by sounding with a long handled ball pin hammer. The majority of the post oaks at the study site were hollow. Of the 44 trees cut only 35 cross-sections were used in identifying fire scar years. Nine trees sampled were deleted from analysis because heart rot, indistinct rings, or injury made precise dating of fire scars impossible. Trees ranged in age from 12 to 300 years or more.

Fire scars in this study are defined as basal injuries, which have killed cambial cells, exhibit a localized cambial growth response, and contain callus tissue. Fire scars also are associated with abnormal tyloses formation, general growth responses (from release or crown damage), and false rings. Often there was no external evidence that a post oak tree had a fire scar, although there were many hollow trees with external fire scars in the surrounding area.

Many other types of scars were present on the cross-sections. Damage caused by pin worms and bark scarrers was not common but it was distinctive and not easily confused with fire scars. Lightning scars were identified by their presence in sections well above the ground.

Fire wounds from ground level sections of post oak were used to reconstruct fire frequency. All fire dates were designated as the year of growth response to the injury. Thus, a scar that we dated to 1770 may have been caused by a fire that occurred anytime in the previous dormant season, approximately September 1769 to April 1770. This is of particular importance when considering if fires occur more frequently during drought years as indicated by ring width.

Dendrochronology uses the pattern in tree-rings caused by climate to date annual growth increments (Stokes and Smiley 1968). This enables accuracy in dating to the year, serves as a check on ring counts from live trees, and allows for the dating of wood of unknown age. Post oaks in this study were dated using a post oak chronology from Clayton Ridge (Stahle and others 1985) on the Rolla-Houston Ranger District of the Mark Twain National Forest. Annual rings were dated using skeleton plots of ring-widths, measured ring-width series, signature years, and ring counts.

Post oak is probably the most fire resistant species in the Ozarks, with the possible exception of shortleaf pine. The determination of fire frequency is difficult using post oak

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because this species is very resistant to scarring by low intensity fires. Paulsell (1957) noted that only 10 percent of the post oaks were scarred in annually burned plots, whereas 23 percent of the post oaks were scarred in the periodic burn plots. On the periodically burned plots, litter build up may have resulted in greater fire intensities that were capable of scarring more trees. This relationship between fuel buildup, fire intensity, and ability to scar trees may result in an under estimate of the number of fires in post oaks growing under low intensity surface fire regimes. More important, however, is the under estimation of fire frequency due to scarring resistance in post oak. For example, only one scar may be produced for every four to ten exposures to low intensity fires. Thus, mean fire intervals determined from fire scars on oak trees should be viewed as minimum fire return intervals.

We also attempted to sample trees in various size classes to minimize the effect that tree size has on scarring and to increase the accuracy of the composite fire chronology. Further, we constructed a composite fire scar chronology (Stokes and Dieterich 1980) from all of the 135 fire scars identified on the 35 dated cross-sections. Percent of trees scarred in any given fire year was determined by dividing the number of sample trees with ring records in a fire year by the number of trees with scars and multiplying by 100.

RESULTS AND DISCUSSION

Fire Frequency

A fire scar chronology composed of all the fire scars from the sample of 35 post oaks dated is given in figure 1. The frequency of fire, as mean fire return intervals (MFI), is summarized for various historic or cultural periods over the last 292 years in the 1-km² study area in table 1. The mean fire return interval was similar for the Native American Period (1711 to 1830) and the Modern Period (1961 to 1997), but the fire scar record indicates that fires burned less frequently during Euro-American settlement and development (1831 to 1960). The percent of trees scarred was significantly

Table 1—Mean fire return intervals by historic periods

Historic period	MFI	Range	Trees scarred (percent)	
			All years	Scar years
-- years --				
Native American (1711–1830)	3.7	1 – 13	4.3 ^a	17.5 ^a
Euro-American settlement (1831–1960)	7.6	2 – 17	0.7 ^b	5.6 ^b
Modern agriculture (1961–97)	3.6	1 – 7	3.4 ^{ab}	12.8 ^{ab}
All periods (1711–1997)	4.9	1 – 17	2.6	13.2

Mean fire return intervals (MFI) are for the presence of fire (a fire scar on at least 1 of 35 samples) in all or part of the 1-km² study area.

Statistics with the same superscript letters on different lines are not significantly different ($\alpha = 0.05$).

different ($t=5.1$, $p < 0.0001$) for the two periods, 1711 to 1830 and 1831 to 1960. The mean percent of trees scarred during the Native American and Modern Periods was four to six times that of the period of Euro-American settlement and development (table 1). Fire frequency and percent of trees scarred were not significantly different ($t=1.78$, $p=0.08$) between the two periods, 1711 to 1830 and 1961 to 1997 because of the high variance and short duration of the Modern period. However, there certainly could be significant ecological differences resulting from fires during these two periods. Mean fire return intervals (MFI) at White Ranch State Forest are similar to those at three other study sites (table 2) that also have oak forest and savanna vegetation (Guyette and Cutter 1991; Cutter and Guyette 1994; Guyette and McGinnes 1982) in the Missouri Ozarks.

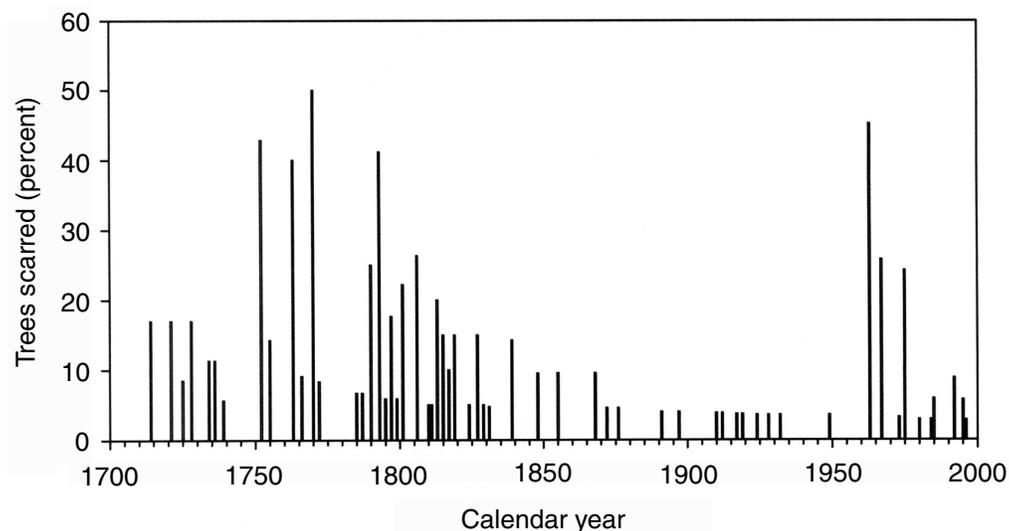


Figure 1—Composite fire scar chronology and percent of trees scarred by fire year for the study site at White Ranch State Forest, Howell County, MO.

Table 2—A comparison of mean fire return intervals at White Ranch State Forest, Caney Mountain Wildlife Refuge, Laclede County, and Cedar Glades

Period	WRSF	CMWR	LACCO	CEDAR
	----- years -----			
1710–1830	3.7	4.8	3.0	3.3
1831–1980	7.6	6.9	12.5	9.4

WRSF = White Ranch State Forest; CMWR = Caney Mountain Wildlife Refuge; LACCO = Laclede County; CEDAR = Cedar Glades.
All sites are more than 50 km from the White Ranch State Forest.

Climate, Fire Occurrence, and Fire Severity

The mean reconstructed Palmer Hydrologic Drought Index (Cleveland and Stahle 1996) for all fire years before 1830 was -0.66 compared to a mean of +0.32 for all fire years after 1830 (table 3). Before 1830, drought was an important factor in the occurrence of fire years, but after 1830 fires burned in years of above average precipitation. This may be because drought increased the probability of fires spreading to the study site or because Native Americans chose the most severe fire weather to ignite fires. Both factors probably contributed to the occurrence of fires in years of growing season drought before 1830. Others (e.g., Sutherland 1997) have noted the general lack of correspondence between fire years with drought years after 1830.

When the percent of trees scarred is calculated based on those years with evidence of fire, there is no significant correlation between growing season drought and the percent of trees scarred before 1830, but there is a significant correlation ($r = -0.47$, $p = 0.01$) between growing season drought and the percent of trees scarred after 1830. This indicates that before 1830 growing season droughts had more of an effect on the year of occurrence of a fire and little effect on the severity of fire at the study site. The opposite relationship occurs after 1830 when growing season drought does not affect the year of occurrence of fire but is related to the severity (percent of trees scarred) of fire.

Table 3—Drought and the percent of trees scarred by historic period

Period	PHDI	%TREE X PHDI	PHDI (%TREE > 6)
Native American (1711–1830)	-0.66 (n = 31)	$r = -0.47$ ($p = 0.01$)	-0.97 (n = 24)
Euro-American (1831–1997)	+0.32 (n = 24)	$r = +0.04$ ($p = 0.80$)	-1.22 (n = 7)

%TREE = percent of trees scarred; PHDI = Palmer Hydrologic Drought Index. Negative values of the reconstructed Palmer Hydrologic Drought Index represent relatively dry periods (Cleveland and Stahle 1996). Correlations are given for the percent of trees scarred and the PHDI (%TREE X PHDI). The PHDI is also given for only those years with multiple scarring of trees (percent trees scarred > 6).

Cultural Interpretations

In 1818, Schoolcraft (1821) observed several abandoned “Indian camps” just below the confluence of Bryant Creek and the North Fork of the White River. These camps were west of the study site separated by 40 km of gently rolling terrain. The study site also lies near the confluence of two streams, the West and South Forks of the Spring River. Schoolcraft also commented on the abundance of bear, elk, deer, and beaver in the area. Thus, geographic location at the confluence of rivers, the distance from sites of known Native American occupation, and the abundance of game suggests that there was reason for a human population within the vicinity of the study site before Euro-American settlement of the area.

Population, Land Use, and Fire

Population and agriculture are two factors that greatly affect anthropogenic fire regimes. Fire history at the White Ranch State Forest shows a changing relationship to these important factors. Fire frequency at the study site was positively correlated ($r=0.53$, $p < 0.01$) with the expansion (Wiegiers 1985) and migration (Wolferman 1997) of the Osage Tribe (Marriott 1974) between 1710 to 1830 (table 4). During the latter part of this period, Shawnee, Delaware, and Cherokee were migrating through the area (Weslager 1978) and they may have contributed to the frequency of fire at the study site. A positive relationship between fire frequency and human population makes sense (Guyette and Cutter 1997) because more people usually cause more ignitions, especially at low levels of human population density. In contrast, exponential increases in Euro-American population density between 1830 and 1900 were negatively correlated ($r = -0.63$, $p < 0.05$) with the scarring of trees. How human population density during this period (1830 to 1900) affected the frequency of fire is not well understood and is addressed in the next section.

Population density is not significantly correlated with the percent of trees scarred during the 1900s. This relationship is expected as population density increases because a complex of cultural factors controls the frequency of fire. Anthropogenic fire is affected by changes in land use, in the type of ownership, in the price of timber and the price of beef, the value of real estate, and by the adoption of fire suppression policies. Since 1960, there has been a

Table 4—Correlations among population density, cattle density, and the percent of trees scarred (an 11-year moving average) by periods

	1711–1830	1830–1900	1900–97	1960–90
Human population density	0.53	-0.63	0.08	-0.73
Cattle on farms	—	-0.52	0.07	-0.74

Cattle data and the correlation for the 1830 to 1900 period are based on the State cattle population from 1867 to 1900. Positive and negative correlations indicate that trends in the percent of trees scarred are coincident with changes in human and cattle production.

decrease in the percent of trees scarred and an increase human population density. The number of cattle on farms follows the same general trends as human population and its correlation with the percent of trees scarred (table 4).

Trends in the Fire Frequency of Forests and Savannas

The trends in fire scarring of trees at the White Ranch State Forest are similar to patterns observed at other fire history sites in oak forest-savanna mosaics in southwestern Missouri (fig. 2). These sites include a site in the redcedar glades in Douglas County (Guyette and McGinnes 1982), a site on an oak-hickory ridge near the Gasconade River in Laclede County, (Cutter and Guyette 1994), and a site in a post oak forest-savanna at the Caney Mountain Wildlife Refuge (Guyette and Cutter 1991). The trend at these sites has been an increase in fire frequency before 1780, an increase in fire frequency and the percent of trees scarred

between 1780 and 1820, and then a steady decline in fire frequency ending circa 1900. A notable exception in fire trends at White Ranch State Forest is that the frequency of fire increases between 1960 and 1997, and it is greater than at the other sites, although differences are not statistically significant.

Differences in the fire regime before and after 1830 may be due to both a change in the frequency of fire and a change in the intensity of fire. The difference in the percent of trees scarred between the Native American period and the period of Euro-American settlement and development could be the result of a number of factors (table 5) that reduced the scarring of trees. These might include changes in fuel continuity, in vegetation type, in fuel characteristics, in farming practices, in the density of large herbivores, in fire frequency, and in the frequency and seasonality of human ignitions.

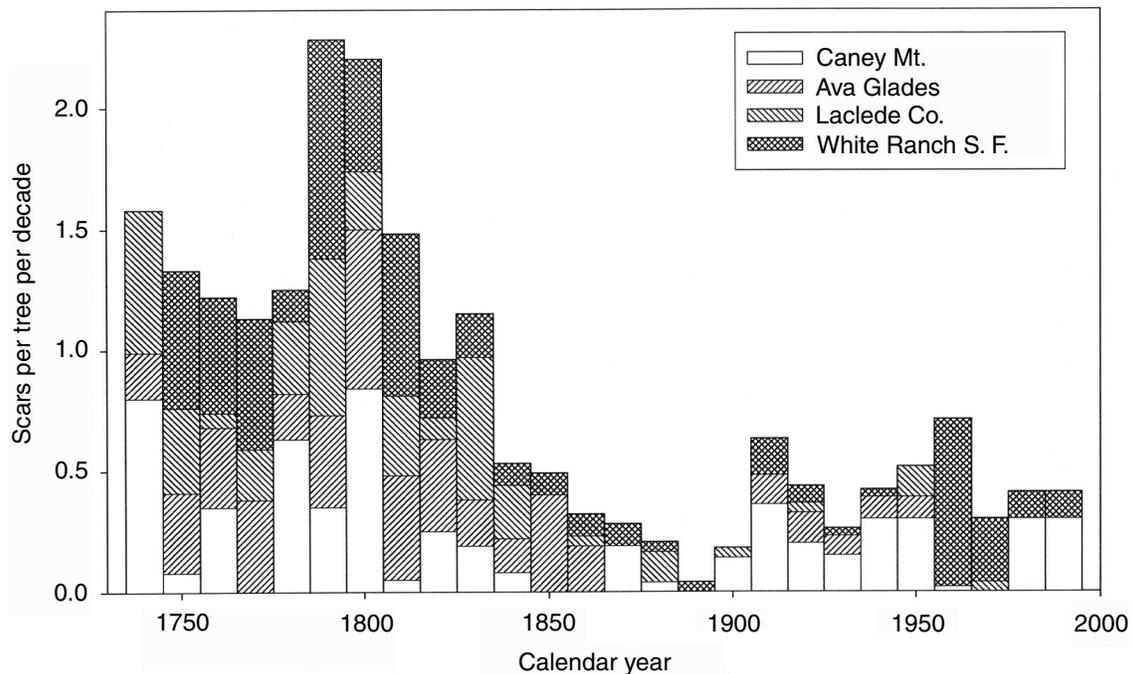


Figure 2—Patterns in fire scarring of post oaks at White Ranch State Forest compared with other fire history sites from oak forests and savannas throughout the Ozark Highlands in Missouri.

Table 5—Possible factors influencing fire frequency and the scarring of trees before and after 1830 in forest-savanna vegetation of the southwestern Ozarks

Before 1830	
1	Fuel buildup during fire free intervals facilitates fire spread and intensity
2	Fires in late summer and fall of year burn hotter than spring fires
3	Warm season grasses create more volatile fuels
4	Effects on fuels by herbivores limited
5	Few firebreaks facilitate continuous spread of fire
6	Native Americans choose the most severe fire weather for burning
After 1830	
1	Fire intensity low from annual fuel reduction by fire
2	Fires in spring cooler than fall fires
3	More cool-season grasses are less volatile
4	Fuel reduction and trampling by more large herbivores
5	Increasing numbers of firebreaks, roads, and fields
6	Fine prairie fuels replaced by slower burning forest litter

Post Oak Regeneration

The year of growth initiation for each post oak stem was determined. No periods of regeneration stood out as exceptional or different from the rest. This is in contrast to an earlier study (Cutter and Guyette 1994) in which the trees sampled indicated that the dominant overstory trees had regenerated in a stand replacement event that resulted in an even-aged overstory. Of the post oaks sampled, none had pith dates (no stems regenerated) between 1815 and 1880, which can be characterized as a period of decline in fire frequency, in percent of trees scarred in a fire year, and in increased settlement and agricultural development. However, because the sample trees were not randomly selected, any inferences regarding stem initiation may give a biased view of oak regeneration in relation to fire disturbance.

CONCLUSIONS

1. Mean fire return intervals by periods were 3.7 years (1705 to 1830), 7.6 years (1831 to 1960), and 3.6 years (1961 to 1997). The percent of trees scarred is significantly different ($t=5.1$, $p < 0.0001$) for the two periods 1705 to 1830 and 1831 to 1960. Since some fires may not have scarred any of the sample trees, these interval estimates are minimum fire return intervals for the study area.
2. Population density is an important factor related to fire frequency. Before 1830 fire frequency is positively related to human population density, a source of anthropogenic ignitions.

3. Later (1830 to 1900) population density is inversely correlated with fire frequency as land use effects reduce the frequency and severity of fires.
4. Fires were more likely to have occurred in drought years before 1830 than after 1830.
5. Droughts are related to the percent of trees scarred after 1830 in years with evidence of fire.
6. Historical documentation of Native American populations 40 km west of the study site in the early 1800s indicates anthropogenic ignitions maintained the level of fire frequency documented before 1830.
7. The trends in fire frequency at White Ranch State Forest are similar to those found at three other sites in the Missouri Ozarks with areas of oak forest and savanna vegetation.
8. A declining trend in the percent of trees scarred at White Ranch State Forest between 1830 and 1900 is the opposite of trends of increasing fire frequency found in highly dissected and forested regions of the Ozarks such as the Current River watershed.
9. Although a complete age structure was not determined for the study forest, dates of stem initiation of the dominant post oaks sampled do not indicate that this was an even-aged forest originating from a stand replacement type disturbance. Dominant post oaks regenerated throughout the past 292 years resulting in an irregular age structure of overstory oaks. Regeneration of dominant post oaks was minimal during a period in the fire chronology when fires burned less frequently and with less intensity.

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A PERSPECTIVE ON *QUERCUS* LIFE HISTORY CHARACTERISTICS AND FOREST DISTURBANCE

Richard P. Guyette, Rose-Marie Muzika, John Kabrick, and Michael C. Stambaugh¹

Abstract—Plant strategy theory suggests that life history characteristics reflect growth and reproductive adaptations to environmental disturbance. Species characteristics and abundance should correspond to predictions based on competitive ability and maximizing fitness in a given disturbance environment. A significant canonical correlation between oak growth attributes (height growth, xylem permeability, shade tolerance) and reproductive attributes (longevity, acorn weight, and the age to reproduction) based on published values indicates that the distribution of oak attributes among species is consistent with r and K selection theory. Growth and reproductive attributes were used to calculate an index reflecting the relative values of the r and K strategies of oak species. This index was used to examine changes in the dominance of oak species at nine sites in the Ozarks. Changes in oak species dominance and differences in their landscape distributions were consistent with predictions based on their r and K index values and estimates of forest disturbance.

INTRODUCTION

Plant strategy theory suggests that life history characteristics reflect growth and reproductive adaptations to population density, environmental disturbance, and stress (Grime 1979, Odum 1997). Species attributes and abundance should correspond to predictions based on competitive ability and maximizing fitness in a given disturbance environment. Thus, selection theory predicts that there should be correlations between growth and reproductive variables among species that are consistent with the species ability to remain competitive and maximize fitness in a given environment. The opposing strategies of r and K selective forces (MacArthur and Wilson 1967) have been used to explain persistence of species in given environments. Generally, r-strategists are those that have a high rate of reproduction and growth providing an advantage in acquiring resources made available through disturbance. A K-strategist has characteristics that allow it to more effectively compete for resources in communities that are near carrying capacity and where resources are predictable and relatively favorable.

Many consider r- and K-selection theory to be valid but an oversimplification (Crawley 1997) because it does not consider fitness attributes that are not influenced by population density. We use this theory because it lends itself to linear quantification among the species of a single genus whose member's life history strategies are similar in many respects. Grime (1979) classifies life history traits into three dimensions based on the overriding factors of stress and disturbance. Using this classification a competitor (C) plant species as one that persists in a low stress, low disturbance environment. A stress tolerator (S) exploits conditions of high stress and low disturbance; and a ruderal (R) represents a reproductively driven strategy and persists in low stress and high disturbance.

Oaks, members of the genus *Quercus*, represent the most important hardwood species group both ecologically and

economically in North America. In addition to the 90 recognized species in North America (Flora Committee 1997) there are at least 70 hybrids in Northeastern Forest (Gleason and Cronquist 1991) and about 23 species in the Central Hardwood Region (Nixon 1997). As a group, oaks have wide ecological amplitude and can dominate highly varied environments. Oaks may all be classified as competitors or stress tolerators, *sensu* Grime (1979), but are not ruderal when compared to many tree species, e.g. *Populus*, *Salix*, *Robinia*. Differences in life history strategies should be especially clear within a genus such as *Quercus*, showing evolutionary divergence and speciation in response to environmental factors including disturbance and stress.

The objective of this study is to provide an understanding of how plant strategy theory can be quantified and evaluated based on numerous variables. The specific hypotheses are: (1) oak reproductive and growth characteristics are significantly correlated; (2) the distribution of these characteristics among species is consistent with r and K life history strategies. Furthermore, we intend to create a preliminary oak r and K Index for quantitative use and to use this index to examine and possibly predict relationships among life histories (the abundance of r and K attributes), disturbance frequency, oak species abundance, and basal area at nine sites in the Ozark Highlands of Missouri.

METHODS

We used data describing 13 oak species from the Central Hardwoods Region: white oak (*Quercus alba*), post oak (*Quercus stellata*), bur oak (*Quercus macrocarpa*), chinquapin oak (*Quercus muehlenbergii*), northern red oak (*Quercus rubra*), black oak (*Quercus velutina*), scarlet oak (*Quercus coccinea*), southern red oak (*Quercus falcate*), pin oak (*Quercus palustris*), blackjack oak (*Quercus marilandica*), swamp white oak (*Quercus bicolor*), overcup oak (*Quercus lyrata*), and nuttall oak (*Quercus texana*). Variables and sources are listed in table 1. Only species with available data for all six characteristics can be used in the statistical analysis, therefore this study explores only 13 species.

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Table 1—Oak species and their growth and reproductive characteristics^a

Species	Acorns	Age	Longevity	Height	Shade	Xylem	Repro.	Growth	r&K
<i>Quercus alba</i>	3.11	40	300	54	3	2	1.46	0.65	1.06
<i>Q. stellata</i>	0.98	25	320	45	1	2	-0.30	-0.60	-0.45
<i>Q. macrocarpa</i>	4.98	35	340	35	4	2	2.77	2.89	2.83
<i>Q. muehlenbergii</i>	0.94	40	250	50	2	2	-0.20	0.07	-0.06
<i>Q. rubra</i>	2.98	25	130	55	3	1	-0.19	-0.41	-0.30
<i>Q. velutina</i>	1.52	20	175	62	3	1	-0.45	-0.53	-0.49
<i>Q. coccinea</i>	1.58	20	120	62	1	1	-0.54	-1.15	-0.84
<i>Q. falcate</i>	0.67	25	150	57	2	1	-0.62	-0.78	-0.70
<i>Q. palustris</i>	0.91	26	130	70	2	1	-0.59	-0.91	-0.75
<i>Q. marilandica</i>	0.94	20	200	30	2	1	-0.55	-0.18	-0.37
<i>Q. bicolor</i>	3.11	20	325	60	3	2	0.44	0.45	0.44
<i>Q. lyrata</i>	2.67	27	350	40	3	2	0.73	1.40	1.07
<i>Q. texana</i>	3.93	5	120	90	2	1	-0.63	-1.03	-0.83

^aThe column headings are species = oak genus, acorn = acorns weight (g), age = age of first reproduction, longevity = estimated maximum tree age in years, height (growth rate) = median site index (feet) at 50 years (the reciprocal was used in index calculations), shade = shade tolerance rating, xylem = wood conductance type, repro. = normalized reproductive variable index, growth = normalized growth variable index, and r&K = r and K index value. Acorn weight (1 pound per number of acorns) and the reciprocal of height were used in calculating indices.

Growth and Reproductive Characteristics

Data on oak growth and reproductive characteristics come from a number of sources. Reproductive data on acorn weight, age of reproduction and tree longevity were found in Schopmeyer (1974), Foster and Ashe (1908), Miller and Lamb (1985), Nixon (1997), Burns and Honkala (1990), Brown and Panshin 1940, Panshin and ed Zeeuw (1970) were sources of data for the growth-related physiological attributes of shade tolerance and potential conductivity as well as longevity, age of first reproduction. Height growth (in feet) derived from median site index curves for oak species were used to estimate the rate of height growth (Carmean and others 1989).

Acorn weight is an important reproductive characteristic because large acorn size confers a reproductive and competitive advantage to oaks in highly competitive environments such as forests and prairies. Long and Jones (1996) found that among 14 oak species larger acorns consistently produced larger seedlings. Large acorns probably represent a K-strategy attribute as light, wind dispersed seeds - common with trees of prodigious seed output- suggests an r-strategy. We used the weight of an acorn in fractions of a pound in all analyses.

Organisms that reproduce early in their life have an advantage in capturing resources in environments with high rates of disturbance that may provide many opportunities for reproduction. Early reproductive age is a r-strategy attribute (Pianka 1999).

Longevity of individual trees confers a variety of selective advantages, including reproduction, in that the trees will have opportunities to reproduce over a longer period. Competitive advantages of longevity are numerous also, e.g. long term site occupation and exploitation of resources. Long-lived species are generally considered K-strategists.

Rapid growth confers an advantage to species in capturing resources in non-competitive environments with high rates of disturbance, thus representing a r-selective attribute. We used both height growth and potential stem nutrient transport as measures of growth potential. We used the reciprocal of height growth at 50 years in calculating the index to match positive trends in shade tolerance and longitudinal permeability among oak species.

The longitudinal permeability of tree stems effects stem water transport and can limit the supply of water and nutrients to the crown (Kozłowski and others 1991) and thus growth. Xylem permeability is conceptualized as a trade off between safety and conductance (Lambers and others 1998). Increased conductance may maximize growth but increases the risk of cavitations and negative physiological effects. The cost of risky anatomical structure of the red oak group corresponds to the r-strategy of many species that maximize growth in response to competitive selection pressures. The red and white oaks have many xylem characteristics that differentiate the potential conductance (and thus maximum growth) of these species groups such as vessel element size, as tyloses formation in vessels, and distinct heartwood-sapwood boundaries. For example, red oak heartwood is about 100,000 times more permeable than white oak heartwood (Siau 1971). Red oak vessel elements are larger than those of white oak (Brown and Panshin 1940). We used a value of 1 for the white group and a value of 2 for the red oak group to reflect differences in potential growth due to xylem conductance.

Shade tolerance can confer a competitive advantage to young oak trees under varying degrees of competition for light. Shade tolerance classes (Burns and Honkala 1990) were quantified as 1 for very intolerant, 2 for intolerant, 3 for intermediate, 4 for tolerant, and 5 for very tolerant. Tolerance for growth under shady conditions is a K strategy attribute.

R and K Index

We created an r and K index for oak species to examine differences among oak species and to test this concept with the spatial distribution of oak species and temporal change in oak species abundance. The r and K indices were constructed for reproductive and growth related factors presented above and based on plant selection theory (Grime 1979). Three reproductive characteristics were multiplied: (1) age of first acorn production (in years), (2) species longevity (in years), (3) and acorn weight (acorns per lb.). These values were then normalized (mean of 0 and a standard deviation of 1) to create a reproductive index. Three growth characteristics were multiplied: (1) height growth at 50 years, (2) shade tolerance class, (3) and heartwood permeability class. These values were then normalized (mean of 0 and a standard deviation of 1) to create a growth index. The mean of the reproductive and growth indices is the r and K index.

Data for the abundance, distribution, and dominance of oak species is derived from studies resulting from the Missouri Ozark Forest Ecosystem Project (MOFEP) (Brookshire and Shifley 1997, Kabrick and others 1997). This project is an experiment to assess the landscape level impacts of management practices on forest ecosystems including wildlife, plants, and forest productivity.

Data describing disturbance frequency, fire frequency, and the development and values of disturbance indices are taken from Guyette and Kabrick (2002). Fire frequency was estimated with regressions developed from fire scar chronologies at 26 sites in the Current River watershed (Guyette and others 2002, Guyette and Dey 2000). Mean fire interval estimates in this study are for the period of maximum variation in fire frequency among sites, the years 1700 to 1850. Only five of the 13 oak species (white, post, black, scarlet and red oak) grow at the MOFEP study sites, thus only five oak species could be used in testing predictions made by the r and K index approach about how species oak may be related to disturbance at these sites.

RESULTS

Oak reproductive and growth characteristics were significantly correlated using two methods. Pearson correlation analysis of reproductive and growth indices showed significance ($r = 0.94$, $p < 0.001$) among oak species attributes (fig. 1). Multivariate analysis using among growth and reproductive resulted in a canonical correlation coefficient of 0.98 ($p < 0.01$). All individual growth and reproductive variables were positively correlated but only acorn weight versus shade tolerance ($r = 0.54$, $p = 0.03$) and longevity versus permeability ($r = 0.94$, $p < 0.01$) were strongly correlated. Correlation analyses indicate that the distribution of all measured characteristics among species is consistent with the theoretical predictions of r and K life history strategies.

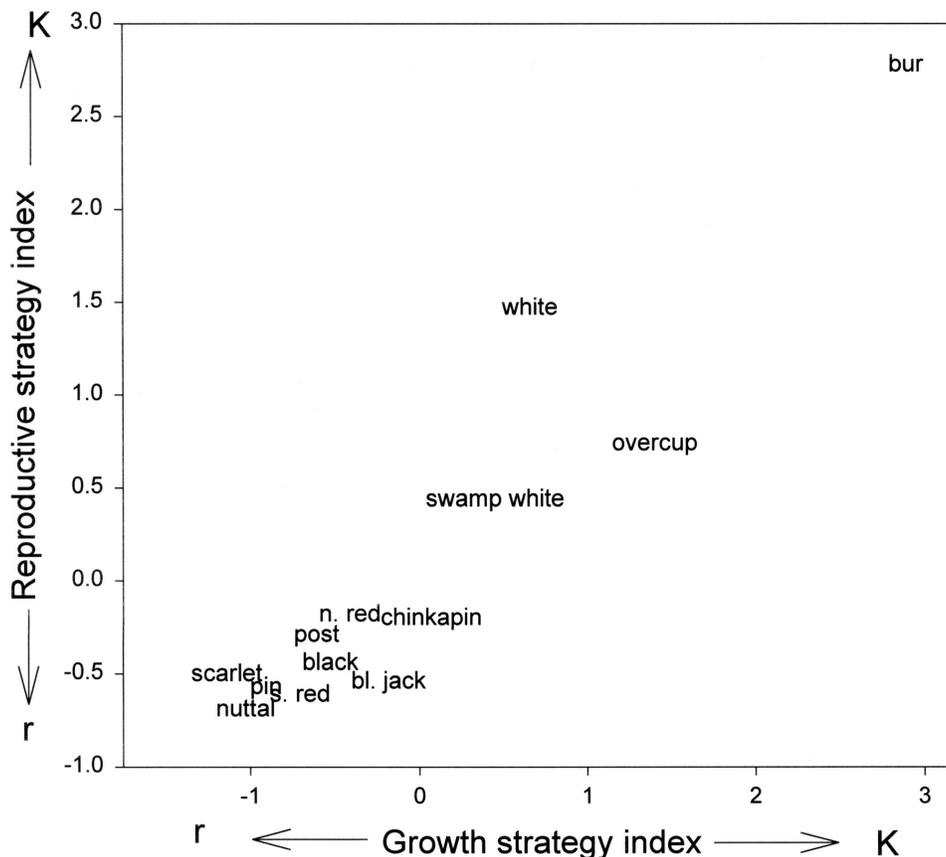


Figure 1—Scatter plot of the relationship between indices of the reproductive and growth strategies of 13 oak species (see table 1 for details).

The distribution of oak species at the nine large (> 314 ha) sites (Missouri Ozark Forest Ecosystem Project) was related to their r and K index values and the long-term disturbance histories of the sites (fig. 2). The abundance of five oak species that grow at these sites was weighted by

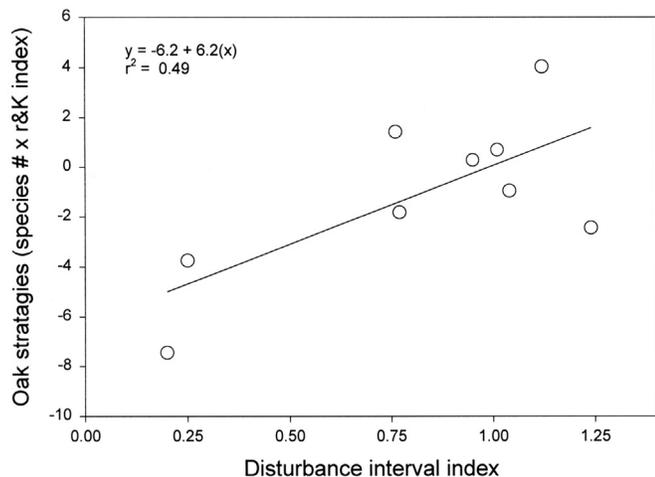


Figure 2—Scatter plot illustrating the relationship between the abundance of oak strategies (number oak by species x r and K index, summed by site) and disturbance history at the nine MOFEP sites.

their r and K index value and was correlated ($r = 0.71$, $p = 0.03$) with index values of long-term disturbance frequency (Guyette and Kabrick 2002).

Recent changes in the abundances of oak species at the nine MOFEP sites are consistent with their life history strategies and their r and K index values. Ten years of inventory data (1992-2002) measured in undisturbed, permanent vegetation plots show that the net basal area of oaks with high r and K indices such as white oak are increasing while those species with low r and K indices such as black jack are decreasing (fig. 3). These abundance changes at these undisturbed sites are roughly correlated with their r and K index values.

DISCUSSION

Non-random associations among growth and reproductive characteristics of oak indicate a distribution of attributes that is consistent with r and K selection processes that has occurred over an evolutionary time scale in response to disturbance and competition. The development of an r and K index among the species of a genus may have utility in management as well as scientific research. Quantification of species strategies could aid in predicting forest composition in response to silvicultural prescriptions. Residual basal area left after logging may be used in the prediction of species regeneration. Scientist might use the r and K index values to explain species distributions. For example,

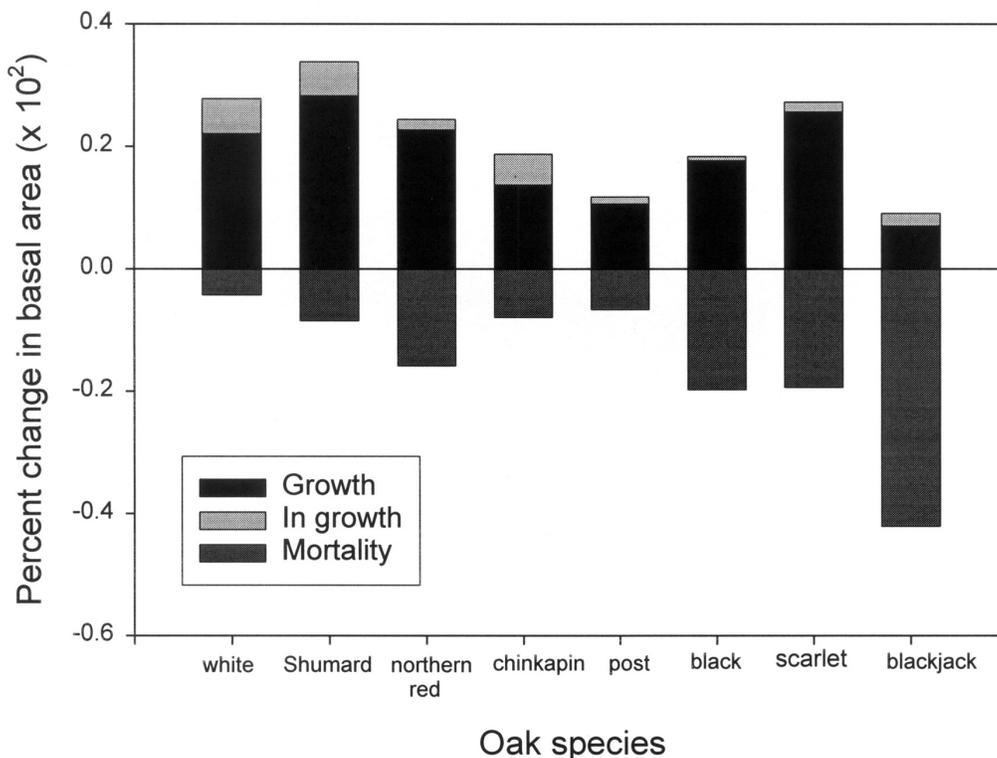


Figure 3—Growth, in-growth, and mortality for oaks at the nine MOFEP sites in undisturbed plots during 1992-2002. Growth is average basal area increases for trees >4.5 in. in diameter at breast height (d.b.h.); in-growth is average basal area increases by trees originally <4.5 in. in d.b.h. that grew into the larger size class during the sampling period; mortality is basal area of trees that died during the sampling period.

bur oak, an extreme K strategist (table 1), only occurs in many areas in extremely competitive environments such as flood plain forests and in tall grass prairies where large seeds and a high degree of shade tolerance allow for initial regeneration.

CONCLUSIONS

Quantitative comparisons among the life history strategies of oak and other large genera via index values are possible, may prove of value, but have limitations. We used values found in the oak literature. There is considerable difficulty in finding precise quantitative data that are comparable among a number of species. For instance, although we found excellent data on acorn weight, other variables such as the age of first reproduction or shade tolerance were more qualitative – more expert opinion than actual measured quantities. Thus, we believe that it should be understood, that when using the numeric values of *r* and *K* indices, these values only qualitatively estimate differences among species life history traits.

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SURVIVORSHIP AND GROWTH OF OAK REGENERATION IN WIND-CREATED GAPS

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Abstract—The effects of wind on upland hardwood forest structure and composition have been studied mostly in the context of either one to two tree mortality gap-phase openings or in retrospective studies of ancient disturbances. Larger (> 0.1 ha) wind-created openings are common across Southern Appalachian landscapes and can be an important factor in shaping understory colonization, growth, and survival. I investigated the relationships of oak seedling survivorship and growth to spatial and structural gradients in and around large hurricane-created gaps on the Bent Creek Experimental Forest. I related 2-year tagged-seedling survivorship to distance from gap edge and physical site through logistic regression. Seedling survivorship declined progressively on a linear distance gradient from gap exterior to gap center. Survivorship also declined as microsite soil moisture increased. I used multiple nonlinear regressions to relate 2-year tagged-seedling basal diameter growth and height growth to distance from gap edge, initial seedling height, canopy cover, and physical site. Basal diameter growth increased as midstory canopy cover declined, at gap positions close to gap center, as initial seedling height increased, and as microsite soil moisture increased. Seedling height growth increased with decreasing overstory canopy cover, at locations near gap center, as initial seedling height increased, and as microsite soil moisture increased.

INTRODUCTION

Hurricane-force winds frequently initiate forest structural and compositional changes in the Southern Appalachians. The effects of wind on upland hardwood forest structure and composition have been studied mostly in the context of either small gap-phase openings, or in retrospective studies of ancient disturbances. Larger (> 0.1 ha) wind-created openings, which are common across Southern Appalachian landscapes (Greenberg and McNab 1998), can be an important factor in shaping understory colonization, growth, and survival (Runkle 1985).

Increases in light created by wind-generated gaps change the dynamics of understory plants. Generally, seedling survivorship and growth improve as gap size increases, as canopy cover decreases, and in the photosynthetically active radiation (PAR)-rich north end of gaps (Ashton 1996, Chen and others 1995, Dale and others 1995). PAR and attendant plant growth and survivorship gradually decline from gap center to exterior forest (Chen and others 1995). Many investigators have linked tree seedling survivorship and growth with gap size and categorical position (gap center, gap edge, outside gap) within and around gaps (Sipe and Bazzaz 1995). Analyzing understory vegetation as a function of categorical covariates is attractive to many investigators, because these discrete approaches yield easily understood mean responses. However, continuous variables lend themselves to predictive equations that enable managers to understand where responses take place along a gradient of change. If managers could predict survivorship and growth along linear distance gradients, they could then also predict the extent of gap partitioning for arborescent species of interest.

Windstorms create massive amounts of woody debris in hardwood forests (Greenberg and McNab 1998). This debris may either enhance or hinder seedling survivorship and growth.

Hurricane Opal, which struck the Bent Creek Experimental Forest on October 5, 1995, provided a firsthand opportunity to evaluate the effects of wind damage, particularly large area gaps, on forest understory vegetation. I investigated the relationships of oak (*Quercus*) seedling survivorship and growth to spatial and structural gradients in and around large Hurricane Opal-created gaps.

OBJECTIVES

My objective was to test the hypotheses that 2-year oak seedling survivorship and growth increase as gap size increases, on a linear distance gradient toward gap center, in the north end of gaps, and as hurricane-created woody debris decreases.

METHODS

Hurricane Opal struck Bent Creek on the morning of October 5, 1995. Opal created sustained winds of 8.9 miles per second and maximum peak gusts of 25.9 miles per second at the nearby Asheville, NC, airport. Within a 259-ha surveyed parcel at Bent Creek, an average of 0.89 canopy gaps/ha were created by Opal-generated windfalls. Single-tree gaps were the most common opening, averaging 57 ± 34 m². Multiple-tree gaps averaged 171 ± 117 m² (Greenberg and McNab 1998).

Gap Selection

Selected gaps are located within the 2 400-ha Bent Creek Experimental Forest, about 16 km south of Asheville, NC (35.5° N, 82.6° W) in the Southern Appalachian Mountains. Gaps were restricted to openings at least 0.1 ha in size. Also, at least six canopy trees per gap must have fallen as a result of Hurricane Opal. Beck (1988) commented on the 0.1-ha size as being a reasonable minimum for the successful colonization and development of the most shade-intolerant eastern hardwoods. By restricting gap areas to > 0.1

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ha, I ensured that all native hardwoods had enough light to colonize and grow successfully.

Using Runkle's (1992) definition of the extended gap to determine perimeters, I located 12 gaps meeting the above criteria ranging from 0.13 to 1.26 ha from October 1995 to June 1996.

Project Site

Of the 12 gaps, 6 are located in dry oak-hickory vegetation communities, 4 in acidic coves, and 2 in rich coves (Schafale and Weakley 1990). The frost-free growing season extends from approximately May 1 to mid-October. Annual precipitation ranges from 120 cm at 670 m elevation to 150 cm at 850 m elevation. Soils are derived from gneisses and schists, with occasional intrusions of mafic minerals found in amphibolite deposits. All soils are > 80 cm deep and acidic (pH < 5.2).

Hurricane-created windfall trees mostly were uprooted and did not snap off from the bole. All selected gaps supported some residual hardwood overstory and midcanopy trees; residual tree distribution was highly variable.

Gap Sampling Design

Sampling points were installed during May to July 1996. Two horizontal perpendicular axes were located within each gap: north-south and east-west. Axes intersected at gap center. Axis orientation was changed when realignment allowed a gradient along the entire length of a gap. Transect lines extended from center along established axes in the cardinal directions. Sampling points were located at:

1. gap center
2. out from center along transects 7.3 to 10.67 m apart until gap edge was reached
3. at the north, south, east, and west gap edges
4. progressively outward beyond gap edges 7.3 m apart.

The most extreme points were installed outside gaps where ground-level solar radiation approximated that of forests unaffected by windthrow.

This design resulted in 15 to 32 sampling points per gap and 269 points among all 12 gaps. Established sampling points formed the centers of 13 m² circular quadrats.

Tree Seedling Measurements

One or two oak seedlings ≤ 3.81 cm in diameter at breast height were selected at random within each of the 13 m² circular quadrats and tagged for long-term identification and measurement. Tagged oaks included 54 northern red (*Q. rubra* L.), 38 chestnut (*Q. prinus* L.), 69 black (*Q. velutina* L.), 2 southern red (*Q. falcata* Michx.), and 73 scarlet (*Q. coccinea* Muenchh.).

Tagged oaks were pooled into one analysis group, because survivorship rates, growth, and response to disturbance are similar for these species (Personal communication, 2000. David Loftis, Project Leader, USDA Forest Service, Southern Research Station, Bent Creek Experimental Forest, Asheville, NC 28806). Seedlings were measured twice: June to October 1996 and October to November 1998.

Variables

A wide array of variables were measured and tested as covariates (see table 1 for detailed descriptions of covariates used in final models):

Variables that directly relate to hypotheses:

- distance/gap attributes: gap area, gap perimeter, ratios of gap length to width, distance from gap center to edge, distances from north and south gap edges to center, cardinal direction from center, and gap aperture (angle from gap center to canopy treetops at gap edge (Runkle 1992)
- cover: canopy cover of overstory, midstory, and total canopy
- debris resulting from Hurricane Opal: crown debris, coarse woody debris, tree-fall pits or mounds.

Covariates that help explain background variability:

- site: slope, aspect, categorical indices of soil moisture potential (xeric, subxeric, submesic, mesic), elevation, landform index (McNab 1993), and terrain shape index (McNab 1989)
- vegetative competition: overtopped vs. not-overtopped (dichotomous estimate of subject seedling position relative to surrounding vegetation), shrub coverage, tree seedling densities
- tagged seedling condition: sprout vs. seed origin, broken vs. whole seedling top, microtopography where the seedling is located, initial height, and initial basal diameter.

Data Analysis

I used regression analysis to test all hypotheses.

Seedling survivorship—I employed logistic regression to test the seedling survivorship hypothesis.

The logistic model (Hosmer and Lemeshow 2000) is

$$P = \frac{\exp(b_i X_i)}{1 + \exp(b_i X_i)}$$

where

P = predicted probability of seedling survivorship

b_i = vector of regression coefficients

X_i = vector of independent variables

\exp = base of the natural logarithm.

Data were pooled across all 12 gaps and 269 quadrats and analyzed with SAS PROC LOGISTIC (SAS Institute 2000).

Basal diameter and height growth—I tested seedling basal diameter and height growth hypotheses with nonlinear regression, using SAS PROC NLIN (SAS Institute 2000).

I regressed basal diameter growth against covariates using the exponential function, $\beta_0(e^{\beta_1 x_1 + \beta_2 x_2 \dots \beta_n x_n})$. I modeled height growth with another exponential function, $\beta_0 + e^{\beta_1 x_1 + \beta_2 x_2 \dots \beta_n x_n}$.

Table 1—Variables used in oak seedling survivorship and growth regression models: data from 12 Hurricane Opal-created gaps within the Bent Creek Experimental Forest

Variable	Mean <i>units</i>	Range	Explanation
GAPPOS (fig. 1)	5.64 (m)	-29.27 – 95.30	Gap position: Linear horizontal distance from gap-edge to quadrat center. Distances from edge towards gap interior are positive, from edge to gap exterior are negative.
MIDCOVER	0.6 (decimal)	0.0 – 1.0	Midcanopy cover: Canopy cover of midcanopy trees. Canopy cover was measured with a go/no-go densitometer (Geographic Resource Solutions 1997) at 17 points within 3.6 m of each quadrat center. The GRS device is essentially a small periscope with level vials and center point for dichotomous calls as to whether or not there is arborescent vegetation overhead. Positive “hits” were then summed and divided by 17 to yield the fraction of the area with overhead canopy.
OVERCOV	0.5 (decimal)	0.0 – 1.0	Overstory cover: Canopy coverage of true canopy species, such as the oaks. Measured as above.
LFI	.19 (decimal)	.08 – .34	Landform Index (McNab 1993): The degree of protection offered by the surrounding topography, expressed as the percent slope from gap center to the surrounding landscape horizon. The mean of 8 readings taken at 45-degree intervals. LFI is a surrogate for soil moisture. Higher values suggest higher soil moisture content.
TSI	3.0 (decimal)	-8.6 – 36.6	Terrain Shape Index (McNab 1989): Microsite topography, expressed as the percent slope parallel to ground surface within 15.24 meters from gap center. The mean of 8 readings taken at 45-degree intervals. TSI is a surrogate for microsite soil moisture. Higher values suggest higher soil moisture content.
SURV	0.9 (decimal)	0.0 – 1.0	Survivorship between 1996 and 1998: Dichotomous response variable.
BDGROW98	0.3 (cm)	-4.3 – 2.5	Basal diameter growth between 1996 and 1998; response variable.
HT96	0.6 (m)	0.1 – 3.7	Initial seedling height: measured in 1996.
HTGROW98	0.2 (m)	-1.5 – 2.5	Height growth between 1996 and 1998; response variable.

GAPPOS = gap position; MIDCOVER = midstory canopy cover; OVERCOV = overstory cover; LFI = landform index; TSI = terrain shape index; SURV = 2-year survivorship probability; BDGROW98 = 2-year basal diameter growth; HT96 = initial height; HTGROW98 = 2-year height growth.

These functions are modifications of the Mitcherlich equation, commonly used to model vegetation growth (Myers 1990). Other investigators have used similar functions to model tree diameter and height growth (Vanclay 1994).

RESULTS

Survivorship

Based on the results of my logistic model (table 2), I rejected the hypothesis that survivorship should increase as gap size increases, toward gap center, in the north end of gaps, and as hurricane-created debris declines.

Oak seedling survivorship declined toward gap center and on high-moisture microsites as indexed by terrain shape index (TSI) (fig. 1). The negative slope of the TSI parameter in the survivorship model makes sense; oak survivorship is superior on drier sites, probably because arborescent seedling competition is less than that of mesic sites (Johnson and others 2002).

My predictive model is weak; standard error of the gap position (GAPPOS) parameter is roughly half the parameter

estimate (table 2). The low rescaled pseudo- R^2 of 0.11 bears evidence that my survivorship model has poor goodness-of-fit. Classification accuracy is poor, as evidenced by the area under the ROC curve (Hosmer and Lemeshow 2000) of 0.774 (1.0 = perfect classification; 0.5 = no classification benefit; < 0.7 generally indicates poor classification) (fig. 2). Also, my model exhibited declining percent correct classifications with increasing cut point values (94 percent at cut point of 0.50 to 83.3 percent at cut point of 0.90), suggesting poor classification ability.

Topography (seedling location: pit, mound, or near large woody debris) was not correlated with seedling survivorship (table 1). Because only a small fraction of gap areas were covered with pits and mounds, few tagged seedlings were located on these microsites, making any statistical relationships improbable. I found no relationship of oak seedling survivorship to hurricane-created debris, including crown debris and log debris > 8 cm in diameter.

Oak seedling survivorship was not related to cardinal direction within gaps or gap size. I found no relationship of

Table 2—Logistic model^a: 2-year oak seedling survivorship

Response variable	n	Likelihood ratio	Prob. > chi-square	Pseudo-R ²	Maximum rescaled pseudo-R ²	Correct classifications (cut point) <i>percent</i>
SURV	234	9.532	.0085	.04	.11	94.0 (.50) 83.3 (.90)
Covariate	Parameter estimate	Standard error	Chi-square	Prob > chi-square		
INTERCEPT	3.392	.410	68.53	<.0001		
GAPPOS	-.029	.016	3.16	.08		
TSI	-.101	.042	5.95	.01		

^a SURV = 2-year survivorship probability; BDGROW98 = 2-year basal diameter growth; HTGROW98 = 2-year height growth; MIDCOVER = midstory canopy cover; OVERCOV: overstory cover; GAPPOS = gap position; HT96 = initial height; LFI = landform index; TSI = terrain shape index (table 1).

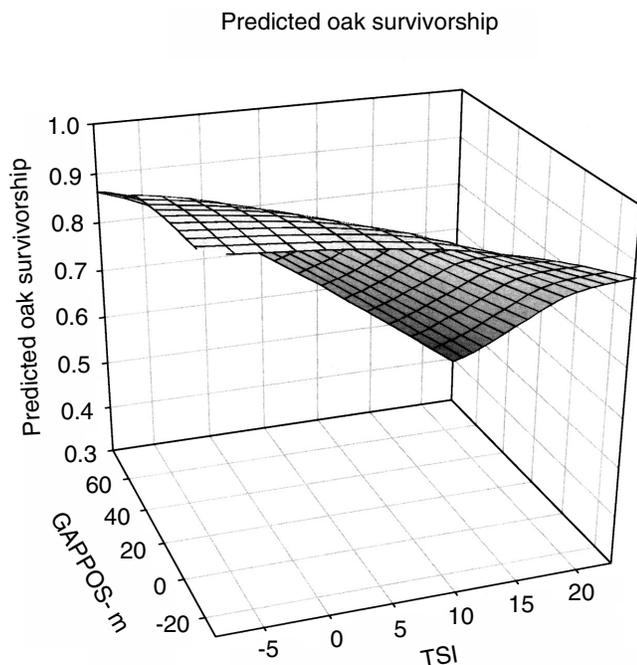


Figure 1—Two-year oak survivorship vs. GAPPOS and TSI. GAPPOS = gap position; TSI = terrain shape index (table 1).

survivorship to surrounding arborescent seedling competition, gap aperture, canopy cover, or tagged seedling condition, including initial seedling height, seedling origin (sprouts vs. propagules from seed), or amount of seedling top damage.

Growth

I encountered significant problems with outliers in all growth analyses. In particular, negative growth observations created enormous modeling problems. Negative basal diameter and height growth are not unusual; oak seedlings frequently lose their tops to herbivory or weather damage (Johnson and others 2002). New tops usually develop after

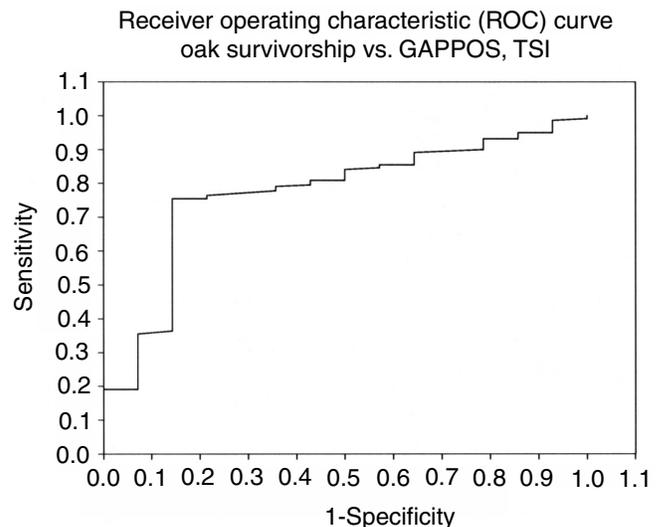


Figure 2—Two-year oak survivorship vs. GAPPOS and TSI: ROC curve (45° diagonal plot suggests poor model accuracy; straight line = perfect accuracy). Area under curve = 0.774 (0.5 = no classification benefit; 1.0 = perfect classification).

resprouting, but the new growth may not make up for increment lost over the 2-year measurement period. Some of these negative growth observations in larger diameter stems created high influence points that actually reversed the sign of initial height (HT96) parameter slopes. I solved this problem by deleting all negative growth observations.

My analyses supported my hypotheses of increased oak basal diameter and height growth toward gap center (table 3, figs. 3 and 4). However, data analyses did not support my hypotheses that growth would increase in larger gaps, in the north end of gaps, and as hurricane-created debris decreased.

Table 3—Nonlinear growth models: 2-year oak seedling basal diameter and height growth^a

Response variable	n	Mean square error	Computed F statistic	Prob. > F	Nonlinear R ²	Covariate	Parameter estimate	Standard error
BDGROW98	169	.09	77.52	<.0001	.31	INTERCEPT	0.463	.065
						MIDCOVER	-1.01	.256
						GAPPOS	0.01	.004
						HT96-LFI	2.24	.260
HTGROW98	169	.0518	12.0	<.0001	.23	INTERCEPT	-.8143	.041
						HT96	.1192	.041
						GAPPOS	.00256	.001
						OVERCOV	-.1702	.001
						HT96-TSI	.0110	.005

^a BDGROW98 = 2-year basal diameter growth; HTGROW98 = 2-year height growth; HT96 = initial height; GAPPOS = gap position; MIDCOVER = midstory canopy cover; OVERCOV: overstory cover; LFI = landform index; TSI = terrain shape index (table 1).

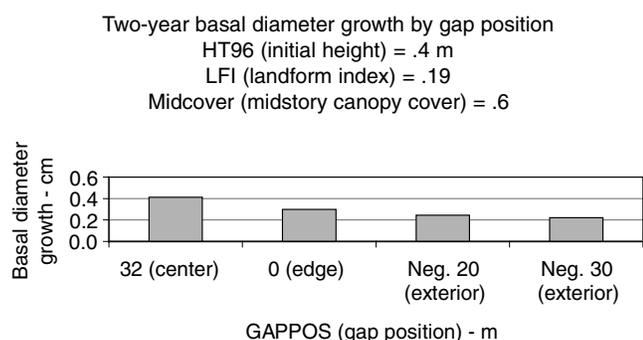


Figure 3—Two-year oak basal diameter growth vs. GAPPOS, HT96, TSI, and MIDCOVER.

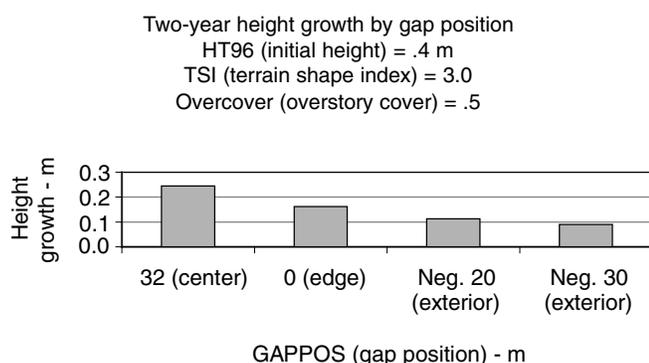


Figure 4—Two-year oak height growth vs. GAPPOS, HT96, TSI, and OVERCOV.

Seedling basal diameter and height growth were highly variable. Basal diameter growth mean square error was 0.09 with mean of 0.3 cm; height growth mean square error was 0.0518 with mean of 0.2 m. Accordingly growth relationships are weak; the basal diameter growth model R² is 0.31, and

the height growth model R² is 0.23. Also, the distance gradient covariate GAPPOS explained little of the variability in growth, as evidenced by high GAPPOS standard errors relative to parameter estimates in both the basal diameter and height growth models (table 3).

HT96 contributed substantially to explaining variability in basal diameter and height growth (table 3). Basal diameter and height growth correlated with seedling origin (sprouts vs. propagules arising from seed). However, initial height was so highly collinear with origin that origin had to be eliminated from all models.

Site variables, TSI, and landform index (LFI) explained much of the variation in growth (table 3). I have no rational explanation why LFI proved valuable in the basal diameter growth model as opposed to TSI in the height growth model. The positive slopes of TSI and LFI (HT96-LFI in the basal diameter growth model, and HT96-TSI in the height growth model) make sense; growth of surviving seedlings should be superior on mesic sites.

Both overstory canopy cover (OVERCOV) and midstory canopy cover (MIDCOVER) (table 1) were negatively correlated with oak seedling height growth. However, OVERCOV was much more strongly related to height growth than was MIDCOVER. In fact, MIDCOVER was not significant in the presence of OVERCOV when both variables were included in the height growth model.

The interaction terms HT96-LFI in the basal diameter growth model and HT96-TSI in the height growth model include covariates not included as main effects in the nonlinear functions (table 3). This contradicts recommendations of some statisticians to always include main effects in “hierarchically well formulated models” (Glantz and Slinker 1990). However, including both interaction and all main effect terms created substantial collinearity, so I deleted problematic main effects from both the basal diameter growth and height growth models.

DISCUSSION

Survivorship declined toward gap center and increased at gap edge and in microsites up to 20 m beyond gap edge in the unaffected forest (fig. 1). My results of higher seedling survivorship in microsites closer to gap edge than gap center mirror those of McNab (McNab, W.H. 2002. Poor American chestnut seedling survivorship in gap-centers. Unpublished data analysis. U.S. Department of Agriculture, Forest Service, Southern Research Station) and Sipe and Bazzaz (1995). Meiners and others (2000) found that oak, ash (*Fraxinus americana* L.), and red maple (*Acer rubrum* L.) survivorship suffered in the subdued light environment at gap perimeters; seedling survivorship was enhanced near gap centers. Why are my findings of low survivorship toward gap center diametrically opposed to the results of other investigators such as Meiners and others (2000)? Perhaps seedling competition increases toward gap center, which may be contributing to early oak seedling death. This trend may reverse through time for seedlings near gap center that are able to attain dominance. Eventually, oak seedlings outside gaps probably will die at an increasing rate, because they will not be able to acquire sufficient sunlight to achieve their compensation points (Kramer and Kozlowski 1979).

My findings of increasing basal diameter and height growth along a linear distance gradient toward gap center are consistent with those of Brown (1996). He found that height growth of tropical hardwoods increased linearly on a distance gradient from gap exterior to gap center. Brown's study is one of few relating seedling performance to linear distance gradients.

Tree seedling survivorship and growth generally improve as gap size increases because of solar radiation gains at ground level (Sipe and Bazzaz 1995). However, improvements in growth often attenuate beyond thresholds in gap size. For example, Coates (2000) found substantial seedling growth enhancement as gap size increased up to 0.1 ha but discovered no growth improvements in sizes beyond 0.1 ha to 0.5 ha. However, I found no correlations of oak seedling survivorship or growth with gap size. I suspect that having my gaps > 0.1 ha in size diluted the effect of gap size on oak survivorship and growth.

The lack of relationship of oak survivorship and growth to hurricane-created crown debris is surprising. Crown debris intercepts substantial solar radiation and should be negatively correlated with survivorship and growth. Crown debris was heavily distributed throughout gaps as a result of wind-thrown trees. I suspect that one reason for this lack of correlation is deterioration of crown debris over the 2-year measurement period. Crown debris coverage declined from a mean of 10.6 percent in 1996 to 0.7 percent in 1998.

Generally, tree seedling survivorship and growth increase as midstory and overstory canopy densities decrease (Buckley and others 1998, Dey and Parker 1997). As expected, I found that seedling growth was negatively correlated with cover. Why did I not find a significant negative relationship of seedling survivorship to canopy cover? I suggest that the tagged seedlings had sufficient carbohydrate reserves to sustain life over the 2-year response

period, even under residual tree canopies. However, the answer eludes me, because my logistic model only measured the dichotomous response of live vs. dead, not physiological condition.

Most surprising is the lack of relationship between oak survivorship and initial size (Johnson and others 2002). Oaks are advance-regeneration-dependent (Johnson and others 2002, Loftis 1989). Probability of their survival and subsequent competitive status is based on size, as represented by basal diameter or height (Battaglia and others 2000, Loftis 1990). Having large initial size confers competitive advantages in high-density cohorts of regeneration. My findings of no survivorship relationship with initial size may be because my analysis includes only 2 years of response time. Many authors suggest that oak survivorship is quite high for the first few years after disturbance before severe competition takes place (Johnson and others 2002).

Topographic factors can serve as surrogates of available soil moisture (Vanclay 1994). TSI and LFI apparently captured important differences in soil moisture across all 12 gaps to explain much of the variability in survivorship and growth (tables 2 and 3).

This study validates the use of LFI and TSI to explain site difference impacts on seedling survivorship and growth. Previously, these indices had been used solely in site classification studies (Hutto and others 1999) (W.H. McNab. 1995. Field guide to site classification in the Bent Creek Experimental Forest. Unpublished manuscript. On file with: U.S. Department of Agriculture, Forest Service, Southern Research Station). Because many forestry investigations are better analyzed with regression than through agricultural-style field-blocked studies, physical site variables such as LFI and TSI are invaluable in explaining vegetation response by differing site qualities.

CONCLUSIONS

1. Oak seedling survivorship declined on a continuous horizontal distance gradient from gap exterior to gap center.
2. Seedling basal diameter and height growth increased on a continuous horizontal distance gradient from gap exterior to gap center.
3. Arborescent overstory cover proved useful in explaining reductions in seedling height growth; midcanopy cover substantially reduced basal diameter growth. Seedling survivorship was not related to cover.
4. Hurricane-created debris had no discernible effect on seedling growth or survivorship.
5. Gap size did not affect 2-year oak seedling survivorship or growth in the range of gap sizes investigated (0.1 to 1.3 ha).
6. Gap-edge effects on oak seedling survivorship and growth persisted at least 20 m into the unaffected forest.
7. Physical site variables enable oak seedling growth and survivorship comparisons among a wide variety of sites.

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COMPARISON OF SAPROXYLIC BEETLE (COLEOPTERA) ASSEMBLAGES IN UPLAND HARDWOOD AND BOTTOMLAND HARDWOOD FORESTS

Michael D. Warriner, T. Evan Nebeker, Steven A. Tucker, and Terence L. Schiefer¹

Abstract—Insects dependent upon dead wood, wood-decaying fungi, or other organisms within dead wood for some portion of their life cycle have been termed saproxylic. Beetles comprise a large component of the saproxylic fauna within forests and play vital roles in the initial fragmentation and breakdown of dead woody debris. To evaluate the influence of forest type on saproxylic beetle assemblages, we surveyed upland and bottomland hardwood stands in east-central Mississippi. Overall, the two forest types shared a number of similarities in terms of their saproxylic beetle faunas. However, ecological differences between these two forest types were evident, most notably in diversity and abundance of beetle species dependent upon wood-decaying fungi.

INTRODUCTION

Dead, decaying wood is known to play a number of important roles in terrestrial ecosystems from nutrient cycling, moisture retention, to habitat complexity (Harmon and others 1986). Due to involvement in such diverse ecological functions and processes, dead wood has been recognized as an important forest resource (Stevens 1997). With this recognition, has come a growing awareness of the contribution dead wood makes to forest biodiversity (Lofroth 1998).

Of the various organisms that make use of dead wood, insects represent one of the most species-rich and abundant components (Hanula 1996). Some insects spend the majority of their life cycle living within, and feeding on, dead wood. Once dead wood is fragmented by wood-boring species, other insects enter, feeding on the decaying wood or the hyphae of wood-decaying fungi. These species, in turn, represent prey for a variety of predaceous insect species.

Speight (1989) termed insect species dependent upon dead wood, wood-decaying fungi, or other organisms within dead wood for some portion of their life cycle as saproxylic. Saproxylic insects represent a fundamental component of most forest ecosystems, playing vital roles in the initial fragmentation and breakdown of dead woody debris (Ausmus 1977, Edmonds and Eglitis 1989) as well as comprising a food base for other organisms (Beckwith and Bull 1985).

Saproxylic insects, beetles in particular, have received much attention in Europe as regards their diversity, conservation, and potential to serve as indicators of forest condition (Hågvar and Økland 1997, Nilsson and others 1995, Väisänen and others 1993). A number of European studies have noted variations in saproxylic beetle faunas in relation to forest structure (Barbalat 1998), successional stage (Gutowski 1995), and management practices (Barbalat 1996).

Outside of insects considered to be pests of wood products, little base-line information exists regarding species composition and status of saproxylic insects in forests of the southeastern U.S. Though little studied, there has been a call for additional research concerning the role dead wood plays in the maintenance of southern forest biodiversity (McMinn and Crossley 1996). Basic assemblage-level data concerning the community composition and structure of saproxylic species within different forest types, and across successional stages, could provide a standard by which disturbances, human-induced or natural, could be evaluated (Kaila and others 1997). In that light, our objective in this study was to compare and characterize the saproxylic beetle assemblages of upland and bottomland hardwood forests. Both upland and bottomland hardwood forests are characterized by significant ecological differences in moisture, tree species composition, and site conditions. Such factors may play important roles in shaping the saproxylic beetle fauna of both forest types.

STUDY SITES

This study was conducted at the Noxubee National Wildlife Refuge in east-central Mississippi (Noxubee County). Study sites were established in two upland hardwood and two bottomland hardwood stands on the refuge. Dominant tree species in both upland hardwood stands included white oak (*Quercus alba* L.), mockernut hickory (*Carya tomentosa* (Poir.)), and black oak (*Q. velutina* (Ell.)). A number of large shortleaf pine (*Pinus echinata* (Mill.)) occurred in one of the upland hardwood stands. Dominant tree species in the bottomland hardwood stands included willow oak (*Q. phellos* L.), cherrybark oak (*Q. falcata* var. *pagodifolia* Ell.), red maple (*Acer rubrum* L.), and American sweetgum (*Liquidambar styraciflua* L.). The bottomland hardwood stands occurred along the floodplain of the Noxubee River and flooded for four to six days in early April 2000 when the Noxubee River overflowed its banks. All four stands used as study sites ranged in age from 45 to 60 years of age.

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MATERIALS AND METHODS

Insect Sampling Protocol

Saproxylic beetles were sampled using Malaise traps and window traps (flight-intercept traps). Malaise traps are large tent-like structures that passively trap low-flying insects and collect them in a container filled with a preservative/killing agent. Collecting containers were filled with 70 percent ethanol. One Malaise trap was placed in each upland hardwood and bottomland hardwood stand.

Window traps were also deployed at each study site. Window traps, modified from Økland (1996), consisted of two perpendicular clear plastic sheets (35 cm x 40 cm) attached to a collecting container (33 cm diameter). Collecting containers were filled with propylene glycol. A roof was placed on top of the intersecting clear plastic sheets to prevent rainfall from flooding the collecting container. Window traps were hung between two trees at a height of 2 m. A total of six traps, spaced 20 m apart, were operated at each study site.

All traps were operated continuously from May to October 2000. Malaise and window traps were serviced, and collected insects removed, on a biweekly basis. Beetles collected from both trap types were sorted to morpho-species and stored in 70 percent ethanol.

Selection of Target Saproxylic Groups

One obstacle confronting insect-related projects is the overwhelming diversity of species that can be collected (Disney 1986). As an alternative to identifying all insects, assemblages of select species representing different functional groups have been suggested for use as monitoring tools or indicators of environmental change (Kremen and others 1993). Based upon that rationale, we identified target groups for use in our analyses. The groups selected comprised saproxylic beetles representing major functional groups within dead wood. The represented functional groups, and associated beetle taxa, used in our analyses were as follows:

Xylophagous beetles

Coleoptera: Cerambycidae (longhorned beetles)

Predaceous beetles:

Coleoptera: Cleridae (checkered beetles)

Fungivorous beetles:

Coleoptera: Erotylidae (pleasing fungus beetles)

Longhorned beetles include a number of species that feed as larvae within trees and shrubs. A small number of species feed on healthy hosts, however, most species feed on dead, decaying wood (Yanega 1996). Most checkered beetles feed on the larvae of wood-boring beetles (Cerambycidae, Scolytidae) as both larvae and adults. Pleasing fungus beetles are a group of mostly fungivorous species, many of which feed on wood-decaying fungi.

Data Analysis

Species diversity between sites was evaluated using rarefaction (Simberloff 1972). Rarefaction estimates the number of species in a random subsample to the entire sample. The resulting value can then be interpreted as a measure of diversity because the technique takes into account both species richness and abundance. The main advantage of

using rarefaction is that it is independent of sample size. Abundances of target taxa were compared between upland and bottomland hardwood stands using t-tests. Similarities in faunal composition among study sites were assessed using the Morisita-Horn index. The Morisita-Horn index was chosen because sample size and diversity of the sample have little influence on its calculation (Morisita 1959, Wolda 1981). Distribution of numbers of species and individuals representing each functional group (xylophagous, predaceous, fungivorous) were compared among upland hardwood and bottomland hardwood stands using a Chi-square test.

RESULTS AND DISCUSSION

Saproxylic Beetle Diversity and Abundance

Overall, a total of 56 saproxylic beetle species were collected from the bottomland hardwood study sites and a total of 48 species from the upland hardwood sites. Species diversity, as measured by rarefaction, varied between the forest types for two of our three target saproxylic groups (fig. 1). For longhorned beetles, predicted diversity was slightly higher in the bottomland hardwood stands than in the upland hardwood sites. Species diversity of pleasing fungus beetles

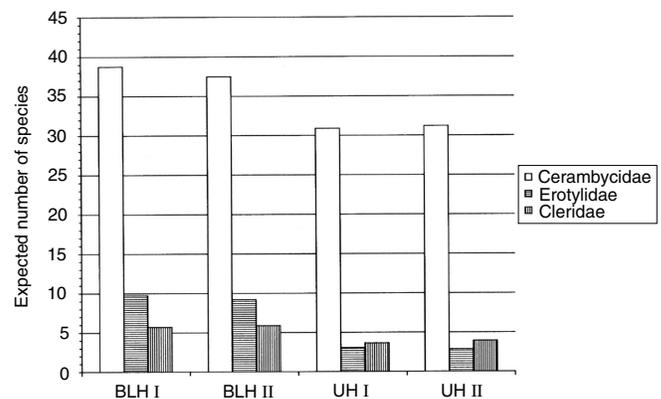


Figure 1—Species richness of target saproxylic beetle groups, as estimated by rarefaction, in upland and bottomland hardwood study sites.

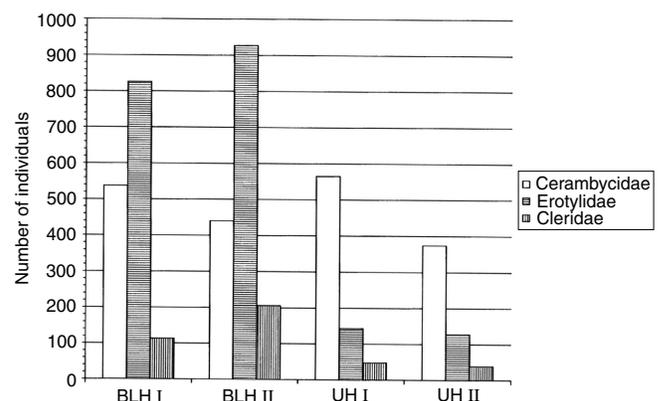


Figure 2—Abundances of target saproxylic beetle groups in upland and bottomland hardwood study sites.

was considerably higher in bottomland hardwood stands, reflecting the presence of a number of species not present in the upland hardwood sites. Checkered beetle species diversity was relatively equitable across all four study sites. Abundances of longhorned beetles were found to be relatively similar ($t=-0.36$, $df=145$, $P=0.3597$) in bottomland hardwood and upland hardwood forests (fig. 2). Conversely, pleasing fungus beetle ($t=1.71$, $df=29$, $P=0.0489$) and checkered beetle ($t=1.75$, $df=21$, $P=0.04735$) abundances varied significantly in relation to forest type, with larger numbers of both groups present in bottomland hardwood forests.

Comparisons of saproxylic beetle assemblages between stands of the same forest type displayed relatively high degrees of complementarity. The Morisita-Horn value calculated for saproxylic beetle assemblages from the two bottomland hardwood sites indicated a high level of similarity at 0.92. A similar level of congruence was found to exist between the two upland hardwood sites as well (0.91). Comparisons between upland hardwood and bottomland hardwood forest types yielded lower values (BLHI/UHI=0.77, BLHI/UHII=0.75; BLHII/UHI=0.72, BLHII/UHII=0.68), indicating a lesser degree of similarity in saproxylic beetle species composition. Analysis of numbers of species representing each functional group revealed no major differences among the four study sites ($\chi^2=2.29$, $df=6$, $P=0.8912$). Differences were noted when abundances of each functional group were compared across study sites. Upland hardwood stands were characterized by significantly lower numbers of individuals from predaceous and fungivorous functional groups ($\chi^2=672.80$, $df=6$, $P<0.001$). Numbers of xylophagous individuals did not differ across the four study sites.

Of the three target groups, longhorned beetles exhibited the smallest amount of variation between the two forest types. The most commonly collected longhorned beetle species from both forest types included *Strangalia luteicornis* (Fabricius), *Neoclytus acuminatus* (Fabricius), *S. bicolor* (Swederus), and *Elaphidion mucronatum* (Say). *Strangalia luteicornis*, and *S. bicolor* are known to feed on decaying hardwoods. *Neoclytus acuminatus* is known to prefer recently dead, as well as weakened and dying hardwoods. *Elaphidion mucronatum* feed primarily on the branches of dead hardwoods.

Although both upland hardwood and bottomland hardwood forests contained different tree species, larval host preference did not seem so specific as to limit large numbers of longhorned beetle species to one forest type. Many of the longhorned beetles collected possess relatively broad larval host preferences in terms of hardwood trees, with individual species known to feed on a range of hickory (*Carya*), oak (*Quercus*), elm (*Ulmus*), and/or ash (*Fraxinus*) species. Notwithstanding that, both forest types did contain species either trapped only within a specific forest type or characterized by higher abundances in one forest type. For instance, *Orthosoma brunneum* (Forster) occurred in larger numbers in bottomland hardwood stands than in upland hardwood stands. This species is known to prefer well-decayed wood in moist conditions. Higher numbers within a moist, flood-prone forest type is understandable. Likewise,

Parandra polita Say were only collected from upland hardwood stands. The larvae of *P. polita* feed on the heartwood of hickory and beech, tree species common in our upland hardwood study sites. The pine component of one upland hardwood stand was also evident in the presence of *Prionus pocularis* Dalmeister, a species known to feed on dead pine logs, and *Typocerus zebra* (Olivier), a species that mines dead pine roots.

Checkered beetles exhibited some variation between upland and bottomland hardwood forests. Although number of species did not differ significantly between the two forest types, numbers of individuals did. This difference was largely attributable to much larger numbers of *Enoclerus ichneumoneus* (Fabricius) in the bottomland hardwood stands than in the upland hardwood stands. *Enoclerus ichneumoneus* is a checkered beetle known to feed on a variety of wood-boring beetle larvae, particularly those under the bark of hardwood trees.

Although upland and bottomland hardwood stands could not be strictly differentiated based upon longhorned beetle and checkered beetle species composition, they could be based upon trap collections of pleasing fungus beetles. Both species composition and abundance of pleasing fungus beetles differed between the two forest types. Upland hardwood stands contained only four of the 10 species collected in the bottomland hardwood stands. The most commonly collected species from both forest types were *Tritoma biguttata* (Say) and *T. thoracica* (Fabricius). Both species were collected in numbers four to seven times higher in bottomland hardwood stands than in upland hardwood stands. Species only collected from bottomland hardwood stands included *Ischyryus quadripunctatus* (Olivier), *Megalodacne heros* (Say), *T. pulchra* (Say), and *T. puncticeps* (Fabricius). These beetles are all known to feed on the fruiting bodies of fungi. *Megalodacne heros*, for instance, feeds on bracket fungi (*Ganoderma* spp.), while the various *Tritoma* and *Triplax* species feed on gilled fungi (*Amanita* spp., *Polyporus* spp.). Upland hardwood stands were largely characterized by a lack of these beetle species. Upland stands were also characterized by lower numbers of pleasing fungus beetles (406), when compared to bottomland stands (2024).

The pleasing fungus beetle fauna of bottomland hardwood stands is likely a reflection of the mesic conditions of these forests. Although we did not quantify number of fruiting bodies, the supposition can be made that the warm, humid conditions of bottomland hardwood forests may be more conducive to fungal growth and development than the drier conditions found in upland sites. Availability of wood-decaying fungi has been demonstrated to be an important factor affecting the diversity of saproxylic beetles in Europe (Økland and others 1996). Quantification of wood-decaying fungi fruiting bodies, in relation to pleasing fungus beetle diversity and abundance, could aid in elucidating any similar relationships in forests of the southeastern U.S.

CONCLUSIONS

Pleasing fungus beetles represent a saproxylic group that could be potentially sensitive to changes in forest condition, particularly as it pertains to suitable levels of moisture for

fungal growth and availability of dead wood for wood-decaying fungi. These beetles are easily sampled with Malaise traps (Goodrich 1997) and relatively easy to identify. Their use as potential indicators seems especially appropriate for mesic forest types, such as bottomland hardwood stands, where they may be more diverse and abundant. Overall, longhorned beetles and checkered beetles did not appear to be a defining group in terms of either forest type. However, longhorned beetles have been shown to respond to changes in forest condition brought about by certain silvicultural practices (Warriner and others 2002). In that sense, they represent a potentially useful group when evaluating the impact forest management practices have upon dead wood resources within a stand.

ACKNOWLEDGMENTS

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LITTER DECOMPOSITION IN LOW AND HIGH MORTALITY NORTHERN RED OAK STANDS ON EXTREMELY ACIDIC SOUTHWESTERN PENNSYLVANIA SOILS

Michael C. Demchik and William E. Sharpe¹

Abstract—Previous research has shown that decomposition of organic matter is slower in soils with high levels of soil acidity and available aluminum (Al). The objective of this experiment was to determine if differences in decomposition rates of northern red oak leaves occurred between extremely acidic and less acidic sites that also differed in oak mortality. Leaf litter from red oaks on high and low acidity soils was reciprocally transplanted into both high and low acidity sites. After one growing season, neither site of decomposition or leaf origin had a significant effect on the rate of decomposition. Litter that decomposed in low acidity stands tended to lose more calcium (Ca) and sodium (Na) and gain more phosphorus (P) than litter that decomposed in high acidity stands. Litter with origins in the low mortality stands tended to lose more potassium (K) and gain more P and zinc (Zn) than litter with origins in the high mortality stands. The stand with the highest oak mortality did not have the highest rate of decomposition indicating that soil acidity (low Ca/Al ratio) may have operated to reduce decomposition at that site.

INTRODUCTION

In southwestern Pennsylvania, mortality of northern red oak has occurred that is related to low levels of available Ca and high levels of available Al (Demchik 1998). In a review of the literature, Cronan and Grigal (1995) suggested that at molar ratios of Ca/Al of 1 or less a 50 percent chance of growth reduction of forest trees exists. Ca/Al ratios of less than 1 were found for all B-horizons in high mortality stands. Soil conditions such as these reportedly reduce litter decomposition rates (Tamm 1976, Wolters 1991). Reduced decomposition rates slow nutrient cycling.

On sites that have experienced a large thinning (as experienced with increased rates of mortality), decomposition rates may increase. Increased exposure of forest soil to sunlight can increase rates of nutrient cycling from litter (Zhang 1995). For this reason, if all other factors were equal, the rates of decomposition on a site that has undergone substantial mortality would be expected to increase. However, low Ca/Al ratios (soil acidity) may serve to reduce decomposition rates, thus potentially canceling out such increases.

Litter quality is also important to the rate of decomposition. Lamb (1976) found Monterey pine (*Pinus radiata*) decomposition rates to be most influenced by soil nutrients at the site of litter origin. The difference in soil nutrients at the site of origin was potentially an index of litter quality. Foliar samples taken from the canopy of high mortality stands on the Laurel Hill were found to be lower in Ca and K than foliar samples from low mortality stands (Demchik 1998). Soils in these high mortality stands had lower Ca/Al ratios (Demchik 1998).

In addition to physical breakdown, minerals released from the litter are an important component of decomposition. In general, leaf matter contains the highest ash content of litter fall and is approximately 70 percent of total litter fall

(Bray and Gorham 1964). Laskowski and others (1995) reported that litter turnover of Ca, magnesium (Mg) and manganese (Mn) was governed by biological processes, litter turnover of K and Na was controlled by physical processes (leaching) and litter turnover of Zn was controlled by both fixing to humic materials and leaching. In general, base nutrients in organic matter decrease with time (O'Connell 1988) while iron (Fe), Zn, copper (Cu) (Laskowski and others 1995) and Al (McBrayer and Cromack 1980) may increase with time. Bases decrease with decomposition and leaching but proposed causes for increases in the absolute quantity of metals have not been firmly defined. Laskowski and others (1995) suggested a natural process but they proposed no mechanisms to explain how it occurred.

Because base nutrient availability on acidic soils is governed in large part by organic matter decomposition, changes in rates of decomposition could drastically alter nutrient cycling. Assessing the effect of both litter origin and site of decomposition on changes in nutrient release from litter is useful in assessing the impact of soil acidification on forests.

The objectives of this study were to determine if differences occurred between high and low mortality oak stands for decomposition rates, element concentrations and absolute level of elements in northern red oak leaves between high and low mortality oak stands on the Laurel Hill.

METHODS

The Site

Three blocks of land on the Forbes State Forest (Hickory Flats, Linn Run and Jones Mill) were selected that contained stands with high mortality (40 to 60 percent standing dead oak timber) and low mortality (0 to 10 percent standing dead oak timber) of northern red oak in the Laurel Hill region of southwestern Pennsylvania. The overstory trees were 85-90 years old. The geology of the area is dominated by parent material from the Pottsville, Mauch Chunk and

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Table 1—SrCl₂ extractable Ca/Al ratios and soil pH from low mortality and high mortality plots of northern red oak on Hickory Flats, Linn Run, and Jones Mill^a

Parameter	Hickory Flats		Linn Run		Jones Mills	
	Low	High	Low	High	Low	High
0.01M SrCl₂ extractable Ca/Al ratios and soil pH^b						
O-horizon	37.9 ± 7.6	9.1 ± 1.2	12.6 ± 4.1	7.9 ± 1.2	6.4 ± 0.8	27.8 ± 7.9
	3.74 ± 0.04	3.77 ± 0.04	3.99 ± 0.02	3.95 ± 0.04	4.4 ± 0.03	4.0 ± 0.04
A-horizon	2.3 ± 0.4 ^c	1.2 ± 0.6 ^c	2.2 ± 1.0 ^c	1.1 ± 0.4 ^c	1.6 ± 0.5	1.2 ± 0.3
	3.65 ± 0.04	3.60 ± 0.02	4.01 ± 0.04	3.65 ± 0.03	4.26 ± 0.03	4.09 ± 0.04
B-horizon	1.3 ± 0.5 ^d	0.7 ± 0.4 ^d	1.2 ± 0.4 ^c	0.40 ± 0.3 ^c	1.1 ± 0.2 ^c	0.66 ± 0.3 ^c
	3.78 ± 0.04 ^c	3.68 ± 0.03 ^c	4.12 ± 0.03 ^c	3.82 ± 0.02 ^c	4.26 ± 0.02 ^d	4.2 ± 0.03 ^d

^a n = 8-20 for each cell.

^b Data presented as means±SE.

^c Denotes significant difference between low and high mortality stands of decomposition within each block at 5 percent.

^d Denotes significant difference between low and high mortality stands of origin within each block at 10 percent.

Burgoon formations. The soils were Typic Dystrachrepts of the Hazelton very stony sandy loam, Calvin very stony silt loam, and Dekalb very stony loam series, Aquic Fragiudults of the Ernest very stony silt loam series and Typic Hapludults of the Gilpin very stony silt loam series. All soils were extremely acidic (table 1). Soils on the high mortality stands had Ca/Al ratios in the A and B horizon that would indicate high probability of expression of aluminum toxicity in plants. Ca/Al ratios in the A and B horizon of low mortality stands were higher and would have a low probability of expression of aluminum toxicity (table 1; Data summarized from Demchik 1998). High mortality stands for Hickory Flats and Linn Run had lower overall leaf mass production compared to the low mortality stands. No difference in leaf mass production was found between high and low mortality stands in the Jones Mill block (Demchik 1998). For a more complete description see Demchik (1998).

Litter Collection

Approximately 500 grams of northern red oak leaf litter was collected in April 1996 from all six stands. The leaf litter was oven-dried at 90 °C until a consistent mass was reached and then two weeks more in order to limit resident microflora. Thus a total of 6 bulk samples, one from each stand was available for use.

In order to assess decomposition, litter bags were used. Bags made of 0.2 mm nylon mesh with dimensions of 20X10 cm were filled with 3 grams of the dried northern red oak leaves. The mesh bags were closed with standard size carbon steel staples. Twenty litter bags were filled with litter from each stand. A total of 120 bags were prepared (20 samples for each of six litter sources).

A reciprocal transplant within blocks was the design used for placing the litter bags in the field (fig. 1). Within each stand, 10 litter bags with litter of "origin" in that stand and 10 litter bags with litter of "origin" in the other stand in that

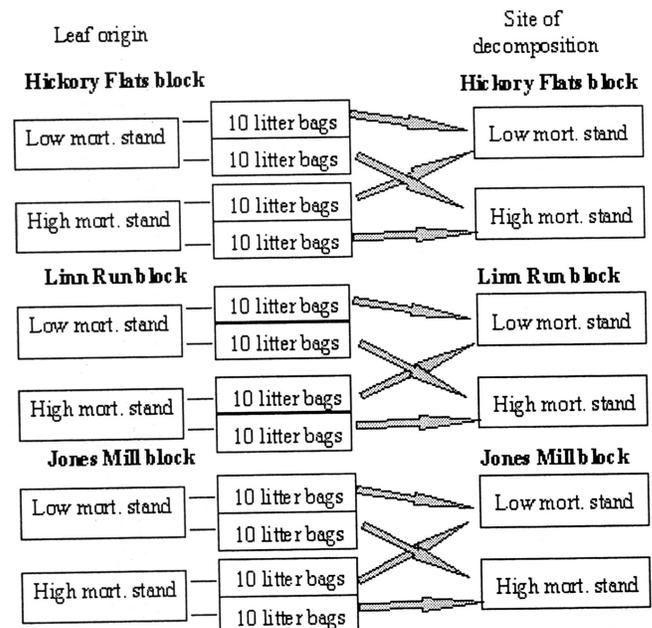


Figure 1—The reciprocal transplant design for decomposition of northern red oak leaf litter from low and high mortality stands (leaf origin) that was allowed to decompose on low and high mortality stands.

block were buried. The litter bags were buried between the organic layer and the A-horizon under 5 cm of leaf litter in early May 1996. The litter bags were collected in mid-October after 167 days in the field. The leaves were removed from the bags and washed with deionized water over a 0.01 mm sieve to remove clinging soil mineral fraction and root material that had grown into the bag. All visible leaf material was salvaged. The washed leaves were oven dried at 90 °C until a consistent mass was reached. Results were analyzed using nested ANOVA with blocks.

Mineral content analysis was conducted on randomly selected samples using Inductively Coupled Plasma Emission Spectroscopy at the Pennsylvania State University Agricultural Services Laboratory following procedures of Dahlquist and Knoll (1978). Three randomly chosen replicates of each of the 12 possible combinations of litter by origin and site of decomposition were selected for a total of 36 samples. Three replicates of fresh 1995 oak litter from each of the 6 stands were also analyzed to determine mineral content prior to decomposition. Data were analyzed using ANOVA. In addition to physical decomposition and concentration of minerals in the sample before and after decomposition, changes in total quantity of a mineral in the sample were determined. Due to high variance in sample nutrient levels both prior to decomposition and after decomposition, mean total quantity of a nutrient prior to decomposition was determined by summing the estimates for each litter origin. This gave a single estimate of total quantity of the nutrient in a sample bag for each litter origin (i.e. low and high mortality stands for each block). Variance was determined for each pooled estimate from differences between samples. Total nutrient level was determined after decomposition by essentially the same procedure. This resulted in 12 estimates of total nutrient level (i.e. leaf litter from low and high mortality origin that decomposed in low and high mortality sites of decomposition in each block). Percent of absolute gain or loss was determined by the formula:

$$\text{percent change} = \frac{(C_a M_a) - (C_b M_b)}{(C_b M_b)} 100 \quad (1)$$

where

C_a = concentration of nutrient after decomposition

M_a = mass of sample after decomposition

C_b = concentration of nutrient before decomposition

M_b = mass of sample before decomposition

Results were compared using computed standard errors.

RESULTS

Decomposition Rate

Significant decomposition occurred on all blocks. However, the only block where a difference in rate of decomposition was found between high and low mortality stands (site of decomposition) was the Hickory Flats block (table 2). The low mortality stand lost less mass (30 percent \pm 3 percent) than the high mortality stand (47 percent \pm 3 percent; $P < 0.01$).

The only block where litter origin had an effect on rate of decomposition was also the Hickory Flats block (table 3). The litter that came from the low mortality stand lost less mass (35 percent \pm 3 percent) than the litter that came from the high mortality stand (42 percent \pm 3 percent; $P < 0.05$).

A significant litter origin by site of decomposition interaction was found ($P < 0.009$). Litter from the low mortality stands of all blocks decomposed more slowly when in the low mortality stands than when in the high mortality stands (table 4) and rates of physical decomposition were not related to soil Ca/Al ratio.

Chemical Changes

Effect of site of decomposition—After decomposition, litter originating from the low mortality stands tended to have greater concentrations of P, Mn and lower concentrations of Mg and Ca than litter originating from the high mortality stands (table 2).

Table 2—Percent of physical decomposition^a (n = 20 per cell) and concentration of minerals^a (n = 6 for each cell) in remaining sample of northern red oak leaf litter that decomposed in low mortality and high mortality stands (site of decomposition) of northern red oak in block established on Hickory Flats, Linn Run, and Jones Mill

Parameter	Hickory Flats		Linn Run		Jones Mills	
	Low	High	Low	High	Low	High
Decomp.(%)	30 \pm 3 ^b	47 \pm 3 ^b	43 \pm 1	43 \pm 2	23 \pm 3	26 \pm 5
Mass lost(g)	0.9 \pm 0.09 ^b	1.41 \pm 0.09 ^b	1.29 \pm 0.03	1.29 \pm 0.06	0.69 \pm 0.09	0.78 \pm 0.15
Ca(%)	0.56 \pm 0.05 ^b	0.75 \pm 0.05 ^b	0.58 \pm 0.06 ^b	0.93 \pm 0.05 ^b	0.67 \pm 0.04 ^b	0.74 \pm 0.04 ^b
Mg(%)	0.021 \pm 0.001 ^b	0.024 \pm 0.001 ^b	0.037 \pm 0.001	0.038 \pm 0.001	0.031 \pm 0.001 ^b	0.035 \pm 0.001 ^b
K(%)	0.071 \pm 0.012	0.085 \pm 0.008	0.094 \pm 0.006	0.10 \pm 0.011	0.129 \pm 0.016	0.095 \pm 0.011
P(%)	0.058 \pm 0.01 ^b	0.054 \pm 0.003 ^b	0.065 \pm 0.006 ^b	0.061 \pm 0.001 ^b	0.073 \pm 0.005 ^b	0.059 \pm 0.005 ^b
Mn(ug/g)	882 \pm 46 ^b	820 \pm 50 ^b	922 \pm 34 ^b	624 \pm 65 ^b	583 \pm 30	647 \pm 78
Fe(ug/g)	419 \pm 87	312 \pm 62	313 \pm 58	349 \pm 48	228 \pm 67	248 \pm 87
Cu(ug/g)	10.0 \pm 2.6	9.8 \pm 0.4	8.5 \pm 0.75	8.4 \pm 0.63	8.6 \pm 0.75	8.2 \pm 0.75
B(ug/g)	14.9 \pm 2.1	16.8 \pm 1.0	18.4 \pm 2.7	17.7 \pm 3.3	16.8 \pm 2.3	17.8 \pm 1.9
Al(ug/g)	998 \pm 293	1014 \pm 200	437 \pm 31	356 \pm 20	322 \pm 36	321 \pm 88
Na(ug/g)	82 \pm 7.4	92 \pm 6.5	38 \pm 24	33 \pm 11	54 \pm 11	55 \pm 10
Zn(ug/g)	115 \pm 40	127 \pm 20	155 \pm 21	154 \pm 18	157 \pm 12	224 \pm 10

^a Data presented as means \pm SE.

^b Denotes significant difference between low and high mortality stands of decomposition within each block at 5 percent.

Table 3—Percent of physical decomposition^a (n = 20 per cell) and concentration of minerals^a (n = 6 for each cell) in remaining sample of northern red oak leaf litter that originated in low mortality and high mortality stands (litter origin) of northern red oak in blocks established on Hickory Flats, Linn Run, and Jones Mill

Parameter	Hickory Flats		Linn Run		Jones Mills	
	Low	High	Low	High	Low	High
Decomp.(%)	35 ± 3 ^b	42 ± 3 ^b	41 ± 2	43 ± 4	23 ± 3	24 ± 3
Mass lost(g)	1.05 ± 0.09 ^b	1.26 ± 0.09 ^b	1.23 ± 0.06	1.29 ± 0.12	0.75 ± 0.09	0.72 ± 0.09
Ca(%)	0.67 ± 0.06	0.65 ± 0.06	0.66 ± 0.08 ^b	0.84 ± 0.06 ^b	0.75 ± 0.07 ^b	0.66 ± 0.08 ^b
Mg(%)	0.021 ± 0.001 ^b	0.024 ± 0.001 ^b	0.034 ± 0.002 ^b	0.040 ± 0.003 ^b	0.032 ± 0.004	0.034 ± 0.004
K(%)	0.084 ± 0.01 ^b	0.072 ± 0.006 ^b	0.112 ± 0.008 ^b	0.083 ± 0.006 ^b	0.138 ± 0.005 ^b	0.086 ± 0.004 ^b
P(%)	0.056 ± 0.01	0.056 ± 0.008	0.074 ± 0.006 ^b	0.052 ± 0.01 ^b	0.071 ± 0.005 ^b	0.061 ± 0.005 ^b
Mn(ug/g)	918 ± 116 ^b	784 ± 84 ^b	915 ± 185 ^b	631 ± 128 ^b	625 ± 105	605 ± 87
Fe(ug/g)	239 ± 61 ^b	491 ± 57 ^b	379 ± 41 ^b	282 ± 27 ^b	280 ± 111 ^b	196 ± 45 ^b
Cu(ug/g)	10.0 ± 1.2	8.8 ± 1.0	8.8 ± 0.5 ^b	8.2 ± 0.4 ^b	8.8 ± 0.2 ^b	8.0 ± 0.3 ^b
B(ug/g)	15.0 ± 1.0 ^c	13.8 ± 0.8 ^c	16.3 ± 0.8 ^b	19.7 ± 0.8 ^b	15.3 ± 0.9 ^b	19.3 ± 1.0 ^b
Al(ug/g)	510 ± 293 ^b	1,501 ± 636 ^b	422 ± 31 ^b	371 ± 20 ^b	377 ± 36 ^b	265 ± 88 ^b
Na(ug/g)	97 ± 7	62 ± 65	37 ± 25	34 ± 11	57 ± 17	52 ± 6
Zn(ug/g)	123 ± 46	119 ± 7	205 ± 65 ^b	104 ± 30 ^b	195 ± 25	186 ± 77

^a Data presented as means ± SE.

^b Denotes significant difference between low and high mortality stands of decomposition within each block at 5 percent.

^c Denotes significant difference between low and high mortality stands of origin within each block at 10 percent.

Table 4—Percent decomposition and mass loss of leaf litter from low mortality and high mortality stands (origin) that decomposed in low and high mortality stands (site of decomposition) of northern red oak in blocks established on Hickory Flats, Linn Run, and Jones Mill

Leaf origin ^{a,b}	Hickory Flats		Linn Run		Jones Mills	
	Low	High	Low	High	Low	High
Low mortality	21 ± 3%	38 ± 3%	33 ± 2%	53 ± 2%	18 ± 3%	24 ± 3%
	0.63 ± 0.09g	1.14 ± 0.09g	0.99 ± 0.06g	1.59 ± 0.06g	0.54 ± 0.09g	0.72 ± 0.09g
High mortality	43 ± 4%	62 ± 4%	45 ± 1%	43 ± 4%	23 ± 4%	20 ± 5%
	1.29 ± 0.12g	1.86 ± 0.12g	1.35 ± 0.03g	1.29 ± 0.12g	0.69 ± 0.12g	0.60 ± 0.15g

^a n = 10 for each cell.

^b Data presented as means ± SE.

Litter that decomposed in the low mortality stands tended to lose more Ca and Na and gain less Zn than litter that decomposed in the high mortality stands (fig. 2). Litter that decomposed in the low mortality stands tended to gain P while litter that decomposed in the high mortality stands lost P (fig. 2).

Prior to decomposition, litter from the low mortality stands had significantly greater concentrations of Ca than litter from the high mortality stands. This difference was significant for the Hickory Flats and Linn Run blocks (P < 0.01). Boron was greater for the low mortality stand on Jones Mill than the high mortality stand (P < 0.01).

After decomposition, no effect of litter origin was found in concentration of Ca (except in Hickory Flats block); how-

ever, since the litter from the low mortality stands started the experiment with greater concentrations of Ca, the portion that was lost was calculated. A tendency to lose more Ca from the litter from the healthy sites was found (P < 0.07). After decomposition, the litter from the low mortality stands had greater concentrations of K, P, Mn, Zn and Cu than the litter from the high mortality stands (table 3). In absolute terms, litter with origin in the low mortality stands lost more K than litter with origin in the high mortality stands (fig. 3). Litter with origin in the low mortality stands gained more Zn and less Al than litter from the high mortality stands (fig. 3). Litter from the low mortality stands tended to gain Na and P while litter from the high mortality stands tended to lose both elements (fig. 3). Across all samples, total amounts of B, Mn, K, Mg and Ca after decomposition were lower and Al and Zn were higher (figs. 2 and 3).

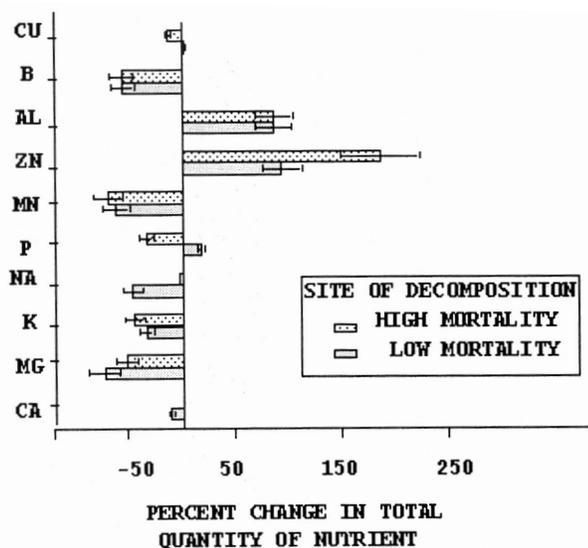


Figure 2—The change in total mineral content of northern red oak leaf litter after decomposition for 167 days during the growing season of 1996 for the leaf litter allowed to decompose in low and high mortality stands (n=6 bags per bar).

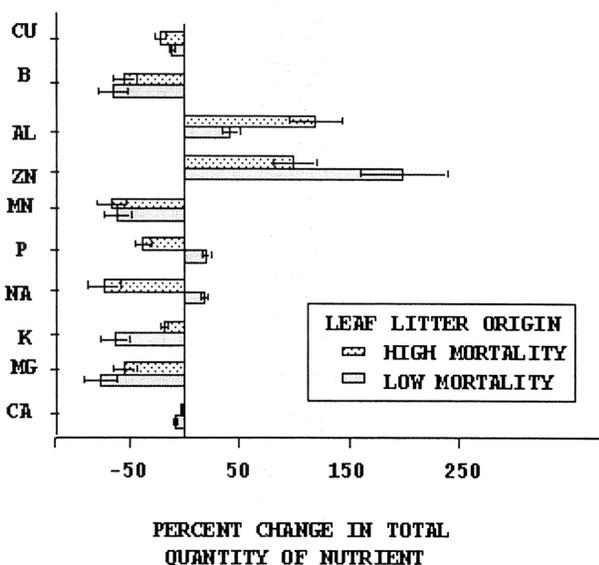


Figure 3—The change in total mineral content of northern red oak leaf litter after decomposition for 167 days during the growing season of 1996 for the leaf litter from low and high mortality stands (n=6 bags per bar).

DISCUSSION

The high mortality stands selected for this study had a considerable amount of standing dead timber and lower Ca/Al ratios in the A and B-horizons (Demchik 1998). These two factors could have quite opposite effects on decomposition. Increases in canopy gap size can increase decomposition (Zhang 1995), but sites with low Ca/Al ratios may have reduced rates of decomposition (Tamm 1976, Wolters 1991). Of the blocks, only Hickory Flats showed significantly higher decomposition rates in the high mortality stand. The more open canopy may have resulted in greater decomposition rates. This indicates that the difference in soil chemistry

between the sites, specifically the low Ca/Al ratios in the soils of the high mortality site, did not reduce the decomposition rates.

The overall lack of significant difference in rates of decomposition between high and low mortality sites may be related to the position of the litter bags in the soil column. The litter bags were buried at the interface of the O-layer and A-horizon. The O-layer was not different in Ca/Al ratio between stands (Demchik 1998). Even with differences in Ca/Al ratio observed in the A-horizon, the actual effect of the Ca/Al ratio may have been limited by bag placement.

While only limited differences occurred in rates of decomposition, the litter that decomposed in the low mortality stands lost more Ca and Na and gained more P than litter that decomposed in the high mortality stands. Transport of Ca is controlled primarily by biological action (Laskowski and others 1995). More favorable soil conditions on the low mortality sites and greater site occupation by trees and other vegetation may have resulted in greater Ca uptake and processing by soil organisms. Ca that was not taken up by vegetation may be more susceptible to leaching. The gain of P is documented to occur in the early stages of decomposition for Scots pine (*Pinus silvestris*) (Berg and Staaf 1980). Leaf litter from the low mortality stands lost more K and gained more P and Zn than leaf litter from the high mortality stands. Potassium loss is primarily controlled by leaching (Laskowski and others 1995). More K was leached from the litter from the low mortality stands probably because the amount tended to be a function of the amount present. The greater accumulation of Zn and P in the litter originating in the low mortality stands is probably caused by either strictly chemical transport or by fixation with humic compounds (Laskowski and others 1995) that are produced in the earlier stages of decomposition (Edwards and others 1970). More research is required to elucidate the reason for these differences.

While much variation was evident, some general observations can be made about the nutrient transport observed. Of the soil bases, total level of Ca seemed to be the most stable. Magnesium, K and Na had much higher rates of loss. Laskowski and others (1995) found K and Mg to be more mobile than Ca; however, Na was found to be less mobile than all other soil bases (although this varied with litter origin). Locally, the mobility of Na was of less importance than the other soil bases. For most forests of the east, Na is only a major soil cation near the coast or adjacent to roadways, where NaCl is used to de-ice surfaces.

While Mn and B leached from the sample at rates roughly similar to rates of decomposition, Zn and Al increased in absolute mass. Laskowski and others (1995) found increases in total level of Zn in litter and McBrayer and Cromack (1980) found increases in Al. While Laskowski and others (1995) suggested this as a natural process, they offered no explanatory mechanism. Possible explanations may include fecal deposition of soil mineral fraction by soil invertebrates, adhesion of soil particles by leaching foliar polysaccharides and root exudates. Additionally, since plant available Al was problematic on these soils (Demchik 1998), possible formation of complexes of Al with P could explain these increases.

SUMMARY AND CONCLUSIONS

Collectively, more Ca and Na were lost from samples decomposing on sites with low mortality of northern red oak, even though the overall rates of physical decomposition were similar. Potentially, Ca was being actively transported from this litter by plants and processed by soil biota. Ca remaining in litter may be more likely to leach with subsequent inputs of hydrogen ions.

Origin of litter affected the loss and gain of nutrients. Litter originating in the low mortality stands tended to lose more K and gain more P and Zn than litter originating in the high mortality stands. This litter had higher concentrations of these minerals to begin with; consequently, more could be expected to be lost as a consequence of mobile anion driven leaching. The greater accumulation of Zn and P in the litter originating in the low mortality stands was probably caused by either chemical transport or by fixation with humic compounds and Al. More research is required to elucidate the reasons for these differences.

In general, of the soil bases, total level of calcium seemed to be the most stable. Magnesium, K and Na had much higher rates of loss. Manganese and B leached from the samples at rates roughly similar to rates of decomposition. Zinc and Al increased in absolute mass.

Overall, while several potentially important differences were seen in the quantity of nutrients remaining after decomposition, no important differences in decomposition were found. The more acidic soils of the high mortality stands may have balanced the increased decomposition rates expected in these more open stands.

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CHARACTERIZATION OF AN OLD-GROWTH FOREST IN THE CROSS TIMBERS OF OKLAHOMA

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INTRODUCTION

Many cross timbers forests in central Oklahoma were neither extensively logged nor farmed and may contain some of the largest tracts of old-growth forests, particularly those dominated by oak, in eastern North America (Therrell and Stahle 1998). We studied a 90 ha old-growth forest in Osage County, Oklahoma which is one of the few designated forest preserves in the cross timbers. Our objectives were (1) to examine changes in species composition and structure across a topo-edaphic gradient and (2) to determine how well these stands conform to traditional models of old-growth stand structure.

MATERIALS AND METHODS

We delineated three stands based primarily on aspect and elevation, sampled overstory and understory tree species, and evaluated site characteristics in randomly placed 0.3 ha plots in each stand. We used detrended correspondence analysis (DCA) to identify important gradients in species composition and canonical correspondence analysis (CCA) to determine if measured site characteristics could help explain such gradients. We fit the negative exponential and rotated sigmoid curves to the diameter distributions for *Quercus stellata* in each stand using least-squares regression. Distributions of estimated total and exposed crown area by diameter class were predicted from regression equations using measurements from a subset of *Q. stellata* trees.

RESULTS AND DISCUSSION

Q. stellata dominated in all stands and *Q. marilandica* was the second most common overstory tree. *Juniperus virginiana* was relatively rare as an overstory tree, but appeared to be

increasing in abundance, particularly in the most open stand. The DCA and CCA revealed a moisture gradient along the first axis. More mesic tree species, such as *Q. velutina* and *Q. shumardii*, had the lowest scores along the first axis, while more xeric species, such as *Q. stellata* and *J. virginiana*, had the highest scores. Sandy soil texture and northeasterly slope positions were associated with more mesic forest species. Neither the negative exponential nor the rotated sigmoid curve accurately described the diameter distributions in any stand ($R^2 < 0.95$). The primary deviations from the models were the constant or increasing abundance from small to large saplings. The stands did not show equal allocation of growing area among size classes, but tended to have bimodal distributions with reduced crown area in the mid-diameter classes. These stands may exhibit natural population structures different than those of shade tolerant species growing in mesic forests, for which previously developed models of old-growth structure have been developed. However, deviations from models of balanced stand structure may be the result of recent fire disturbances.

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**Upland Oak Ecosystem
Restoration and Management**

UPLAND OAK REGENERATION AND MANAGEMENT

David L. Loftis¹

Abstract—In oak-dominated plant communities and in other communities where oaks are important, the keys to natural regeneration of upland oak components are (1) to ensure presence of competitive regeneration sources, and (2) to provide timely, sufficient release of these sources. Regeneration sources vary significantly among different types of plant communities and disturbance regimes. Options for timely, sufficient release of oak regeneration sources include stand structures associated with even-aged, two-aged, and uneven-aged silvicultural systems. I discuss the nature and management implications of these variations, the regeneration options, and stress the importance of evaluating oak regeneration potential.

INTRODUCTION

The remarkable book by Johnson, Shifley, and Rogers (Johnson and others 2002) covers much of what I am going to say either directly or indirectly, and in greater depth. However, I will provide a few additional insights based on my work in oak silviculture over the last 30 years.

Upland oaks have two fundamental requirements for successful regeneration and subsequent management, both in oak-dominated systems and in systems where oaks are important components of mixed hardwood forests. These two requirements are:

1. the presence of competitive sources of oak regeneration
2. timely, sufficient release of these oak regeneration sources.

The first requirement—competitive oak regeneration sources—is a restatement of the First Law of Oak Silviculture; i.e., successful oak regeneration after harvest will come from advance reproduction that exists in the current stand and stump sprouts from trees that are harvested from the current stand. I will discuss progress that has been made in assessing (1) the competitiveness of oak regeneration sources and (2) silvicultural practices to develop competitive oak regeneration sources.

The second requirement—timely, sufficient release—concerns the timing and pattern of tree removal from the existing stand to ensure the regeneration sources develop, ultimately, into overstory trees. I will discuss a broader range of silvicultural systems that can provide timely, sufficient release than we envisioned 30 years ago.

COMPETITIVE REGENERATION SOURCES

Assessing Regeneration Potential

When I began research in oak regeneration, the notion was well accepted that advance reproduction and stump sprouts were the sources of successful regeneration after harvest cutting. This First Law of Oak Silviculture was based on early work done by Leffleman and Hawley (1925), Korstian (1927), Liming and Johnson (1944), and on work in the 1950s, 1960s, and 1970s (Clark and Watt 1971, Sander 1971, Sander and Clark 1971).

The next logical step was important—the development of methods and models to predict the oak component of the next stand, based on the population of regeneration sources in the current stand. The foundation of the models was the relationship between the size of advance reproduction and postharvest development (Sander 1971), and the relationship between tree size and age, and stump-sprout development (Johnson 1977). Researchers developed models for the Ozarks (Dey 1991, Sander and others 1984) and for the Southern Appalachian (Loftis 1990a). The models were applied to sample data collected from stands considered for harvest. For example, I developed a simple model that predicted the probability of success of advanced red oak reproduction 20 years after harvest (dominance probability) based on the size of advance reproduction and oak site index (Loftis 1990a). I also adapted dominance probabilities for stump sprouts from Paul Johnson's work (Johnson 1977). Therefore, knowing the site index and the size distribution of red oak regeneration sources, a silviculturist could predict what the oak component would be in the next stand. This development of prediction models was an important step forward. Previously, when we cut stands, we were either satisfied with the outcome, or we lamented that the oak component in the new stand was much less than we desired or much less than was in the previous stand. With the development of these models we had tools to give us information on regeneration outcomes before we made the cut, and an opportunity to apply different management techniques to achieve a different outcome.

Even before I completed development of this model, I was uneasy. It considered competition only implicitly as a function of site index. That is, my interpretation of the inverse relationship between site index and dominance probability was that competition increases as site quality increases. For a stem of a given size, it is reasonable to expect that it would have a better chance to become dominant or codominant on site index 70 than on site index 90. What bothered me was the assumption of an “average competitive environment” when the competitive environment within even a single stand can vary widely. In reality, it makes a huge difference whether a 1-inch basal diameter advance red oak stem is going to be competing against a yellow-poplar stump-sprout or against other small advance reproduction.

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Another thing bothered me. On higher quality sites where I observed oaks competing successfully after crown closure (stem exclusion stage), there was an absence of yellow-poplar. Apparently, at least on a patch-wise basis, abundant, well-developed advance reproduction of oaks (and other species) competitively excluded yellow-poplar of seedling origin. Height-age (site index) curves for yellow-poplar and oak (Beck 1962, Doolittle 1958, Olson 1959) indicate that even when oak is free to grow at crown closure, if surrounded by free-to-grow yellow-poplar, oak is going to lose the battle. Only where yellow-poplar is excluded prior to crown closure will oaks be successful. The patchy nature of early regeneration development might not be apparent in older stands, since a patch might ultimately contribute only one or two dominant or codominant oak trees, and, by age 60, these big oaks would appear intimately mixed with other species.

Since the 1980s I have been trying to flesh out an intuitive, conceptual model that addresses these phenomena, a model in which competition among regeneration sources is the main driver (Loftis 1989). The prediction system builds on the concepts of Egler (1954) and Noble and Slatyer (1980), as well as the applied work of Johnson (1980) and Marquis (1984). The predictions of postharvest species composition at the time of crown closure are driven by data collected from small plots, say 0.01 acre, in the mature stand in which all existing regeneration sources are enumerated by size class. The model will stochastically add new seedlings of some species, e.g. yellow-poplar to plots when appropriate, and it will stochastically add stump sprouts from trees present on the plot. The model chooses several “winners” on each plot from the existing reproduction sources and from added seedlings on that plot, based on a ranking of expected postharvest performance. The model then combines the winners from each plot into a summary of stand-level species composition; including, but not restricted to oaks. This modeling approach provides the capability to deal with altered competition situations resulting from silvicultural practices. These practices might include the elimination of stump sprouts with herbicides or an altered size class distribution of regeneration sources resulting from silvicultural treatments designed to enhance advance reproduction development. I have developed a computer prototype of this model and an enhanced version should be available in 2004.

In the last two decades researchers have developed useful evaluation tools and prediction models. I hope managers will use these models in the silvicultural prescription process in the future. Assessing regeneration potential is the critical first step in regenerating oaks.

Enhancing Regeneration Potential for Oaks

If these models predict an unsatisfactory oak component in the next stand, we must do one of the following:

1. make the oaks more competitive
2. reduce competition from other species
3. do a combination of the two.

Either directly or indirectly, successful silvicultural treatments are going to cause one of these outcomes. This simple construct provides a useful context for discussing silvicultural treatments designed to favor oaks.

In a given stand, there is not a lot we can do to alter the population of oaks that will produce stump sprouts. To make oaks more competitive, we must increase the number and size of advance reproduction, enhancing their ability to sustain more rapid height growth after release. For oak-dominated ecosystems on more xeric sites, oak advance reproduction that can compete successfully after disturbance accumulates over time in mature stands. However, on more mesic sites oak advance reproduction that can compete after disturbance does not accumulate in mature stands (Johnson and others 2002, Loftis 1983a). Rather, it cycles in and out of the system with new seedling establishment after good acorn crops followed by mortality. But the survivors at any point do not develop into advance reproduction of a size that would be competitive if released by overstory removal (Loftis 1983a, McGee 1967). Interrupting this cycle of establishment and mortality to enhance survival and growth of advance oak reproduction requires a silvicultural treatment that alters stand structure and the light environment. By removing midcanopy and some lower canopy trees with herbicides, leaving a main canopy with no large gaps, we have increased survival and growth of small oak advance reproduction in the Southern Appalachians (Loftis 1990b). This treatment allows the population of small oak advance reproduction to develop after a few years into a population of larger advance reproduction, making oaks more competitive after release. This process also reduces competition from other species. Potential sprouts from midcanopy and lower canopy trees are treated with herbicides, thereby directly reducing competition from these trees both before and after overwood removal. The reduction in competition from yellow-poplar is more subtle. First, while the residual canopy with no canopy gaps is sufficient to allow oak seedlings to develop, it is not sufficient to allow the establishment and development of yellow-poplar. Secondly, new yellow-poplar seedlings that become established after overwood removal will be in an inferior competitive position, at least on a patch-wise basis, because of the development of large advance reproduction of oaks and other species.

Prescribed burning is another silvicultural treatment that has received a great deal of attention over the past 20 years. A number of hypothetical mechanisms might favor oak reproduction:

1. burning could alter stand structure and the light environment, providing for the development of larger advance reproduction—making oaks more competitive
2. burning could top-kill poorly formed oak advance reproduction, transforming them from stems that would respond slowly to release into thrifty sprouts that respond quickly to release—making oaks more competitive
3. burning, particularly recurrent burning, could kill or inhibit the development of competing vegetation—reducing competition from other species

4. burning could alter the seedbed, resulting in increased establishment of more oak seedlings—making oaks more competitive
5. burning could adversely affect insect predators of acorns, resulting in more oak seedlings—making oaks more competitive.

Understanding the role of fire in oak ecosystems and devising useful prescriptions to effect desired oak regeneration outcomes requires that these and other hypotheses be tested. Several ongoing studies are testing these hypotheses in various places and in different kinds of oak ecosystems. For example, after a single fire on relatively mesic sites in the Southern Appalachians, I found that survival of northern red oak seedlings was reduced on burned plots, and that, over time, surviving oak seedlings grew no better or worse than seedlings on nonburned plots (Loftis 1990b). Burning had no apparent effect on stand structure and the light environment. On somewhat less mesic sites, prescribed burning reduced the number and vigor of yellow-poplar competitors after burning in stands where a shelterwood cut had been conducted several years before (Brose and Van Lear 1998). Several other studies are ongoing (Dey and Hartman, in press; Iverson and others, in press) and viable prescriptions for prescribed burning may emerge from some of these studies. Workable prescriptions may differ from one upland oak ecosystem to another, and there may be some ecosystems where prescribed fire may play no role at all.

Another area of silvicultural practice is planting. Researchers have expended a good deal of effort developing technology to produce oak seedlings that can perform satisfactorily after outplanting (Johnson 1988, 1989; Kormanik and others 1998) making oaks more competitive. Some have suggested that the best opportunities for planting oaks successfully are on sites of intermediate quality, in a site index range from 60 to 75 feet (Johnson and others 2002) where competition is less severe. Attempts to plant oaks on higher quality sites have certainly met with limited success (Loftis 1979, McGee and Loftis 1986). Planting in clearcuts on mesic sites in the Southern Appalachians where site index exceeds 80 feet requires herbicides to reduce competition of other species, yellow-poplar in particular (Personal communication, 2000. Paul Kormanik, Silviculturist, USDA Forest Service, Southern Research Station, Forestry Sciences Laboratory, Athens, GA 30602-2044).

Another approach to planting oaks is planting under a shelterwood (Johnson and others 1986; Weigel and Johnson 1998a, 1998b). This approach is somewhat analogous to the shelterwood method described above for natural regeneration. However, in this case, the advance reproduction is planted in conjunction with a shelterwood and given a few years to become well established and to expand root systems before a partial or final removal cut opens the stand and the associated competition develops, making the oaks more competitive. Treating understory and midcanopy trees during the period under the shelterwood both increases light for the planted oaks and reduces competition from other species after overwood removal (Johnson and others 2002).

In my opinion, devising and implementing silvicultural strategies to favor oaks should usually involve treatments that both make oaks more competitive and that reduce competition from other species. The modeling approach I outlined is designed, at least conceptually, to provide insights into how well treatments accomplish these objectives on a stand-specific basis.

Intermediate stand treatments can also be used to directly favor oak and typically do so by reducing competition from other species in such operations as cleanings and thinning (Shifley, in press).

TIMELY, SUFFICIENT RELEASE OF OAK REGENERATION SOURCES

A generation ago the prevailing opinion was that even-aged silviculture was the preferred approach to managing oak: "Oak grows best in full sunlight, and oak silviculture should be even-aged." (Clark and Watt 1971: p. 38).

In the ensuing 30 years, we have found a number of ways to provide timely, sufficient release of oak regeneration sources that result in silviculture classified as other than even-aged.

Where competitive oak regeneration sources are present, either as a result of intrinsic processes or as a result of prior disturbances, clearcutting or overstory removal will result in successful oak regeneration (Beck 1988, Johnson and others 2002, Roach and Gingrich 1968). Successful oak regeneration has also been achieved by applying a two-cut shelterwood when competitive advance reproduction was present at the initial cut (Loftis 1983b). In this case, residual basal areas after the initial cut included plots with 33 and 66 square feet, and the level of overwood retention did not result in any differential species response. Yellow-poplar and other less shade-tolerant species developed about as they would have in a clearcut, although with some reduction in height growth. Normally, a final removal cut would be made no more than 10 to 20 years after the initial cut to ensure continued development of the oak regeneration.

The shelterwood method I designed to take advantage of differential species response between northern red oak and yellow-poplar may not work everywhere (Shuler and Miller 1995) or may need to be modified for different ecosystems. And in some ecosystems, an aggressive, shade-tolerant species, e.g. sugar maple, might be better able to take advantage of the modest increase in the light resource than oak.

Even-aged silviculture has been successful for oak regeneration. As noted earlier, when competitive regeneration sources are present as a result of intrinsic processes, disturbance, or treatment, a shelterwood will result in successful oak regeneration. Therefore, it is reasonable to believe that a lower residual basal area shelterwood—a shelterwood with reserves—designed to create a two-aged stand would also successfully regenerate oak. Oak did regenerate well on one lower quality site where we reduced basal area to about 20 square feet per acre, where stump-sprout potential was high, and large advance reproduction was present at the time of the cut. In another stand on a

high-quality site where we had reduced midcanopy and lower canopy trees to favor the development of large oak advance reproduction, successful oak regeneration is occurring at crown closure 5 years after creating a shelterwood with reserves. The patches at this site are large enough to ensure that oak will be a component of the next new stand. These methods create stands that “may be two-aged or tend towards an uneven-aged condition as a consequence of both an extended period of regeneration and the retention of reserve trees that may represent one or more ages classes” (Helms 1998: p. 151). Two-aged methods provide more complex stand structures to satisfy nontimber objectives.

Uneven-aged silviculture applied to oak stands offers intriguing possibilities and uncertainties. Managers may have some concerns over whether to apply group selection as an extension of the structural control methodology developed for single-tree selection, or as small-scale area control. However, in terms of biological response, oaks can be successfully regenerated if competitive regeneration sources are present when the openings are created. In the Southern Appalachians, in group-selection openings of one-fifth acre or larger, the same species composition develops as in much larger clearcut openings (Beck 1988). Yellow-poplar, one of our more shade-intolerant species, regenerated quite well in these small openings 25 years after they were created. An intriguing possibility is related to a common response observed along edges of group-selection openings and extending into the surrounding stand. The increase in light penetrating into the surrounding stand usually results in development of oak advance reproduction if small oak seedlings are present when openings are created, providing an opportunity to favor oaks in regeneration with a subsequent enlargement of the opening. In addition, group selection should provide, at least theoretically, the flexibility necessary to take advantage of the sometimes patchy distribution of competitive, large advance reproduction in forest stands.

Regenerating oaks using single-tree selection has generally been viewed negatively. In a Southern Appalachian study of single-tree selection on relatively mesic sites (Della-Bianca and Beck 1985), oak regeneration and regeneration of other overstory species generally has been far from sufficient. Since 1946, managers have applied structural control using a reverse-J distribution with residual basal area target of 65 square feet, a maximum diameter of 34 inches and a q of 1.4 (2-inch classes). After more than 50 years and four cutting cycles, we have a stand that roughly approximates a reverse-j (negative exponential) distribution, but most of the smaller diameter trees are noncanopy, shade-tolerant species. In the study, the recent addition of the application of herbicides has produced some encouraging trends with respect to development of large oak advance reproduction. However, how or if we can provide timely, sufficient release of this advance reproduction using single-tree selection remains to be seen.

On the other hand, there is at least one documented success using single-tree selection in the relatively more xeric western range of oaks (Lowenstein 1996). It seems reasonable to wonder whether or not some form of single-tree selection

might also work on xeric sites in other parts of the oak range where advance reproduction capable of competing after release tends to be abundant.

CONCLUSIONS

There are a number of conclusions about regeneration and management for which we can find general consensus:

- The First Law of Oak Silviculture has not been repealed. We have to have competitive oak regeneration sources present when we begin removing the stand
- These competitive oak regeneration sources can result from natural stand processes including natural disturbances, or
- We can implement silvicultural treatments to develop competitive regeneration sources.
- These silvicultural treatments can (1) make oaks more competitive, (2) reduce competition from other species, or (3) both of the above
- Management of oak stands can potentially be even-aged, two-aged, or uneven-aged
- We still have a lot to learn

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EFFECTS OF DIFFERENT LARGE-SCALE PRESCRIBED BURNING REGIMES ON ADVANCE REPRODUCTION IN THE MISSOURI OZARKS

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Abstract—In 1997, The Nature Conservancy initiated a large-scale prescribed fire management study on approximately 2,500 acres of their Chilton Creek property located in Shannon and Carter counties, Missouri. Since the spring of 1998, five management units, of roughly 500 acres each, have been burned in the dormant season to simulate a range of fire regimes that vary from annual fires to fire free intervals that average from 1 to 4 years. The intent is to simulate high frequency, low intensity fires that occurred historically in the watershed and study fire effects on the biota. The overstory was inventoried on half-acre permanent plots located in the different burn treatments. Survival and height growth of the advance reproduction was recorded on smaller plots nested within the half-acre plots. In this paper, we present the effects of the different burning regimes on the advance reproduction.

INTRODUCTION

Over the past 400 years or more, fires burned throughout the Ozarks, shaping the nature of the vegetation (Ladd 1991, Guyette and Cutter 1991, Cutter and Guyette 1994, Guyette and others 2002). The frequency of fire varied across the Ozarks with changes in topography and was modified throughout time by humans. The net result was a mosaic of pine and oak savannas and woodlands and mesic hardwood forests (Batek and others 1999). Today, however, fire occurrence in the Ozarks has been drastically reduced. In Missouri, fires usually burn less than 50,000 acres per year throughout a 16 million acre area that encompasses the Ozark Highlands (Westin 1992). Individual fires average less than 20 acres, and humans cause nearly all (> 99 percent) of these fires.

Since the advent of fire suppression in the 20th century, savanna and woodland communities have developed into mature, closed-canopied forests as tree density and stocking and vertical structure of woody species have increased. Managers of federal and state natural resource agencies are reintroducing fire using prescribed burning to restore oak/pine savannas and woodlands, to restore glade and fen communities, to promote native biodiversity, and to restore historic disturbance regimes. Large area burns (500 acres to 7,000 acres) are being done throughout the Ozarks.

The Nature Conservancy (TNC) is restoring fire through prescribed burning on approximately 2,500 acres of their Chilton Creek Preserve in the Missouri Ozark Highlands. Their fire plans are guided by information provided by Guyette and others (2002) who have documented mean fire intervals of 3.6 and 4.1 years just west of Chilton Creek during the historic period 1700 to 1820, which predates most European settlement in the area. TNC's management objective is to use fire to restore the quality and ecological integrity of terrestrial natural communities and improve habitat for species of conservation concern in the Ozarks where fire has long had a strong influence on ecosystem

structure and function. They are intensively monitoring the response of vegetation and other selected biota to a set of fire treatments that differ primarily in the frequency of burning. In this paper, we present the response of tree advance reproduction after four years of implementing the fire treatments.

METHODS

The Chilton Creek Preserve is a 5,657 acre site located along the Current River in Shannon and Carter Counties, Missouri (T 28 N, R 1 W) (fig. 1). The site lies within the Current River Hills subsection of the Ozark Highlands (Keys and others 1995), an area characterized by rugged, steeply dissected valley and hollows and narrow ridges (approximately 500 foot relief). The area is covered in relatively continuous oak-hickory and oak-pine woodlands and mature forests growing on excessively drained cherty clay residuum. Based on an inventory of overstory trees [with diameter at breast height (d.b.h.) \geq 4.5 inches], we found that basal area averaged 79 ft² per acre (range 38 to 160), and stocking was 69 percent (range 36 to 120) [according to Gingrich (1967)] on the subset (n = 26) of circular half-acre plots used in our study.

The Chilton Creek watershed was divided into five management units (fig. 1) of approximately 500 acres each (table 1). All units were burned in the spring of 1998 to initiate the process of restoring fire. Thereafter, units were burned during the dormant season (usually in March or April) on a randomly selected 1 to 4 year return interval basis, with the exception of the Kelly North management unit, which was burned annually (table 1).

We sampled individual stems of advance reproduction on 26 of the 250 (0.5-acre) permanent vegetation plots (fig. 1). Initial stem measurements were done in the fall of 1997, before the first burn. We recorded species, stem basal diameter one-inch above the ground, d.b.h., and height on 2,741 stems that were distributed among the five management units (table 1). Overall, the basal diameter of all stems

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Chilton Creek Preserve

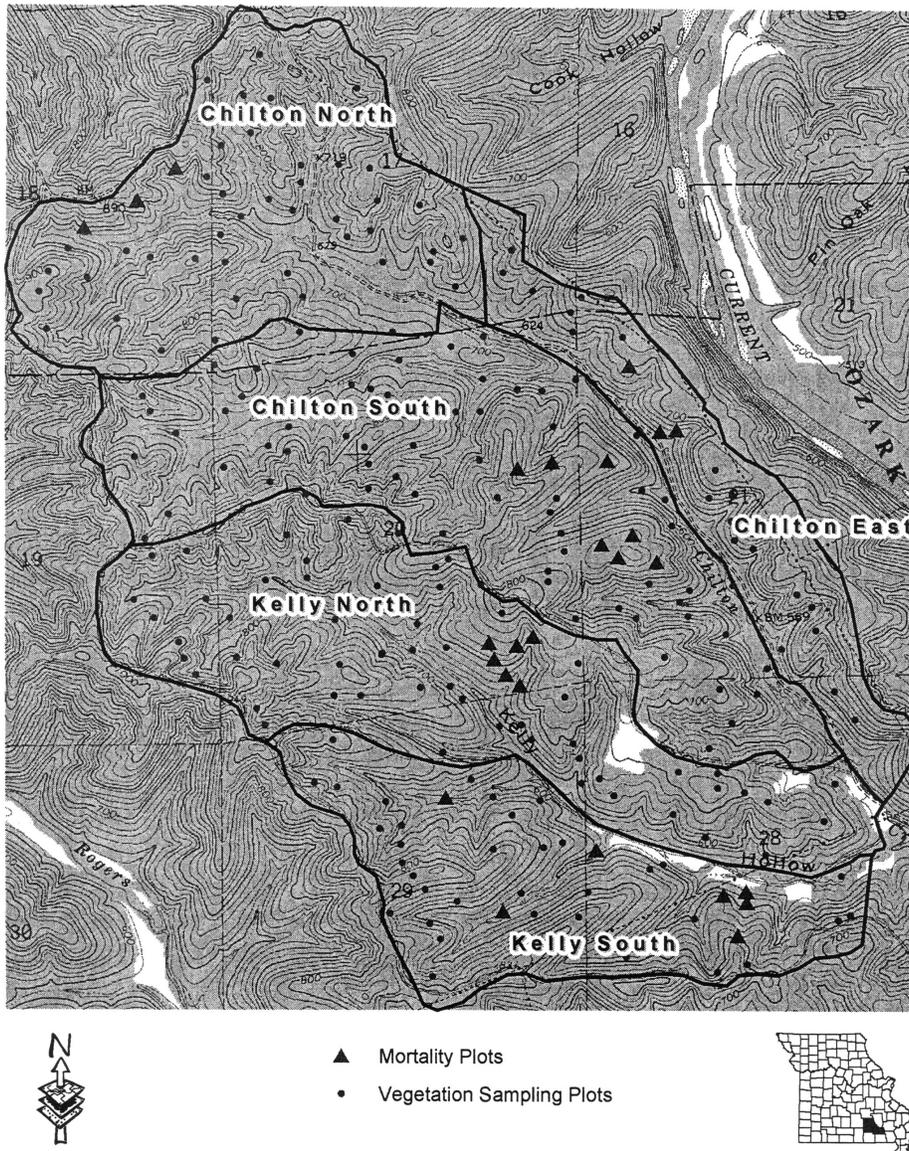


Figure 1—Location of the Chilton Creek Preserve and study area with locations of vegetation sampling plots (circles) and the subset of plots (triangles) we used to evaluate the effects of fire on advance reproduction.

Table 1—Schedule of prescribed burns conducted at Chilton Creek during the dormant season in each of the management units; size of each unit with the distribution of study trees is also presented

Burn unit	Dormant season fire				Acres	Advance reproduction (N)
	1998	1999	2000	2001		
Kelly South	X		X	X	403	363
Kelly North	X	X	X	X	603	542
Chilton South	X	X	X		725	1,123
Chilton North	X				464	358
Chilton East	X				254	355

ranged between 0.1 and 6.0 inches, and heights varied from 0.1 to 50 feet (table 2). In the fall of 1998 and 2001, we inventoried all stems and counted the number of sprouts and measured the height of the tallest sprout for surviving trees that had been topkilled by previous fires.

Fuel loading was estimated before each burn using two permanent 50-foot transects on each plot following the methods of Brown (1974) and Brown and others (1982). Total fuel loads averaged 4.3 to 5.9 tons per acre for any given burn year, and herbaceous/litter fuels accounted for much of the total tonnage (table 3). Weather conditions before each burn were recorded onsite using a belt weather kit or Kestrel 3000 weather meters. Weather during the burn was recorded at the National Park Service station located 4 miles from the study area. Temperatures during most burns were between 60 to 75 °F, winds were generally less than 4 miles per hour, and relative humidity ranged from 33 to 44 percent (table 3).

During each burn, we estimated flame length, rate-of-spread and flaming front temperature (table 3). Flame length was measured with passive flame height sensor arrays, which consisted of 20 lengths of cotton string soaked in flame retardant that were suspended from wires positioned 10 feet above the fuel bed. Visual measurements of flame angles were used to convert flame height to flame length according to Ryan (1981) and Finney and Martin (1992). Visual estimates of flame lengths were also made during the burns by observers. Flame lengths were highly variable but often were in the range of 1 to 3 feet. Rate-of-spread was determined by direct observation using a stopwatch to time the movement of the flaming front over a known distance or by using arrays of modified clock assemblies that were buried in the soil along a transect (Grabner 1996). Rates-of-spread were also variable, but the fire front usually moved at a rate of 3 to 16 chains per hour. Fire temperature along the flame front was measured using temperature sensitive paints applied to aluminum tags that were suspended from 9 gauge

Table 2—Pre-burn seedling and sapling basal diameter, diameter breast height, and total height^a

Species	N	BD	D.b.h.	HT
		----- inches -----		feet
White oak	346/185	1.4 ± 1.5	1.9 ± 1.2	10.8 ± 11.7
Scarlet oak	156/56	1.0 ± 1.4	1.9 ± 1.3	7.3 ± 11.4
Blackjack oak	56/25	1.7 ± 1.8	2.9 ± 1.1	9.6 ± 10.5
Chinkapin oak	106/31	0.6 ± 0.9	1.2 ± 1.0	4.6 ± 6.3
Post oak	180/79	1.2 ± 1.4	2.0 ± 1.1	7.8 ± 9.4
Black oak	224/92	0.9 ± 1.3	1.6 ± 1.3	7.5 ± 10.6
Pignut hickory	299/179	1.4 ± 1.4	1.8 ± 1.0	10.7 ± 10.8
Black hickory	128/53	1.1 ± 1.2	1.6 ± 1.1	6.9 ± 7.5
Mockernut hickory	296/153	1.0 ± 1.1	1.3 ± 0.9	7.5 ± 7.4
Flowering dogwood	316/192	1.4 ± 1.3	1.7 ± 1.0	10.1 ± 12.2
Blackgum	240/156	1.3 ± 1.2	1.5 ± 0.9	9.7 ± 7.8
Persimmon	32/10	0.5 ± 0.5	1.0 ± 0.5	4.3 ± 4.9
White ash	65/29	0.9 ± 0.9	1.2 ± 1.0	6.7 ± 6.0
Sassafras	286/115	0.8 ± 1.0	1.4 ± 0.9	7.3 ± 8.0
Shortleaf pine	74/53	1.9 ± 1.5	2.0 ± 1.2	11.5 ± 7.9

BD = basal diameter; d.b.h. = diameter at breast height; HT = total height; N = the first sample size.

^a The first sample size is given for BD and HT, and the second is for d.b.h. (means and one standard deviation are presented).

Table 3—Fuel conditions, fire weather, and behavior for each of the prescribed burns

Burn year	Slope	Fuel characteristics								Weather					Fire behavior		
		Moisture			Load					Wind	Temp.	RH	FL	ROS	Temp.		
		1-hr.	10-hr.	100-hr.	1-hr.	10-hr.	Herb.	Total	Surface						1-ft.	2-ft.	
----- percent -----		----- tons per acre -----							mph	°F	%	ft.	ch/hr	----- °F -----			
1998	4 – 36	8	8	13	0.24	0.94	3.5	5.9	2 – 4	65 – 75	39	3.2	15.8	589	309	246	
1999	11 – 25	8	8	16	0.27	1.4	1.8	4.3	0 – 2	59 – 69	44	1.0	5.9	361	179	154	
2000	4 – 33	7	7	14	0.3	1.6	2.2	5.2	0 – 2	68 – 76	36	1.5	6.5	470	232	184	
2001	4 – 33	7	7	12	0.24	1.3	1.9	4.6	0 – 2	50 – 64	33	1.1	2.7	250	153	150	

steel rods (Cole and others 1992). Tags were hung at the fuel surface, and at 1- and 2-foot heights above the fuel surface on each rod. Temperatures were highest at the fuel surface (ground level) and reached 250 and 600 °F.

For each species, we used logistic regression (Allison 1999) to model the probability of survival in 1998 (after one burn) based on initial basal diameter, initial height, and the interaction between basal diameter and height. Similarly, we modeled the probability that a stem of advance reproduction would be alive in 2001 (4 years after burn treatments were begun) based on initial stem size and number of times the reproduction was burned. We used an information-theoretic approach to modeling the probability of survival for advance reproduction that had experienced prescribed burning (Burnham and Anderson 2002). The set of apriori models for each species was ranked using Akaike's Information Criterion, AIC, which were adjusted for small sample sizes (AIC_c) when necessary. AIC values were used to compute the Δ AIC and Akaike weight (w_i) for each model. These statistics (i.e., Δ AIC and w_i) were used to identify models that performed well and for estimating the support a model had for being the best. Models with a lower Δ AIC and a greater w_i have more support for being the better models of those being compared. In all comparisons for a species, we included the null (intercept only) model.

RESULTS AND DISCUSSION

1998 Fire Damage – After One Burn

Mortality of advance reproduction after one spring burn was generally below 10 percent for most species (table 4). Mortality was low (i.e., < 5 percent) in hickory (*Carya*), black-

gum (*Nyssa sylvatica* Marsh.), sassafras (*Sassafras albidum* (Nutt.) Nees), chinkapin oak (*Quercus muehlenbergii* Engelm.), and blackjack oak (*Quercus marilandica* Muenchh.). Sassafras had the lowest mortality (0.3 percent) and shortleaf pine (*Pinus echinata* Mill.) had the highest (38 percent). White oak (*Quercus alba* L.), post oak (*Quercus stellata* Wangenh.), black oak (*Quercus velutina* Lam.), scarlet oak (*Quercus coccinea* Muenchh.), and flowering dogwood (*Cornus florida* L.) experienced relatively moderate levels of mortality (i.e., 5 to 10 percent). For all species, stems of advance reproduction averaged about 1 inch in basal diameter (table 2), and diameters ranged from 0.1 to 6.0 inches.

We found that initial basal diameter and height of advance reproduction were significantly ($\alpha = .05$) related to the probability of survival one year after a dormant season fire, regardless of species, based on logistic regression analyses. The full model used to predict survival after one burn, which included initial basal diameter and height, and their interaction, had strong support for being one of the best models considered for flowering dogwood ($w_i = 0.94$) and for black oak ($w_i = 0.88$). The full model had moderate support ($w_i = 0.62$) in explaining blackgum's response to a prescribed burn. For the other species, subset models that contained initial basal diameter, initial height, or a combination of the two variables had moderate support for being in the set of best survival models (w_i varying from 0.25 to 0.63). For all species, there was no support ($w_i = 0$) for the null hypothesis model (intercept only model). The Hosmer Lemeshow goodness-of-fit test on the full model showed a good fit of the model for all species except black oak. In

Table 4—Fire damage to advance reproduction one growing season after one or more (i.e., 3 to 4) springtime prescribed burns

Species	Sample size (1/3+) burns	Mortality		Topkill with sprouts		Total damage		Minimum basal diameter for < 10 percent mortality	
		1	3+	1	3+	1	3+	1	3+
		burn	burns	burn	burns	burn	burns	burn	burns
		----- percent -----						----- inches -----	
White oak	346/255	5	22	52	63	57	85	0.2	4.5
Post oak	180/145	9	21	64	74	73	95	0.3	2.0 (3 burns) 2.6 (4 burns)
Chinkapin oak	106/54	5	17	76	74	81	91	0.2	0.1 (3 burns) 2.2 (4 burns)
Scarlet oak	156/121	10	44	65	53	75	97	0.3	5.1
Black oak	224/170	10	28	70	69	80	97	0.7	1.6 (1 foot) 1.8 (5 foot) 2.2 (10 foot)
Blackjack oak	56/37	4	41	80	59	84	100	0.2	> 6
Hickory	723/520	3	17	94	70	97	87	0.1	6 (< 10 foot) 1.5 (10 foot)
Flowering dogwood	316/245	5	52	82	38	87	90	1.75	> 6
Blackgum	239/185	2	50	49	38	51	88	0.1	> 6 (1-10 foot)
Sassafras	286/216	0	9	79	84	79	93	0.1	0.1
White ash	65/44	14	25	61	70	75	95	0.5	0.6 (1-5 foot)
Shortleaf pine	74/18	38	39	18	39	56	78	3.75	> 6

other studies, tree stem diameter has been correlated to survival after burning because it is directly related to bark thickness and tree height, and hence to a tree's ability to resist heat injury to the cambium or to the crown (Hare 1965, Loomis 1973, Hengst and Dawson 1994, Regelbrugge and Smith 1994).

The probability of survival increased rapidly with increasing basal diameter for most species, but less so with flowering dogwood and shortleaf pine (fig. 2). In general, the minimum basal diameter needed for survival to be at least 90 percent was less than 0.5 inch for most species (table 4).

However, flowering dogwood and shortleaf pine advance reproduction had to be larger than 1.8 and 3.8 inches, respectively, before their chances of survival exceeded 90 percent.

Total fire damage (sum of mortality and topkill) was high after one dormant season fire (table 4). Most of the fire damage to advance reproduction was topkilled seedlings that sprouted during the following growing season. Waldrop and Lloyd (1991) observed that low to moderate intensity surface fires can topkill most hardwood stems that are less than 4 inches in diameter, and that mortality declines as

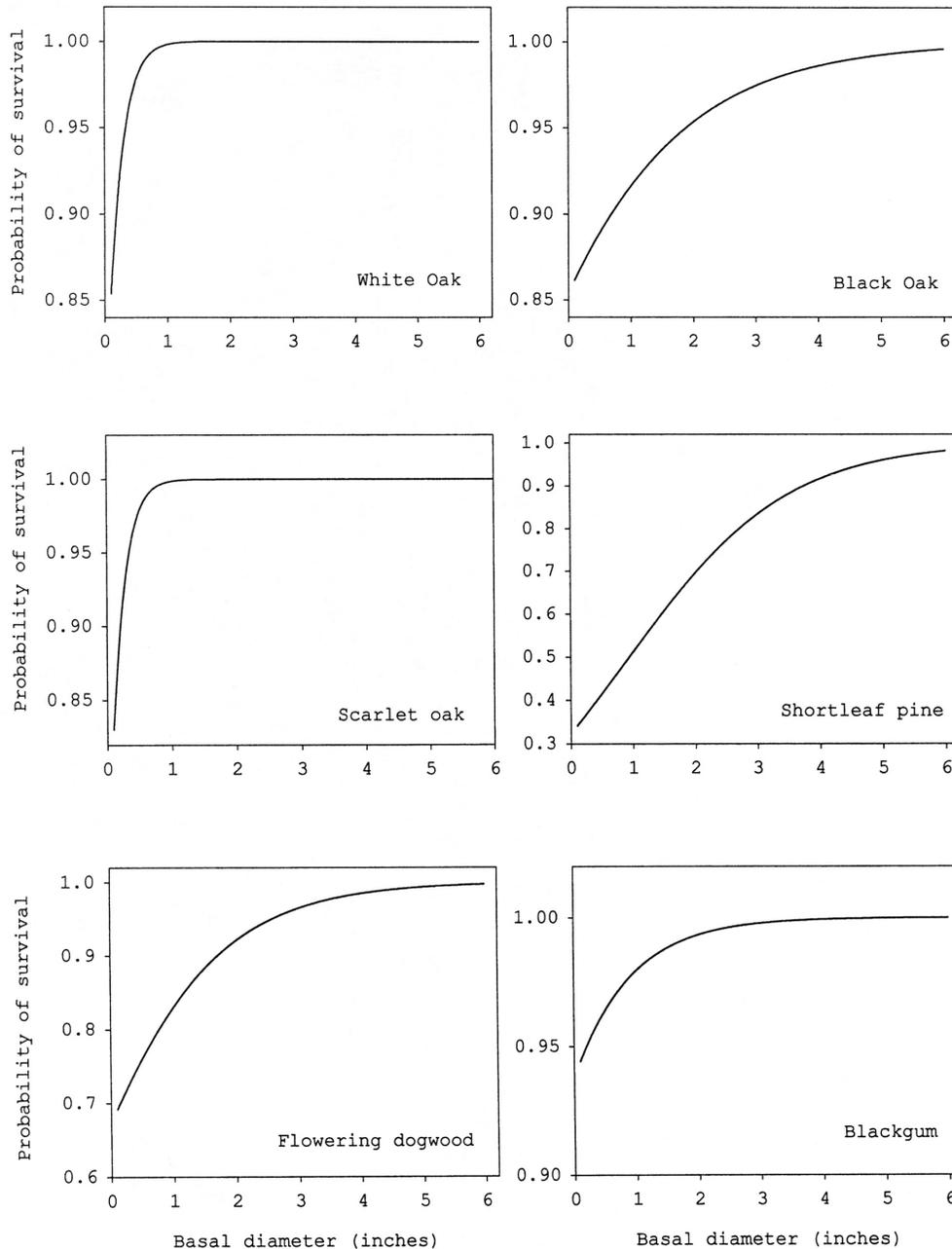


Figure 2—The probability that advance reproduction will be alive one growing season after a dormant season prescribed fire based on the initial basal diameter and species. All logistic models shown were significant ($\alpha = 0.05$) and had at least moderate support according to the Akaike weight (w_i).

tree diameter increases above 4 inches. Dormant season fires also promote hardwood sprouting after topkill because carbohydrate reserves in the root system are still at relatively high levels. White oak, blackgum, and shortleaf pine had the lowest overall amount of fire damage.

2001 Fire Damage – After One, Three, or Four Burns

After three or four burns, total fire damage (mortality and topkill) was high for all species and was often greater than it was after one burn (table 4). For advance reproduction that was burned three or four times, a higher proportion of the damage was due to mortality and less of the damage was topkill compared to trees that had been burned only once. Mortality after three or more burns increased notably in scarlet oak, blackjack oak, flowering dogwood, and blackgum. Moderate increases in mortality were seen in the other species. Sassafras showed the greatest tolerance to being burned repeatedly. For most species, basal diameters associated with 90 percent or greater survival were substantially higher after three or more burns than they were after one burn (table 4). For some species, the threshold diameter varied with tree height or with the number of burns experienced by the advance reproduction. Sassafras showed a tremendous ability to tolerate being burned repeatedly with more than 90 percent of the stems surviving even for small diameter trees (e.g., 0.1 inches).

For most species, initial basal diameter, initial height, and number of burns were significantly ($p < 0.05$) related to the probability of survival one growing season after either one, three or four dormant season burns. The full logistic model, which included initial basal diameter and height, their interaction and the number of burns, had strong support for being the best model ($w_i = 0.99$) for blackgum and hickory, and moderate support (w_i ranging from 0.32 to 0.65) for black oak, flowering dogwood, and white oak. The initial basal diameter and number of burns model had moderate support (w_i varying from 0.22 to 0.47) for white ash (*Fraxinus americana* L.), post oak, chinkapin oak, scarlet oak, and white oak. For blackjack oak, the initial basal diameter model ($w_i = 0.54$) and the number of burns model ($w_i = 0.36$) had the most support in predicting survival of advance reproduction. The survival of blackjack oak advance reproduction was as low as 62 percent after four consecutive burns and as high as 87 percent after one burn. The number of burns model also had moderate support ($w_i = 0.42$) for predicting survival in chinkapin oak, where survival ranged from 98 percent for trees subjected to only one burn to 84 percent for trees burned as many as four consecutive years. Survival of sassafras advance reproduction was high enough, even after four consecutive burns (i.e., 91 percent), that all models tested were statistically insignificant ($p > 0.05$). For all species, there was no support ($w_i = 0$) for the null hypothesis model (intercept only model). The Hosmer Lemeshow goodness-of-fit test on the full model showed a good fit of the model for all species except scarlet oak and hickory.

The probability of survival increased with increasing initial basal diameter for all oak species (fig. 3) and white ash. In contrast, survival probabilities declined with increasing stem diameter in hickory, blackgum and flowering dogwood species regardless of tree height or number of burns. In

these species, tall trees had higher chances of surviving than did short trees of the same basal diameter, regardless of the number of fires. In flowering dogwood, the effect of height on survival was most pronounced in smaller diameter trees, whereas the opposite was observed in blackgum and black oak advance reproduction.

Survival for all species was greatly reduced after three or four fires (fig. 3). In many cases, survival of advance reproduction was 20 to 30 percent less after four fires than after one. Differences in survival between trees subjected to one or four burns were greatest for small diameter trees, but survival probabilities converged at larger basal diameters (e.g., 3-inch and larger trees). In general, multiple burns lowered survival in flowering dogwood and blackgum more than in most of the oaks, with the exception of scarlet oak and blackjack oak. Survival in scarlet oak was reduced by nearly 40 percent for small diameter advance reproduction, but it improved with increasing basal diameter, though not to the extent that was seen in other oak species.

Recovery of Height and Understory Woody Structure

The effect of fire and time since the last fire on the height of sprouts from advance reproduction that were topkilled was similar among the species. We compared pre- and post-burn height distributions in the single burn and four burn treatments for oak species combined and for flowering dogwood, a major competitor of oak reproduction (Dey and others 1996). Post-burn height distribution of oaks was substantially different than the initial distribution four growing seasons after a burn (fig. 4). One burn caused densities of sprouts in the smallest height classes (< 4 feet tall) to increase above initial levels, and eliminated many of the taller advance reproduction. The tallest oak sprouts had only made it into the 10-foot height class in four years since the burn, approximately 14 feet or more shorter than the tallest pre-burn stems. This slow recovery in height after each fire may be due to sprouts growing under a forest canopy that averaged 79 ft² per acre (range 38 to 160) and 69 percent stocking (range 36 to 120). Dey and Jensen (2002) found that overstory densities that averaged 62 ft² per acre inhibited the height growth of oak stump sprouts. Further, we found that the tallest oak sprouts were less than 4 feet one season after four consecutive burns, and most of the advance reproduction were less than 2 feet tall. Similar results were seen in flowering dogwood. Waldrop and Lloyd (1991) also found that fire increased the density of trees in the smaller size classes by causing shoot dieback and formation of sprout clumps, and by promoting the establishment of new seedlings in South Carolinian Coastal Plain forests, where relatively young stands had been subjected to a range of periodic fire treatments over 40 years.

SUMMARY

One dormant season prescribed burn reduced the size distribution of advance reproduction for common hardwood species found in the Missouri Ozark Highlands. Most stems of advance reproduction less than six inches in basal diameter were damaged by fire, usually by shoot dieback followed by formation of sprout clumps. Mortality of advance reproduction was generally low in all species after one burn. We found that the probability of survival was significantly

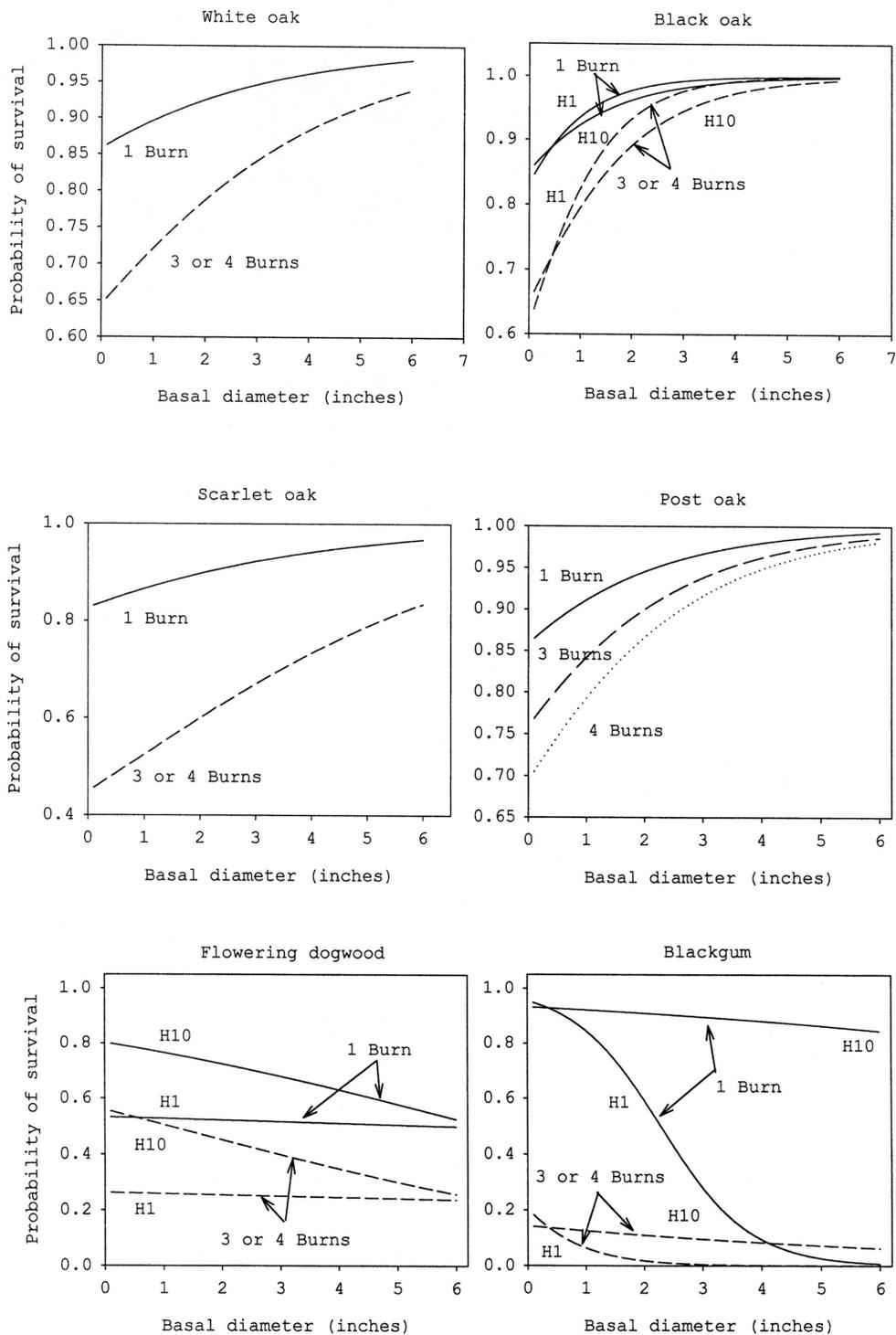


Figure 3—The probability that advance reproduction will be alive one growing season after four consecutive dormant season burns, two years after three burns, or four years after a dormant season prescribed fire based on the initial basal diameter, initial height and species. All logistic models shown were significant ($\alpha = 0.05$) and had at least moderate support according to the Akaike weight (w_i).

related to size of advance reproduction and that there were real differences among the species studied. Recovery of height by the hardwood sprouts is slow under a mature forest canopy. Thus, one fire can significantly modify the structure of the woody understory in upland oak forests for

up to four years, but it does little to alter the composition of the advance reproduction. By virtue of reducing the diameter and height of advance reproduction, a single prescribed burn predisposes sprouts to experience more severe damage and higher rates of mortality from subsequent fires.

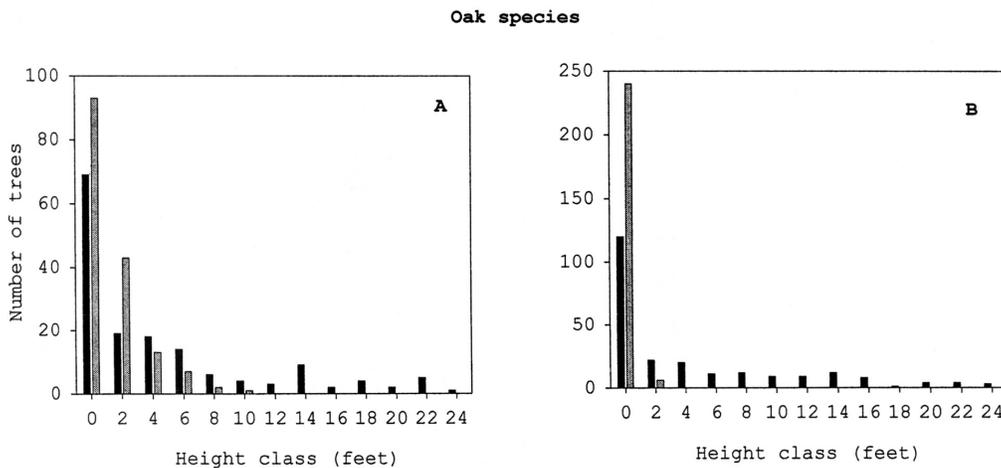
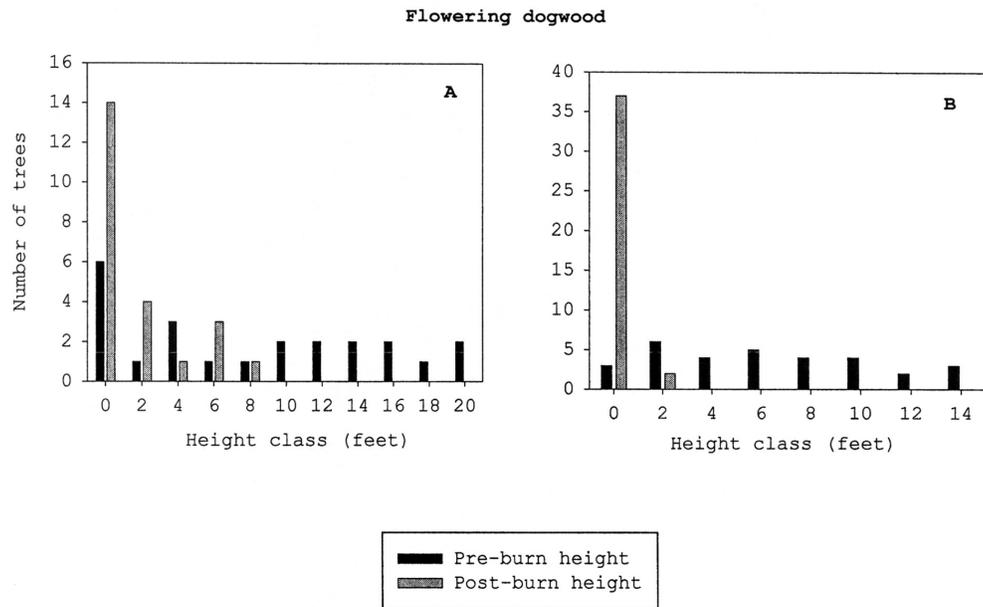


Figure 4—Pre- and post-burn height distributions of flowering dogwood and oak advance reproduction that sprouted after being topkilled by one, or four consecutive dormant season fires. Post-burn heights are shown (A) four years after one burn and (B) one year after four burns.

Three or four consecutive dormant season burns caused substantially higher mortality to advance reproduction and consequently greater levels of total fire damage. Mortality of flowering dogwood and blackgum advance reproduction increased substantially under a regime of frequent to annual fire. Mortality of oak and hickory advance reproduction was also increased to a lesser degree by frequent burning. Among the oaks, scarlet and blackjack advance reproduction were most vulnerable to repeated burning, whereas black, post, and white oak were intermediate. Overall, repeated burning in the dormant season favors oak and hickory reproduction.

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OAK ECOSYSTEM RESTORATION AND MAINTENANCE IN SOUTHERN ILLINOIS

Charles M. Ruffner and John W. Groninger¹

Abstract—Oak dominance in southern Illinois appears to be a consequence of long-term anthropogenic disturbances, including burning, grazing, and cutting. The increased prevalence of thin-barked, shade tolerant species, such as sugar maple and beech on presently oak-dominated upland sites appears to be a result of the extremely low-intensity disturbance regimes of the late 20th century. Our preliminary work indicates that moderate intensity fall burns top-kill 40 percent of pre-burn sugar maple and beech seedlings [< 2 inches in diameter at breast height (d.b.h.)] and increase herbaceous cover between 15-25 percent. However, sapling sized stems are largely undamaged suggesting that burning alone will not effectively restore oak dominance. Thus, a replicated study has been implemented to test the effectiveness of periodic burning and partial cutting, alone and in combination, to control mesophytic tree species and regenerate upland oak stands. Vegetation dynamics will be assessed on a long-term basis to document the effects of fire and cutting towards maintaining oak dominated ecosystems.

INTRODUCTION

Late Holocene forests of southern Illinois were comprised of oak-hickory and mixed mesophytic forests with inclusions of glades, prairies, and savannas. Braun (1950) classified regional forests as Oak-Hickory in the Ozark Hills of southwestern Illinois and Mixed Mesophytic across the Shawnee Hills of southeastern Illinois and western Kentucky. K uchler (1964) mapped the potential vegetation of this region as Oak-Hickory. Much has been published concerning the ecology of these forests, particularly species-site, productivity, and diversity relationships (Fralish 1988, 1997; Fralish and others 1991). While edaphic factors affecting vegetation structure have been explored, few studies have investigated the role that disturbances, particularly human disturbances, have had on these forest ecosystems.

Several key natural disturbance regimes have been characterized across the southern Illinois landscape. Primarily, these include tornado and wind damage, ice storms, periodic drought, and floods (Parker and Ruffner, in press). These occur rather sporadically, and the effects of single events are relatively localized on the landscape. While it is accepted that these natural disturbances have some impact on forest composition and structure, it is widely held that long-term human disturbances, including burning, grazing, and cutting, have been the primary forces shaping the oak-hickory forests of southern Illinois (Olson 1996, Fralish 1997, Ruffner and others 2003, Parker and Ruffner, in press).

Oaks have several biological adaptations to fire. Oak stems have thick, corky bark, a tenacious ability to repeatedly resprout following top-kill due to a high root:shoot ratio and dormant buds near the root collar, and the ability to compartmentalize wounds (Abrams 1992, Johnson 1993, Van Lear and Watt 1993, Smith and Sutherland 1999). In addition, oaks benefit from post-fire site conditions, such as the open understory and reduced impact of fire-intolerant competitors, and verification of the site through consumption of duff and exposure of soil to greater solar radiation, allowing

oak to dominate the advance regeneration pool (Van Lear and Watt 1993).

Despite the conceptual acceptance of the importance of anthropogenic disturbances, little fire scar evidence from the pre-settlement period exists because of the widespread logging of the primary forests and deterioration of cut stumps (Robertson and Heikens 1994, Olson 1996, Batek and others 1999). While pre-settlement fire scar data are likely lost forever, researchers have compiled substantial evidence of fire's role in post-settlement forests of southern Illinois by using an historical ecology approach including analysis of vegetation structure (Anderson and others 2000), witness tree distributions (McArdle 1991), fire scar analysis (Robertson and Heikens 1994), documentary evidence (Hall and Ingall 1910, Miller 1920), and land-use history studies (Ruffner and others 2002, van de Gevel 2002).

Historical accounts depict the region as heavily influenced by natives (Allen 1945, Temple 1966, Brown 1985). The landscape encountered by early European settlers reflected nearly 10,000 years of Native American manipulation and transformation. Native American use of fire and agricultural clearing was probably much greater prior to the 1500-1600s when large epidemics decimated regional native populations. Reduced disturbance regimes allowed an overall expansion of forest canopy cover. Thus, when European settlement began in the late 1700s-early 1800s, the anthropogenic landscape resembled a mosaic of oak-hickory woodlands and forests interspersed with small patches of barrens, savannas, and glades (Olson 1996, Dey and Guyette 2000, Parker and Ruffner, in press).

Regional studies reporting historic period fire histories indicate that fire ignitions were high following European settlement due to farmers clearing underbrush from the forest to enhance regeneration of browse and increase ease of travel and hunting (Hall and Ingall 1910, Miller 1920). The amount of land cleared for agriculture peaked in

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the early 1900s after which badly eroded lands were abandoned and either planted or naturally regenerated to forest. Many abandoned farms and cut-over lands were purchased during the 1920s-30s for public parks and forests and managed as timberlands throughout the 20th century (Parker and Ruffner, in press). With the development of an effective fire-suppression campaign in the 1930s-40s, human caused ignitions dropped, and fire was greatly limited as a force shaping vegetation.

The virtual elimination of fire from the landscape during the early 20th century fostered the expansion of mixed mesophytic species across the region (Fralish and others 1991). Numerous authors have studied central hardwood "old-growth" stands typified by the absence of cutting, burning, and most forms of management over the past several decades (Weaver and Ashby 1971, Nelson and others 1973, Schlesinger 1976, Barton and Smeltz 1987, Fralish and others 1991, Martin 1992, Robertson and Heikens 1994, Spetich 1995, Fralish 1997, Zaczek and others 2002, Ruffner and others 2003, and Groninger and others 2003). These studies report similar and significant shifts in species compositions and forest structure across a spectrum of forested sites. Overwhelmingly, sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*) were found to be increasing in stand density and basal area at the expense of the oak and hickory species that dominated the overstory. In particular, still important, but declining overstory species such as black oak (*Quercus velutina*) and southern red oak (*Q. falcata*) are not represented in younger age classes. Age-diameter figures suggest that a large cohort of mixed maple, beech, ash, and black gum (*Nyssa sylvatica*) recruited only a few years after the control of understory fire and the reduction of harvesting in some forests of the Ozark and Shawnee Hills (van de Gevel and Ruffner 2002, Zaczek and others 2002).

The presence of an understory dominated by mesophytic tree species has been associated with poor oak seedling and sapling development (Loftis 1990, Lorimer and others 1994). However, removal of the mesophytic midstory has aided in the development of the advance regeneration needed for the perpetuation of upland oak ecosystems (Crow 1988, Johnson 1993). Despite this, operational methodologies to remove dense midstories are costly and of uncertain reliability (Miller 1984, Horsley 1990, Groninger and others 1998). The composition of the understory and midstory may play an especially important role in the development of the next overstory in many southern Illinois stands where overstory dominants such as black oak and southern red oak are approaching their maximum ages en masse.

Recent studies have conducted prescribed burns in several transitional forests across southern Illinois with mixed success (Ruffner 2001, Ruffner and others 2003, Ruffner and Davis 2002). Understory prescribed burns have been effective in top-killing seedlings of these mixed mesophytic species with little or no effect on sapling-sized stems, unless subjected to multiple burns. Further, these burns have been ineffective for promoting oak regeneration in these stands. From these initial results we posit that understory burning is not effective in top-killing the larger unwanted stems that are shading the understory and precluding the development

of oak and hickory advanced regeneration. Thus, we have developed an experiment to test the effects of three silvicultural treatments on controlling unwanted species and inducing oak-hickory recruitment. Recent burning activities will be discussed in this paper and the current experimental design and possible implications for oak ecosystem maintenance will be explained.

PHYSICAL AND HISTORICAL CONTEXT OF STUDY AREA

The current project focuses on upland forests of the Ozark Hills of southwestern Illinois and the Shawnee Hills of southern Illinois.

Ozark Hills

The Ozark Hills region (113,340 acres) in southwestern Illinois is characterized by mature dissected topography capped with loess deposits and underlain with cherty limestone (Fralish 1997). Ridgetop sites are relatively narrow spur ridges capped with loess above steep sideslopes of colluvial materials, which descend to narrow riparian zones comprised of alluvial soils. Pre-European settlement forests were dominated by oak-hickory species with increased numbers of American beech, sugar maple, and tulip-poplar (*Liriodendron tulipifera*) across more mesic sites (McArdle 1991). McArdle argued that these forests developed under a moderate to infrequent disturbance regime based on the fact that oak-hickory importance increased after European settlement in response to the more intense disturbance regime of logging, clearing for agriculture lands, and increased grazing and burning. Indeed, much of the region's forests were extensively logged between 1880-1920 and frequent fire was identified as a major problem for forest development in the 1920s (Miller 1920, Miller and Fuller 1922, Fralish 1997). Fires continued through the 1940s until much of the Ozark Hills were purchased by the USDA Forest Service in the late 1930s and effective fire control measures were implemented.

Shawnee Hills

The Shawnee Hills comprise a 950,495 acre, unglaciated east-west escarpment bisecting southern Illinois (Fralish 1997). Topography of this section is characterized by broad ridgetops bearing deep loess deposits dissected by moderately steep sideslopes opening onto broad flat valleys (Fenneman 1938). Pre-European settlement forests of this region were dominated by xerophytic species such as post oak (*Quercus stellata*), black oak, and white oak (*Q. alba*), with mesophytic species tulip-poplar (*Liriodendron tulipifera*), American beech and sugar maple having lower importance across most sites (Fralish 1997).

Stands disturbed during the early 20th century from harvesting, fire or grazing are 58-84 percent similar to pre-settlement oak hickory forests suggesting compositionally stable forests (Harty 1978, Fralish 1997). However, the reduction of harvesting on public land and the eventual near removal of fire from the landscape during the last century has caused a shift in importance values particularly across northern aspects and low slope positions (Fralish 1997). Reduced disturbance patterns have resulted in a distinct increase in sugar maple and American beech recruitment into the mid-story and understory positions (Schlesinger 1976, Fralish

1997, Ruffner and others 2003). Still other midstory species such as winged elm (*Ulmus alata*), hophornbeam (*Ustrya virginiana*), and dogwood (*Cornus* spp.) appear capable of limiting oak recruitment on many sites.

Current management objectives of Illinois Department of Natural Resource agencies across this region focus on increasing oak-hickory advance regeneration while reducing mesophyte stem density with experimental prescribed burns coupled with timber stand improvement cuttings (Allen 2001, Ruffner and Davis 2002). Justification for this rests on the assertion that anthropogenic disturbances (either Native American or Euro-American) have been the driving force influencing forest structure and function across this region for at least the last four hundred years (Fralish 1997, Parker and Ruffner, in press).

PRESCRIBED FIRE TREATMENTS

Prescribed fire has been widely used to reduce competing vegetation, slow successional transition, reduce pest and pathogen populations, enhance wildlife habitat, facilitate site preparation, and encourage recruitment of resprouting species (Mutch 1994). Many authors have called for the re-introduction of prescribed burning in oak forests of the east, but few have documented the efficacy of this practice (Van Lear and Watt 1993, Brose and others 2001).

Perhaps the most successful experiments to date include those in oak forests of the Piedmont region of Virginia (Keyser and others 1996, Brose and Van Lear 1998, Brose and others 1999). Following shelterwood harvests with a 50 percent basal area reduction, these authors conducted repeated prescribed burns to significantly reduce tulip-poplar regeneration and increase advance oak regeneration. They suggest that this harvest/fire disturbance regime closely mimics the conditions that fostered the development of these oak dominated systems (Brose and others 1999). In addition, they report that allowing several years to lapse between the initial cut and burning is critical. This waiting period allows for several key components including the establishment and growth of vigorous oak seedlings and regeneration of the buried tulip-poplar seed pool. Although burns were also conducted in the winter and summer, spring appeared to be the best time period for burning because it presented the most favorable weather conditions such as warm temperatures, lower humidities, and sunny days (Brose and others 1999).

Within forests of southern Illinois, land managers have been utilizing prescribed fire since the mid 1980s. While the US Forest Service fire management program has largely been forced into a "suppression" mode due to extensive litigation, several Illinois Department of Natural Resources Divisions actively manage vegetation with prescribed fire (Ruffner 2001). The Divisions of Forest Resources and Natural Heritage both use fire to maintain unique vegetation and habitat types in glade and oak savannas, improve wildlife habitat, and foster oak regeneration while reducing competing mesophytic species in forestlands (Ruffner 2001).

The effect of a fall prescribed burn in an oak-hickory forest stand was investigated using two 0.10 ha permanent plots at Ozark Hills Nature Preserve, Trail of Tears State Forest.

Despite the low-to-moderate intensity of the burn caused by fall weather conditions, the burn effectively met the primary objectives of reducing understory competition from mesophytic tree species and increasing diversity of herbaceous species. Analysis of pre- and post-burn data indicates that nearly 40 percent of understory sugar maple and American beech seedlings were top-killed and herbaceous cover increased 15-25 percent within the plots. While these numbers indicate reduction of unwanted seedlings, sapling sized stems were left untouched by this level of burning. Thus, a replicated study similar to those conducted by Brose and his associates was designed to test the effectiveness of periodic burning and partial cutting of midstory, mesophytic trees on the development of oak-hickory regeneration.

This newest project evaluates and demonstrates the use of prescribed fire and partial cutting, alone and in combination with one another, on restoring oak forest health and sustainability. All study sites are in upland forest stands in southern Illinois with an oak-hickory dominated overstory and a midstory consisting of shade tolerant tree species. Site index ranges between 50-80 for upland oaks. Stand basal area averaged 110.1 ft² per acre (\pm 4.5 SE) with an average stem density of 226.2 (\pm 26.7 SE) trees per acre. A total of five, four acre blocks (each comprising a burned only plot, a cut only plot, a burned and cut plot, and an unmanaged control) have been installed across southern Illinois. Block compartments have 30-50 percent of standing basal area reduced by cutting stems <12 inches in d.b.h., favoring healthy oak-hickory stems for the residual stand. Burn compartments will be treated three times in five years beginning spring (2003) with a typical fuel model 9 prescription aimed at top-killing mesophytic resprouts and generating an advanced regeneration pool of oak-hickory stems. At each site, permanent plots have been installed to permit repeated measurement of the following variables:

- growth and fire damage for trees larger than 4 inches in d.b.h.
- tree species regeneration, shrub species, and tree saplings up to 4 inches in d.b.h.
- herbaceous species composition, cover, and quality for wildlife.

CONCLUSION

Perpetuation of oak dominated uplands is a priority among a wide range of constituencies in southern Illinois. Managers addressing this problem are faced with an incomplete understanding of past processes that produced the presently dominant oak overstory. Specific questions concern the timing, frequency, and intensity of anthropogenic and natural fires and the potential impacts of native and agricultural animals in stand establishment and maintenance. Equally puzzling is the extent to which overstory and midstory mesophytes must be controlled in order to carry a cohort of oak and hickory from seedling to overstory status. Also, with the prolonged absence of fire, some mesophytes have developed to the extent that they are now overstory trees. Removal of these now fire resistant individuals through cutting may be necessary to meet ecosystem restoration goals, but is inconsistent with esthetic expectations for public lands. Retention of these trees might necessitate

implementation of prescribed fires of greater than historic intensity and or frequency. These hotter fires may negatively impact the quality and value of maturing timber and thereby alienate some landowners with economic incentives for forest management. Alternatively, retaining large mesophytes may preclude adequate fuel development and result in the failure to secure oak and hickory recruitment.

In the face of these uncertainties, the establishment of demonstration plots such as those described here could serve as a focal point to help interested parties in southern Illinois determine where oak ecosystem restoration is desirable and how it may be effectively implemented. This empirical approach may also help address historical questions which often serve as a justification for ecosystem maintenance and restoration. A network of similar installations across fire-influenced oak dominated portions of North America may serve to increase public understanding of the fundamental roles played by humans and fire in the widespread occurrence of these ecosystems.

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EFFECT OF PRE-HARVEST SHADE CONTROL AND FENCING ON NORTHERN RED OAK SEEDLING DEVELOPMENT IN THE CENTRAL APPALACHIANS

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Abstract—Successful oak regeneration is related to the size and number of advanced seedlings present when harvests occur. This study was installed to quantify the effect of microsite light availability and deer on the development of advanced northern red oak (*Quercus rubra* L.) reproduction in mesic Appalachian hardwood stands. Microsite light was manipulated with pre-harvest herbicide treatments. Twelve 0.4-acre plots were randomly assigned to each of three microsite light levels and an untreated control for a total of 48 plots. A woven wire fence was erected around 8 plots in each treatment. Approximately 1,500 individual seedlings were tagged for long-term study. An additional 200 seedlings were tagged for annual destructive tests to measure shoot and root development. Three years after treatment, survival averaged 74 percent in fenced/high-light plots compared to 22 percent in unfenced/untreated plots. Fencing had a much stronger influence on survival than microsite light. Treatments also increased shoot length by 30 percent, root length by 39 percent, shoot weight by 145 percent, root weight by 337 percent, and basal diameter by 26 percent compared to controls. Practical considerations and long-term implications are discussed.

INTRODUCTION

Regenerating northern red oak (*Quercus rubra* L.) on high-quality growing sites is a continuing problem in the central Appalachian region. New stands that develop after harvests often contain fewer oak stems than the preceding stand, and the proportion of oak in the new stand usually does not meet management objectives. The basic problem is that harvests are often applied when there is a lack of competitive advanced oak seedlings present, thus the probability of successful oak regeneration is relatively low.

Competition among various species on a given site determines future species composition. After a significant disturbance to the forest canopy, numerous woody and herbaceous species compete for the light, water, and nutrients freed by the removal of overstory trees. The sources of new woody regeneration include: (1) new seedlings from seed stored in the forest floor, (2) sprouts from cut stumps, wounded roots, and broken shoots, and (3) advanced seedlings that developed before the disturbance. Species that compete with oaks on mesic sites often exhibit faster initial height growth than new oak seedlings and small advanced oak seedlings. If the oaks are not able to keep pace with competing species in the early stages of development, they usually die as the new overstory canopy closes above them (Trimble 1973). Oak stump sprouts are usually competitive with other species, but they contribute relatively few new stems on mesic sites (Loftis 1983a, Sander 1988). As a result, the primary source of successful oak reproduction on mesic sites comes from relatively large advanced oak seedlings. If large advanced oak seedlings are lacking before the harvest, then competing species usually dominate the composition of new stands (Beck and Hooper 1986).

Successful oak regeneration is related to the size and number of advanced seedlings present when harvests occur (Sander and others 1984, Loftis 1990a). For example, on northern red oak site index 80 (base age 50 years), the probability that an advanced oak seedling with a 0.1-inch basal diameter will become dominant or codominant 20 years after a harvest is essentially zero (Loftis 1990a). Even if thousands of such small seedlings are present before a harvest, very few will compete successfully after the harvest due to their small initial size. This probability increases to 1 percent for a 0.2-inch basal diameter, and 8 percent for a 0.75-inch basal diameter. As the seedling size and probability of success increase, fewer seedlings are needed to obtain adequate regeneration after a harvest. A pre-harvest inventory of advanced oak seedlings is recommended to determine if there will be a sufficient oak component in the new stand (Loftis 1990a). If projected oak regeneration is insufficient, silvicultural treatments may be needed to increase the growth and survival of advanced seedlings before the overstory is removed (Loftis 1990b).

In undisturbed mature oak stands, advanced oak seedlings usually exhibit both poor survival and slow growth. In one study, the survival of a cohort of northern red oak seedlings that germinated after a good acorn crop steadily declined from 60 percent after 1 year to only 10 percent after 10 years (Beck 1970). Similarly, the average total height of survivors was less than 1 foot after 1 year and generally did not increase over the next 10 years. In the southern Appalachians, shelterwood treatments that removed more than 50 percent of the stand basal area stimulated the growth of advanced oak seedlings, but also stimulated the development of competing species such as sweet birch (*Betula lenta* L.) and yellow-poplar (*Liriodendron tulipifera* L.), particularly where canopy gaps were created (Loftis

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1983a). Alternative shelterwood treatments that removed only 30 percent of stand basal area from below, with no canopy gaps, increased survival and growth of advanced oak seedlings without stimulating the development of competing species (Loftis 1988). Similar treatments have not been tested in the central Appalachians.

In most central Appalachian hardwood stands, adequate advanced oak reproduction does not develop due to several factors: (1) predation of acorns by deer, insects, rodents, and birds, (2) browsing of seedlings and sprouts by deer, and (3) excessive competition from dense interfering vegetation in the midstory and understory strata. These conditions call for pre-harvest silvicultural treatments that reduce acorn predation, reduce deer browsing of established seedlings, and reduce interfering plants so that advanced oak seedlings can grow to sufficient sizes before overstory removal (Lorimer 1993, Marquis 1981, Marquis and others 1976, Tilghman 1989).

Preparing for successful regeneration requires proper management of stand structure in the overstory, midstory, and understory for many years before a harvest (Carvell and Tryon 1961, Sander and Clark 1971, Gottschalk 1983, Beck 1988, Leak and others 1987, Loftis 1990b, Hannah 1987, Marquis and others 1992). Forest managers in the central Appalachian region need a reliable and efficient treatment for developing adequate advanced oak reproduction before harvest operations. Preliminary results in the region indicate that advanced oak reproduction is more abundant in stands where the canopy is closed and the subcanopy density is reduced (Schuler and Miller 1995, Miller 1997). A key to preparing for successful reproduction is a clearer understanding of the relationship between subcanopy stand density and the survival, growth, and development of oak seedlings and their competitors. This study was installed to quantify the effect of microsite light availability and deer on the development of advanced oak reproduction in mesic Appalachian hardwood stands.

STUDY SITES

The study was installed in 80-year-old second-growth central Appalachian hardwood stands on the Monongahela National Forest in northern Randolph County, West Virginia. Overstory trees in the study area regenerated after landscape-scale logging operations that were conducted between 1915 and 1920. In 1998, northern red oak accounted for 59 percent of the basal area, while yellow-poplar, black cherry (*Prunus serotina* Ehrh.), American beech (*Fagus grandifolia* Ehrh.), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), and cucumbertree (*Magnolia acuminata* L.) also occupied significant proportions of the overstory. Annual precipitation in the study area averages 59 inches and is evenly distributed throughout the year. Soils are described as Dekalb channery loam (loamy-skeletal, mixed, mesic Typic Dystrochrept) (USDA Soil Conservation Service 1967). The study area is located on site index 80 for northern red oak (base age 50). Several layers of dense subcanopy vegetation were present before treatments were applied. This vegetation included striped maple (*Acer pensylvanicum* L.), American beech, red maple, and sugar maple. There were approximately 20 to 25 white-tailed deer (*Odocoileus virginianus*) per square mile in the study area. The stands

contained an average of 5,000 2-year-old advanced northern red oak seedlings per acre when the study was installed.

METHODS

Microsite light on the forest floor was manipulated by treating selected subcanopy stems with an approved herbicide. A 50 percent solution of glyphosate as Accord 41.5 percent SL in a water carrier was used in all herbicide applications. The treatments included three microsite light levels plus a control defined as follows:

Control—no stems were treated

Low—all stems greater than 2.0 feet tall and less than or equal to 2.0 inches in diameter at breast height (d.b.h.) were cut near the ground, and the surfaces of cut stumps immediately were wetted with herbicide solution

Medium—in addition to stems included in the Low treatment, all stems greater than 2.0 inches and less than or equal to 7.0 inches in d.b.h. were injected

High—in addition to stems included in the Low and Medium treatments, all remaining stems that were in the intermediate or suppressed crown classes were injected.

The hack-and-squirt method was used to inject herbicide into target stems in the Medium and High treatments. A hatchet with a 1.75-inch wide blade was used to make the incisions, and incisions were spaced 1.5 inches apart on each target tree. A squirt bottle was used to dispense about 1.5 ml of herbicide into each incision.

In all three herbicide treatments, oak stems were neither cut nor injected in order to retain them as possible sources of advanced reproduction or sprouts.

Each treatment was applied to 12 square plots, resulting in a total of 48 plots, and each plot was 0.4-acre in size. A 6.5-foot tall woven wire deer fence was erected around 8 plots in each of the treatments, for a total of 32 fenced plots. A square 0.1-acre measurement plot was centered within each treatment plot, thus providing a buffer around each measurement plot, and all data were collected within the measurement plots. The fences were erected in July 1998, and the herbicide treatments were applied in late July 1999.

Species, d.b.h., and crown class were recorded for all stems greater than or equal to 1.0-inch d.b.h. before treatment within the 0.1-acre measurement plots. A post-treatment inventory was completed a year later to determine the percent reduction in basal area achieved in each plot. Photosynthetically active radiation (PAR) was measured within each plot in late July before treatment and each year after treatment to quantify changes in microsite light. PAR was measured with synchronized Accupar Ceptometers placed 1 meter above the ground at a fixed location in a nearby open field and at 9 designated points within each plot. Measurements in the open were compared to mean measurements within the plots at synchronized times to determine percent PAR associated with each plot (Parent and Messier 1996, Gendron and others 1998).

Approximately 1,500 individual oak seedlings were tagged for long-term study. Survival and total height of live seed-

lings were recorded in late summer before treatment and each year after treatment.

An additional 50 seedlings in each treatment were tagged within fenced plots to perform annual destructive tests to measure root and shoot response to each microsite light level. All seedlings tagged for the destructive tests germinated in the spring of 2000. Approximately 10 seedlings were extracted from each treatment in September of 2000, 2001, and 2002, thus providing growth response data for each of the first three growing seasons. Measurements taken on extracted seedlings included shoot length, root length, dry shoot weight, dry root weight, and basal diameter.

DATA ANALYSIS

Statistical analyses were completed to provide insight into four important relationships: (1) the effect of herbicide treatments on microsite light, (2) the effect of herbicide treatments and fencing on survival and height of tagged red oak seedlings, (3) the effect of herbicide treatments on third-year shoot and root characteristics of extracted seedlings, and (4) the effect of herbicide treatments on basal diameter of extracted seedlings over 3 growing seasons.

A one-factor repeated measures ANOVA was used to examine the effect of herbicide treatments on microsite light. The fixed effect model has the form:

$$Y_{ij} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \varepsilon_{ij}$$

where

Y = percent PAR

μ = the overall mean

α = the effect of herbicide treatment

β = the effect of time

ε = the random error.

A two-factor repeated measures ANOVA was used to analyze the effect of the herbicide treatments (Factor 1) and fencing (Factor 2) on seedling survival and height. The fixed effect model has the form:

$$Y_{ij} = \mu + \alpha_i + \beta_j + \theta_k + (\alpha\beta)_{ij} + (\alpha\theta)_{ik} + (\beta\theta)_{jk} + (\alpha\beta\theta)_{ijk} + \varepsilon_{ijk}$$

where

Y = survival proportion or height

μ = the overall mean

α = the effect of herbicide treatment

β = the effect of fencing

θ = the effect of time

ε = the random error.

The remaining terms represent the interaction of factors in the full model.

For third-year shoot and root response, data were analyzed using a one-factor ANOVA. The fixed effect model has the form:

$$Y_i = \mu + \alpha_i + \varepsilon_i$$

where

Y = shoot length, root length, shoot dry weight, or root dry weight

μ = the overall mean

α = the effect of herbicide treatment

ε = the random error.

For seedling basal diameter, means were compared for each of the first three growing seasons after treatment. Basal diameter data were collected from the same seedlings used to compare shoot and root development. It was not possible to conduct a repeated measures analysis of basal diameter since the subjects were destroyed each year. Instead, the data were analyzed as a two-factor ANOVA and the fixed effect model used has the form:

$$Y_{ij} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \varepsilon_{ij}$$

where

Y = basal diameter

μ = the overall mean

α = the effect of herbicide treatment

β = the effect of time

ε = the random error.

The general linear models procedure in SAS was used for all statistical analyses (SAS Institute Inc. 1998). The Tukey-Kramer HSD mean separation test was used for all multiple comparisons. Treatment effects were considered to be statistically significant when $P < 0.05$. For each analysis, the residuals were tested for normality using the Shapiro-Wilk test and for homogeneity of variance using the Levene test.

RESULTS AND DISCUSSION

The average basal area on all study plots was 180 ft² per acre before treatment. The herbicide treatments reduced basal area by an average of 22, 10, and 2 percent for the High, Medium, and Low treatments, respectively (table 1). Loftis (1990a) recommended reducing basal area by 30 to 35 percent when applying similar pre-harvest shelterwood treatments in stands on site index 80 in the southern Appalachians. The basal area reduction in this study ranged from 1 to 35 percent, thus all treatment levels were equal to or less than those recommended for stands in the southern Appalachians (table 1).

Microsite Light

Before treatment, the low levels of microsite light beneath the dense subcanopy vegetation were not conducive to oak seedling survival and growth. The average PAR was 1.9 percent before treatment, and none of the plots was receiving the minimum amount of light needed for oak seedling survival. When seedlings do not receive enough light, as is

Table 1—Summary of shade control treatments and effects on basal area and microsite light availability

Treatment	Plots <i>no.</i>	Stems treated		Reduction in basal area		Residual stand PAR	
		Mean	Range	Mean	Range	Mean	Range
Control	12	—	—	—	—	2	1 – 3
Low	12	209	70 – 450	2	1 – 13	4	3 – 8
Medium	12	360	180 – 600	10	3 – 25	8	4 – 16
High	12	410	270 – 640	22	16 – 35	12	8 – 25

PAR = photosynthetically active radiation.

common in stands with a dense subcanopy layer, photosynthesis produces less carbohydrates than are used in respiration, thus the seedlings eventually die (Hodges and Gardiner 1993). Hansen and others (1987) found that small northern red oak seedlings need $PAR \geq 30 \mu\text{mol m}^{-2}\text{s}^{-1}$ to achieve the necessary positive carbon balance. All measures of PAR in untreated plots were below this threshold level. It was clear that low microsite light levels on the forest floor had prevented the development of any large advanced oak seedlings for many years.

One year later, the herbicide treatments resulted in a significant increase in microsite light reaching the forest floor (fig. 1). The High, Medium, and Low treatments increased microsite light to 12, 8, and 4 percent PAR, respectively. The repeated measures ANOVA indicated a significant effect of

treatment ($P < 0.01$), time ($P < 0.01$), and the interaction of treatment and time ($P < 0.01$). The differences among the treatments were still intact after the third growing season, although the subtle changes in microsite light that occurred each year appear to differ by treatment. By the end of the third year, slight reductions in microsite light were evident in the High and Medium treatments, probably due to crown expansion among overstory trees into small canopy gaps. Microsite light in the Low and Control treatments remained relatively stable for the first three growing seasons. As this study continues, more information about the longevity of treatment effects on microsite light will become available.

Seedling Survival and Height

This comparison of survival and height included all 1,076 tagged seedlings that were still alive after 3 years. The repeated measures ANOVA with two factors indicated that time ($P < 0.01$), microsite light ($P = 0.02$), and fencing ($P < 0.01$) had a significant effect on the 3-year survival of oak seedlings. There was no evidence of interaction between microsite light and fencing ($P = 0.78$). At each level of microsite light, fencing increased survival by more than 20 percent (fig. 2). Note that survival was 22 percent in untreated plots, and the addition of a fence increased survival to 44 percent. Also, in fenced plots, each increase in microsite light further increased survival by 10 percent. For example, the Low treatment increased survival to 54 percent, the Medium treatment increased survival to 64 percent, and the High treatment resulted in maximum survival of 74 percent (fig. 2). Repeated measures ANOVA are robust to violations of multivariate normality and homogeneity of covariance matrices, thus applying the arcsine square root transformation to the observed survival proportions yielded similar results. A similar repeated measures ANOVA for seedling height indicated that time ($P < 0.01$) and fencing ($P < 0.01$) significantly affected seedling height, but height did not differ significantly by microsite light treatment ($P = 0.46$). Seedling height in fenced plots averaged 4.7 inches, while those in unfenced plots averaged 3.5 inches after 3 years.

Shoot and Root Response After 3 Years

This comparison is based on a relatively small sample, approximately 10 seedlings per treatment, extracted from fenced plots for laboratory analysis of shoot and root development. Shoot length, root length, shoot weight, and root

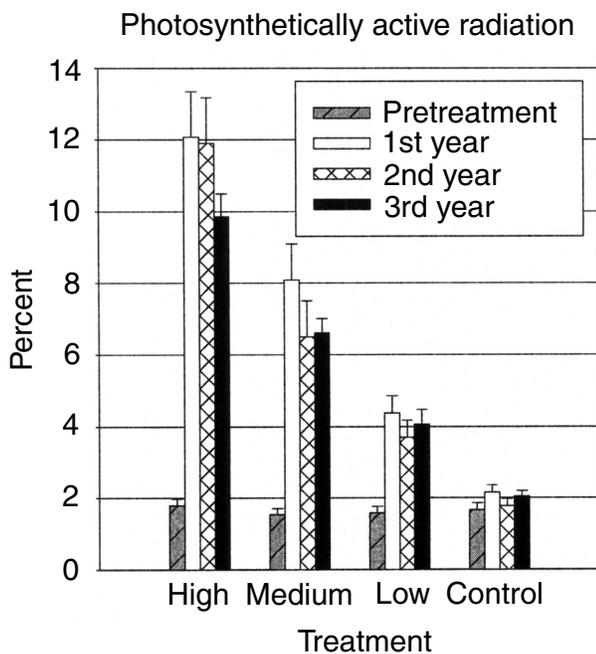


Figure 1—Mean percent of photosynthetically active radiation before and 3 years after shade control treatments, with one standard error bar shown above each mean.

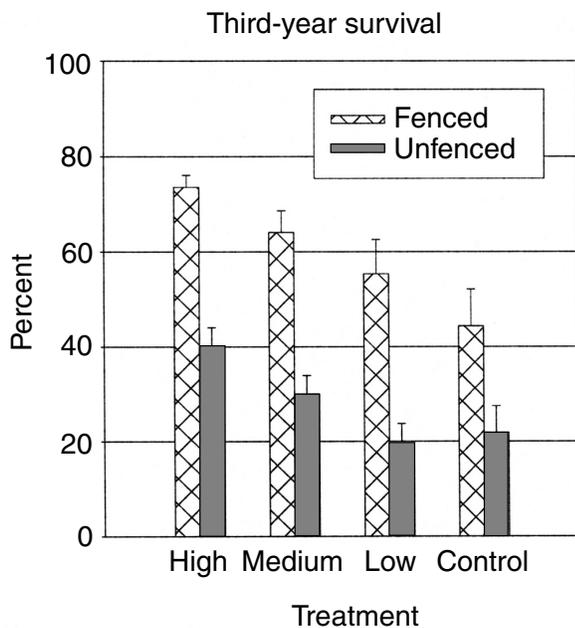


Figure 2—Mean survival of advanced northern red oak seedlings 3 years after shade control treatments and fencing, with one standard error bar shown above each mean.

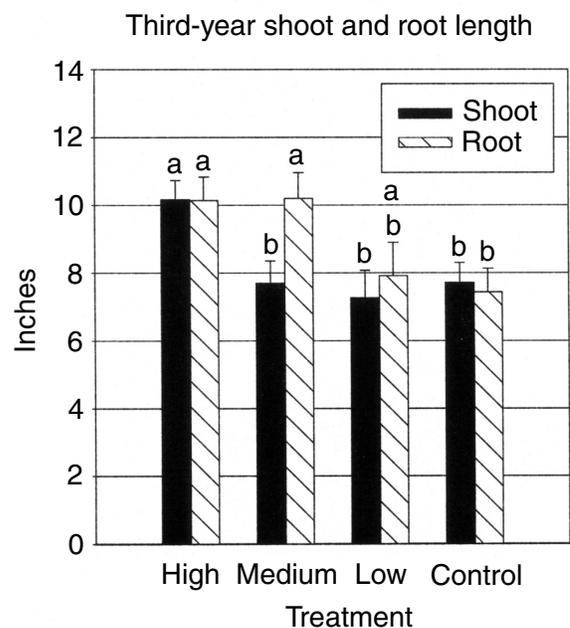


Figure 3—Mean shoot and root length of seedlings extracted 3 years after treatments, with one standard error bar shown above each mean. For each variable, means with the same letter are not significantly different based on Tukey-Kramer HSD multiple comparison test at the 0.05 level.

weight were significantly related to microsite light resulting from the herbicide treatments. In addition, the analysis of residuals exhibited no evidence to reject assumptions of normality or homogeneity of variance in any of the comparisons. Multiple comparisons of treatment means following each ANOVA showed that significant root responses occurred at lower microsite levels than that observed for shoot responses. Shoot length in the High treatment was significantly greater than in other treatments, while shoot length among the Medium, Low, and Control treatments was not significantly different. Shoot length averaged over 10 inches in the High treatment compared to less than 8 inches in the other treatments (fig. 3). By contrast, root length in both the High and Medium treatments was significantly greater than that observed in the Control treatment. Root length averaged over 10 inches in the High and Medium treatments compared to less than 8 inches in the Low and Control treatments (fig. 3). The High treatment increased shoot length and root length by 30 and 39 percent, respectively, compared to controls. Shoot weight in the High treatment was significantly greater than in other treatments, and shoot weight among the Medium, Low, and Control treatments was not significantly different. Average shoot weight in the High treatment was 145 percent greater than that observed in control plots (fig. 4). Root weight in the High and Medium treatments was significantly greater than in the Control treatment. Average root weight in the High treatment was 337 percent greater than that observed in the control plots (fig. 4).

Seedling Basal Diameter

Both time ($P < 0.01$) and microsite light treatment ($P < 0.01$) were significantly related to seedling basal diameter, although there was no evidence of interaction between time and treatment ($P = 0.67$). The residuals were consistent

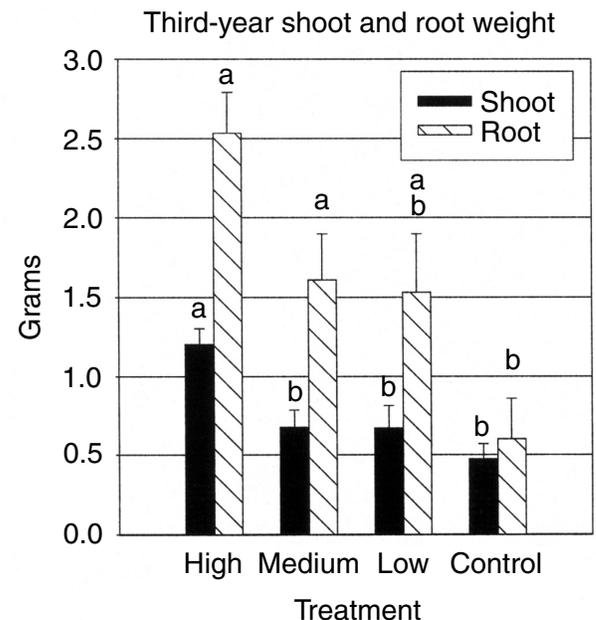


Figure 4—Mean shoot and root dry weight of seedlings extracted 3 years after treatments, with one standard error bar shown above each mean. For each variable, means with the same letter are not significantly different based on Tukey-Kramer HSD multiple comparison test at the 0.05 level.

with normality and homogeneity of variance assumptions. The High treatment led to an increase in basal diameter each of the first three growing seasons, with the greatest increase occurring in the third growing season (fig. 5). After three growing seasons, the Medium and Low treatments

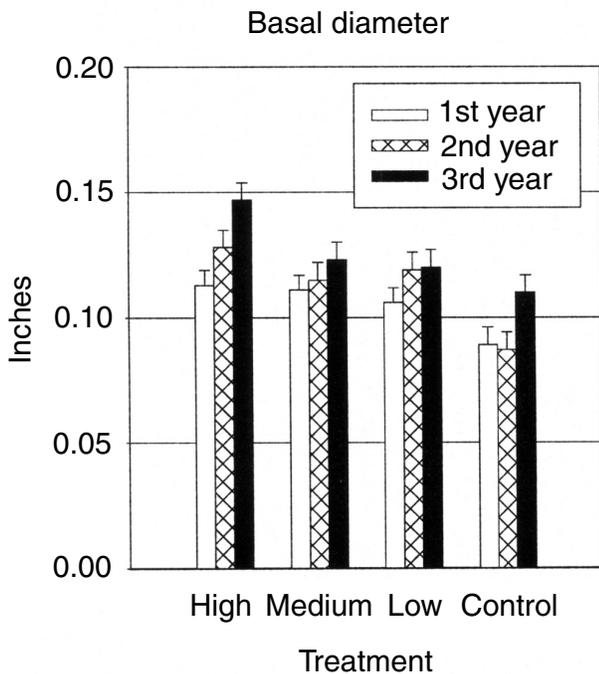


Figure 5—Mean basal diameter of seedlings extracted 1, 2, and 3 years after treatments, with one standard error bar shown above each mean.

did not produce significant increases in basal diameter compared to controls. Basal diameter in the High treatment averaged 0.146 inches, approximately 26 percent greater than that observed in the controls.

In general, the data indicated that enhanced root development occurred in the High and Medium treatments, with some evidence of faster stem development in the High treatment (figs. 3 and 4). Oak seedlings typically exhibit a conservative growth strategy in which surplus photosynthate resources are allocated to root development before notable shoot development occurs (Hodges and Gardiner 1993). Apparently the Medium treatment resulted in enough photosynthate to enhance root development within 3 years after treatment, but increases in shoot development may not be evident for a few more years.

Practical Implications

An example is presented in table 2 to illustrate the practical implications of the results presented here. The example is based on 20-year dominance probabilities for red oak seedlings presented by Loftis (1990b). This approach predicts the number of dominant/codominant (D/C) stems 20 years after overstory removal based on the number and size of seedlings present when the overstory is removed. The number of D/C stems projected to develop in the new stand

Table 2—Predicted number of dominant/codominant oak stems in the new stand based on the size and number of advanced oak seedlings present when harvest occurs

Time between treatment and harvest year	Pre-harvest basal diameter inches	Dominance ^a probability percent	Survival rate percent	Pre-harvest oak seedlings number per acre	D/C stems 20-yr after harvest
Predicted outcome with high shade control and fencing					
0	0.089	0.0	100.0	5000	0
1	0.113	0.0	88.2	4410	0
2	0.128	0.6	83.5	4175	25
3	0.146	0.7	73.5	3675	26
4	0.167	0.8	68.0	3400	27
5	0.191	0.9	63.0	3150	28
6	0.218	1.2	58.0	2900	32
7	0.248	1.4	53.0	2650	37
8	0.281	1.7	48.0	2400	41
9	0.317	2.1	44.0	2200	46
10	0.356	2.5	40.0	2000	50
11	0.398	3.1	36.0	1800	56
12	0.443	3.7	32.0	1600	59
Predicted outcome with no shade control and no fencing					
0	0.089	0.0	100.0	5000	0
1	0.089	0.0	69.6	3480	0
2	0.089	0.0	41.2	2060	0
3	0.116	0.0	21.8	1090	0
4	0.120	0.5	11.0	550	3
5	0.124	0.5	6.0	300	1
6	—	—	0.0	0	0

D/C = dominant/codominant.

^aLoftis 1990a.

is found by multiplying the dominance probability for a given seedling size by the number of such seedlings present. Note that the dominance probability increases as seedling size increases because larger advanced seedlings can compete more successfully against other species as the new stand develops.

The example compares two silvicultural alternatives. One alternative includes fencing and shade control as applied in the High treatment. The other alternative includes no fencing and no shade control. Computations for the first three years are based on actual survival rates and average basal diameters observed in the High and Control treatments. Computations beyond the third year were estimated as a linear projection of basal diameter growth and a negative exponential projection of survival based on the observed 3-year trends in each of the two silvicultural alternatives.

With shade control and fencing—The treatments increased the projected number of successful D/C oaks within 3 years, and continued increases are expected for several years into the future. After 3 years, the survival rate was 73.5 percent and the average basal diameter was 0.146 inches (table 2). Applying the corresponding dominance probability indicates that 0.7 percent of the surviving 3675 seedlings, or 26 stems per acre, would become D/C in the new stand if the overstory were removed after the third year. Postponing overstory removal for several additional years would allow advanced seedlings to grow larger, thus introducing a greater dominance probability and a greater projected number of successful D/C oaks in the next stand. However, natural mortality will also reduce the number of seedlings each year. Projections of both decreasing survival and increasing growth indicate that the projected number of successful D/C oaks generally increases for at least 10 years after pre-harvest treatments were applied. If treatments are applied 8 to 10 years before removing the overstory, projections indicate that the new stand will contain 40 to 50 D/C oaks per acre when the new stand is 20 years old.

With no shade control and no fencing—In the absence of pre-harvest treatments, the projected number of successful D/C oaks remained near zero, and no improvement is expected in the future. After 3 years, the survival rate was only 21.8 percent, and the average basal diameter was 0.116 inches (table 2). These trends suggest that few seedlings will remain after 5 years, and those that survive have little chance of becoming dominant or codominant after the overstory is removed. Even if the overstory had been removed immediately, when there were 5,000 seedlings per acre, the dominance probabilities indicate that none would compete successfully after the harvest because of their small initial size.

For simplicity, this example was based on applying the appropriate dominance probability to a single size class, the mean basal diameter observed in each alternative. In real-world applications, a population of advanced oak seedlings often exhibits a distribution of size classes and each size class has a corresponding dominance probability. It is more accurate to estimate the projected number of successful D/C oaks by applying dominance probabilities to

the number of advanced seedlings in each size class and summing the results (Loftis 1993).

SUMMARY

The example illustrates three important results of this study. First, pre-harvest shade control and fencing increased survival and stimulated faster shoot and root growth. Successful oak regeneration is related to the size and number of advance seedlings present before a harvest, thus the treatments tested in this study increased the probability of successful oak regeneration. In the absence of pre-harvest treatments, especially fencing, the probability of successful oak regeneration remained near zero. Second, significant shoot and root development occurred in the first 3 years, but more time is needed to allow seedlings to fully respond to the treatment. As the seedlings develop larger basal diameters, their corresponding dominance probability will also increase. Data from this study indicated that treatments should be applied at least 8 to 10 years before a planned harvest to assure that seedlings attain at least a 2 to 3 percent probability of becoming dominant or codominant once the overstory is removed. Third, annual measurements of PAR showed only slight decreases in microsite light each year, indicating that observed survival and growth rates will continue for several years. In the High treatment, it is expected that enhanced microsite light will be available for 10 to 12 years after treatment. This extended response period provides a practical window of opportunity for scheduling future activities such as commercial shelterwoods and/or removal of the overstory once competitive advanced oak seedlings develop.

Periodic control of undesirable vegetation can be a valuable long-term practice in forest management. Zedaker (1986) reasoned that applying herbicide treatments at opportune times in the life cycle of hardwood stands is an effective means of allocating site resources to desirable species. In this case, pre-harvest shade control treatments allow advanced northern oak seedlings to acquire the site resources necessary to become competitive with other species and enhance the probability of successful oak regeneration. Oaks are notorious for slow height growth in the early stages of development (Hodges and Gardiner 1993). Small seedlings need at least 8 to 10 years of desirable growing conditions before overstory removal to develop into competitive advanced seedlings. Pre-harvest herbicide treatments provide such conditions, in that interfering plants are eliminated quickly and they do not become reestablished for many years. Forest managers should consider maintaining relatively low levels of undesirable subcanopy vegetation in hardwood stands, even many years before a planned harvest, to keep interfering species in check and continually allocate resources to preferred species.

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FIRE AND THINNING IN AN OHIO OAK FOREST: GRID-BASED ANALYSES OF FIRE BEHAVIOR, ENVIRONMENTAL CONDITIONS, AND TREE REGENERATION ACROSS A TOPOGRAPHIC MOISTURE GRADIENT

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Abstract—Prescribed fire alone and in combination with thinning were accomplished in late 2000 to spring 2001 at Zaleski State Forest in southern Ohio. Sites were monitored before and after the treatments were applied. Light was assessed via hemispherical photographs taken in July 2000 and 2001. Oak and hickory seedlings and saplings were sampled during those same time periods. Soil moisture was monitored eight times in 2001 via time-domain-reflectometry (TDR). Air temperature was recorded every 2 seconds during the fires, and soil temperature was recorded hourly in the months following the fires. These data allow us to evaluate, in concert with the landscape moisture patterns: (1) aspects of fire behavior, and (2) effects of the thinning and burning on soil moisture and temperature, light, and vegetation. The thin-and-burn treatment, relative to the control, generally resulted in more light, higher soil moisture, higher seasonal soil temperatures, but no short-term effects on oak-hickory regeneration. The integrated moisture index (IMI), a GIS-derived index categorizing landscape into three moisture regimes, was related to many of the measured variables: sites modeled as topographically wetter had more soil moisture, lower fire and seasonal soil temperatures, less light penetration, and less oak and hickory regeneration.

INTRODUCTION

Ohio is undergoing a conversion from its oak-hickory (*Quercus* and *Carya*) forests to primarily maple (*Acer* L.) and tulip poplar (*Liriodendron tulipifera* L.) forests. This change is typical among many midwest and eastern states. Data from the USDA Forest Service forest inventories between 1968 and 1991 (Kingsley and Mayer 1970, Dennis and Birch 1981, Griffith and others 1993) indicate that the proportion of total volume in oak and hickory declined substantially relative to maple, tulip poplar, and black cherry (*Prunus serotina* Ehrh.). The relative importance of several oak and hickory species in Ohio declined by at least 22 percent during this same period while maples and tulip poplars increased by at least 38 percent in total volume. This trend corroborates regional patterns in Illinois (Iverson and others 1989, Iverson 1994), Pennsylvania (Nowacki and Abrams 1992), and several other eastern states (Powell and others 1993). This trend has prompted a large scientific effort to assess the problem and search for management solutions (e.g., Loftis and McGee 1993, Abrams 1996, Brose and others 1999, Elliot and others 1999, Huddle and Pallardy 1999, Tybirk and Strandberg 1999, Johnson and others 2002).

Several factors contribute to the decline of oaks in eastern forests. Oaks do not regenerate well under closed canopies and thus are declining while more shade-tolerant species are thriving (Hilt 1985, Loftis and McGee 1993). In addition, when light and moisture are not limiting (e.g., after a clear-cut), tulip poplar and some other species can out-compete the oak (Beck 1990, Marquis 1990). The success of oak regeneration after a canopy-changing disturbance seems to follow a moisture gradient, that is, regeneration of oak is

adequate only under xeric conditions in situations where it can successfully compete with more mesic species (Iverson and others 1997).

Historically, fire has been a component of oak forests in southern Ohio. Dendroecological studies have shown that fires were frequent from the time of Euro-American settlement ca. 1800 to ca. 1930 (Sutherland 1997; Hutchinson and others 2002). However, after ca. 1930, fires usually were suppressed, resulting in a dramatic increase in recruitment of maples and other non-oak species.

Preliminary findings of an earlier study in southern Ohio indicated that several burns did not sufficiently increase light to the forest floor for satisfactory oak regeneration to occur. Therefore, a new study was initiated in 2000 to assess the effectiveness of thinning, in addition to prescribed fire, for its potential to improve oak regeneration. As part of the national Fire and Fire Surrogates Study (FFS), our group is studying these treatments as possible means of reducing maple abundance and fostering oak recruitment in the Oak Hills study region.

Microclimatic effects have been found to be critical in forest ecosystems. Topographic characteristics and surface cover can greatly influence several microclimatic factors, including air temperature, soil temperature, and moisture (Kang and others 2000). Human-controlled factors such as silvicultural cutting and fragmentation, also can have profound influences on microclimatic factors (Chen and others 1999, Zheng and others 2000). Thus, our study stratified sites by moisture class to allow this feature to be evaluated with the applied treatments.

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The objectives of the FFS project are to measure the effects of both fire and thinning on oak regeneration and on components of biodiversity within the ecosystem. In this paper, we present a preliminary analysis, of one site, of how the following characteristics vary among moisture classes and treatments: (1) fire behavior; (2) seasonal soil temperature and moisture following treatment; (3) canopy light penetration before and after treatment; and (4) oak and hickory seedlings and saplings before and the first season after treatment.

METHODS

Site Description and Study Design

The results reported here are from the Zaleski State Forest, located in Vinton County about 80 km southeast of Columbus, OH (82° 25' W, 39° 18' N). This is one of three southeast Ohio sites that are part of the FFS study. The area is part of the unglaciated Allegheny Plateau and is characterized by dissected topography and less than 100 m of total relief. The overstory is dominated by oak, especially in the more xeric positions on the landscape. Oak establishment occurred from ca. 1840-1925, under conditions of frequent fire (Hutchinson and others 2002). Common species include chestnut oak (*Quercus prinus* L.), white oak (*Q. alba* L.), red oak (*Q. rubra* L.), scarlet oak (*Q. coccinea* Muenchh.), black oak (*Q. velutina* Lam.), pignut hickory (*Carya glabra* (Miller) Sweet), mockernut hickory (*C. tomentosa* (Poiret) Nuttall), and bitternut hickory (*C. cordiformis* (Wangenheim) K. Koch). Other common overstory species include red maple, tulip poplar, and American beech (*Fagus grandifolia*

Ehrhart), which are more abundant on mesic positions of the landscape.

Oaks are much less abundant in the midstory and under-story layers, and species composition in these layers is more strongly related to topographic influences. Oak and hickory regeneration is present only on a few highly xeric and open ridge-top positions. Red maple and a few other species tend to dominate the lower strata and will likely dominate the next forest.

The Integrated Moisture Index (IMI) was used to capture the influence of varying topography and soils across the landscape (Iverson and others 1997). The IMI is a GIS model (0-100 scale) of long-term moisture availability based on solar radiation, position on the slope, curvature of the landscape, and water-holding capacity of the soils. IMI has been used to predict forest site productivity and composition, understory composition and richness, soil nitrogen, aluminum, pH, and bird distributions (Iverson and others 1996, Hutchinson and others 1999, Dettmers and Bart 1999, Boerner and others 2000, Dyer 2001). In this study, plots were categorized into three IMI classes: xeric (score 11-34.5), intermediate (34.5-46), and mesic (46-78.5).

A sampling grid (311 points) was overlaid on the Zaleski site by establishing a point every 50 m, using a global positioning device (fig. 1). The site was divided into four (26 to 31 ha) treatment units: control (C), burn only (B), thin only (T) and thin+burn (TB). Only C, B, and TB were evaluated for this paper.

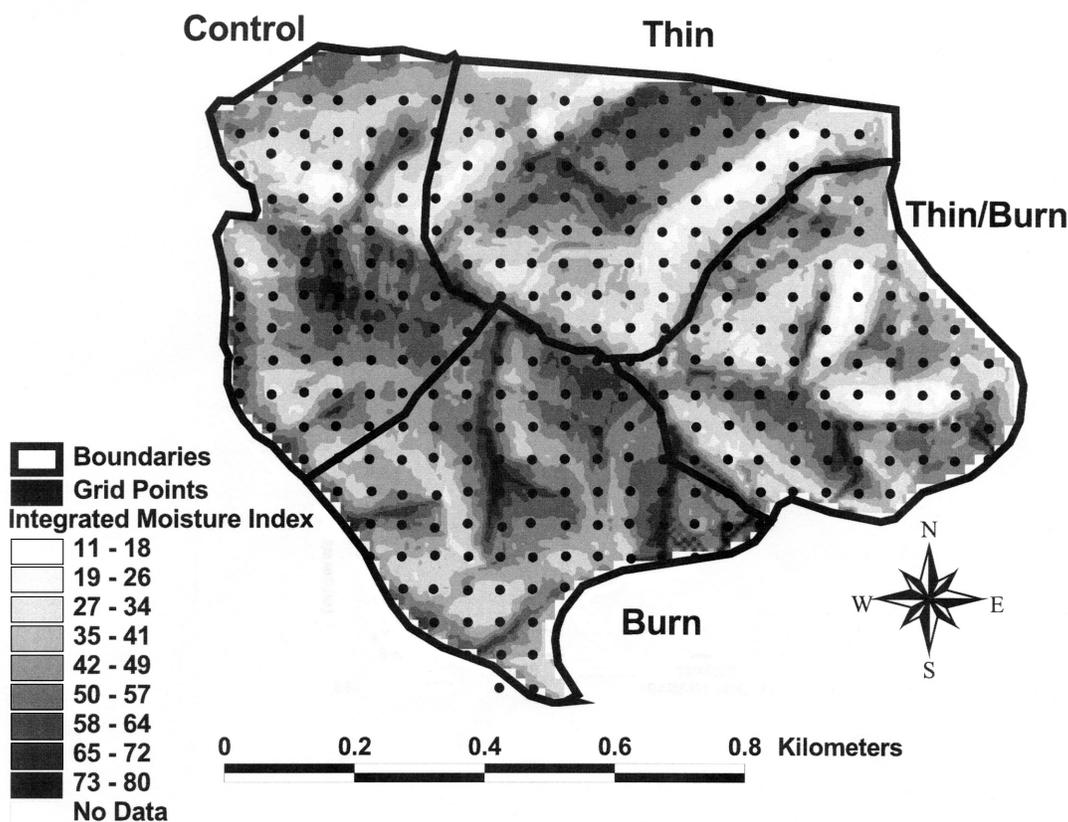


Figure 1—Map of treatment units, grid points, and IMI classes in the Zaleski State Forest.

Thinning occurred during the fall of 2000. For the TB site, basal area was reduced 27 percent, from 25.5 m²/ha to 18.5 m²/ha. The density of canopy trees (dominant/codominant) was reduced 26 percent, from 192 to 142 stems/ha, and midstory density was reduced 41 percent, from 255 to 150 stems/ha.

The fire was conducted on 4 April 2001 between 1300 and 1553 EST. Three firing teams ignited across the north line, across the south line, and down the middle. Each firing team used two or three drip torches, allowing them to set several lines of fire parallel to the control lines. During the fires, air temperature ranged from 15 to 18 °C, relative humidity from 23 to 35 percent, and windspeed from 5 to 6 km/hr. The area received a dusting of snow on April 1 and about 0.3 cm of rain on the morning of April 3, so the coarser fuels were not dry at the time of the burn. However, warm and dry air on April 3 dried fine fuels rapidly.

Fire Temperatures and Analysis

Prior to the burn, stainless steel temperature probes (Type K thermocouple) were installed at 60 grid points in the B unit and 63 points in the TB unit (fig. 1). The thermocouples were placed 25 cm above the soil surface. Hobo® data loggers (Onset Computer Corporation) were buried 2 m away in closed PVC containers and connected to the probes via a buried cable. Extreme care was used to limit disturbance of the litter layer during the burial of the cable; a hatchet was used to cut a small slit in the ground to lay the cable and the litter layer was reconstructed over the closed slit.

The data loggers were programmed to capture air temperature every 2 seconds on the day of the burn. From these data, we calculated the following: (1) maximum temperature; (2) duration of temperature above 30 °C; (3) a heat index, defined as the summed temperatures above 30 °C (an integral under the temperature curve); and (4) time of maximum temperature. An example output from the Hobo data logger software is shown in figure 2.

An animation of the burning fire was created using the data from maximum temperature, duration of elevated temperatures, and time of the maximum temperature. For each of

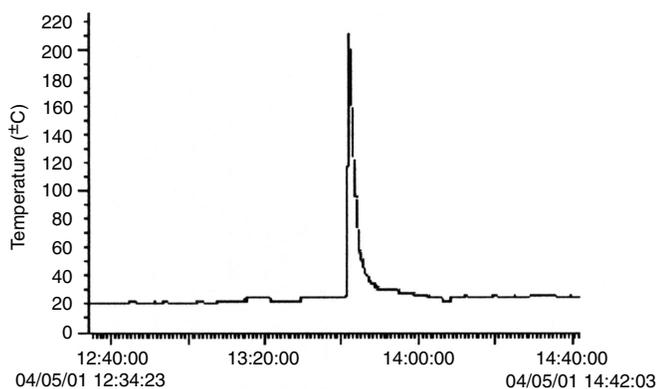


Figure 2—Example output of the air temperature data recorder on the day of the fire.

123 grid points from which the data were successfully collected, spreadsheet functions were built, for each of 248 30-second time periods, to linearly raise the temperatures for each grid point to the maximum and down from the maximum. The duration was used to calculate the beginning and ending times of the elevated temperatures. The 248 time-slice temperatures for each grid point were then linked to 248 maps via ArcView 3.2a (Environmental Systems Research Institute 1996) and interpolated via an inverse-weighted distance function, then merged into a movie.

Environmental Monitoring

Light, soil moisture, and soil temperature were monitored following the burns to assess differences among treatments. Light also was measured before the treatments. Monitoring for all three variables was conducted at each grid point that was not within a 50 m buffer of a treatment boundary, on just the C (45 points) and TB (60 points) units. The two extremes were selected for evaluation because evaluating all four treatments was cost-prohibitive. (Ten 0.1 ha-plots in each treatment unit are used to assess the environmental variables at a less extensive scale. The data are not reported here.)

To estimate understory light levels, hemispherical photographs were taken at each grid point with a digital camera in July 2000 and July 2001. The images were analyzed for percentage open sky and percentage transmittance with the Gap Light Analyzer (GLA) program (Frazer and others 1999).

Soil moisture was recorded eight times during the 2001 growing season: 3 May, 17 May, 7 June, 14 June, 6 August, 20 August, 4 September, and 12 September. The large time gap between June and August was due to equipment failure. Moisture was sampled with a TRIME (Time Domain Reflectometry with Intelligent MicroElements) – TDR (Time-Domain-Reflectometry) sensor. PVC tubes, sealed at the bottom and with a removable cap at the top, were buried in the weeks following the burn to a depth of 50 cm or bedrock. A power auger was used to drill a hole sized equally to the outside diameter (~5 cm) of the tube and the tube was inserted carefully to ensure close contact between the soil and the tube throughout its depth. The sensor measures the volumetric soil water via electromagnetic field measurement of the dielectric constant of the soil.

The temperature probes used to monitor fire behavior also were used to monitor soil temperature following the fires. On the TB grid points, the probes were turned from a vertical to horizontal position into the soil at a depth of 2 cm. On the C grid points, the probes were positioned in a similar fashion. The Hobo data loggers were programmed to acquire soil temperature hourly from setup in April to October 31, 2001.

Oak and Hickory Regeneration

At each grid point, the number of oak and hickory seedlings (<50 cm height) was recorded in a 12.6 m² circular plot (2 m radius) centered on the grid point. Oak and hickory saplings [>50 cm height to 10 cm diameter at breast height (d.b.h.)] were recorded in a 78.5 m² circular plot (5 m radius)

also centered on the grid point. Vegetation data, also recorded at the grid points but not reported here, include the abundance of seedlings and saplings of all tree species, species and basal area of overstory trees (recorded with a 10 basal area factor prism), and the cover of forbs, graminoids, shrubs, woody vines, and tree seedlings on the forest floor.

Statistical Analysis

Analyses and graphic outputs were produced in Splus (Mathsoft 1996). Analysis of variance was used to detect trends due to treatment (B vs. TB for the response variables for fire behavior; C vs. TB for response variables light, moisture, soil temperature, and oak and hickory seedlings and saplings) or moisture class (xeric, intermediate, or mesic). For oak and hickory regeneration, the year (2000 vs. 2001) was also compared with an analysis of variance. Interactions among treatments were also evaluated in each analysis. Where appropriate on the three IMI classes, multiple means were tested with Tukey's multi-comparison test. To test significant differences in oak and hickory seedling or sapling densities between 2000 and 2001, a pairwise t-test was used with 100 paired samples.

RESULTS AND DISCUSSION

Fire behavior

The B unit had an average maximum temperature of 174 °C, while the TB unit averaged 138 °C (fig. 3). The B unit burned later in the day when there was higher air temperature and lower humidity. However, on the TB unit, temperatures exceeding 30 °C lasted an average of about 11 minutes, compared to 9.5 minutes on the B unit; likely the result of fuel moisture differences. The average heat index, which takes into account both temperature and duration, was

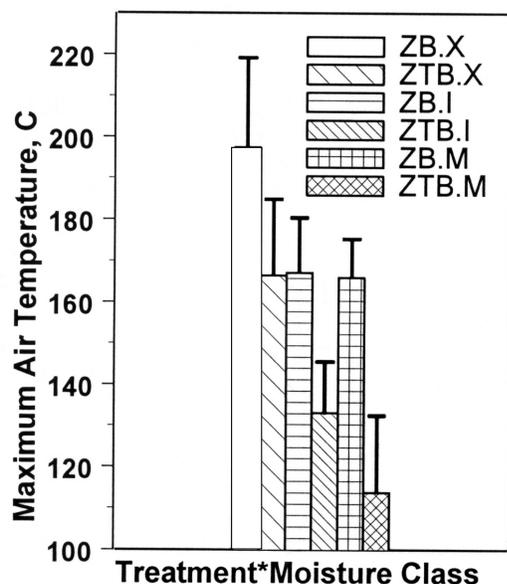


Figure 3—Maximum air temperatures (+ standard error of mean) recorded during the day of the fire, by treatment and moisture class. Legend: (1) site - Z=Zaleski; (2) treatment - B=Burn, TB=Thin and Burn; (3) moisture class - X=xeric, I=intermediate, and M=mesic.

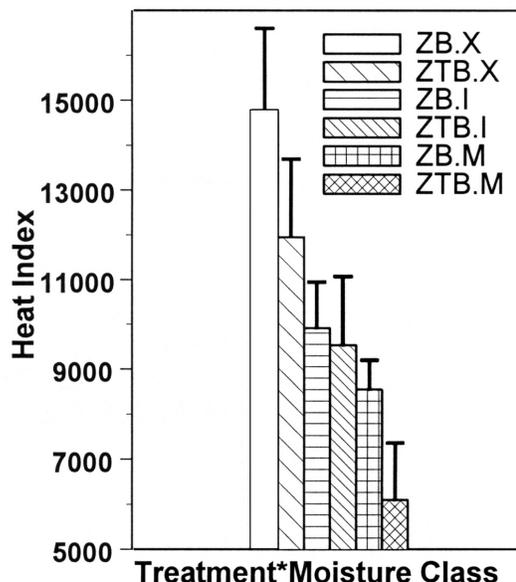


Figure 4—Cumulative heat index, calculated from maximum temperatures and duration, by treatment and moisture class. Legend: (1) site - Z=Zaleski; (2) treatment - B=Burn, TB=Thin and Burn; (3) moisture class - X=xeric, I=intermediate, and M=mesic.

10,556 for the B unit and 9,177, or about 13 percent less, on the TB unit (fig. 4).

There was a significant trend with moisture class for average heat index (ANOVA, $P = 0.02$): 12,734 for xeric, 9,729 for intermediate, and 7,639 for mesic sites (fig. 4). This trend is reflective of conditions where the fuels remained moister in the mesic areas from the rain and snow dusting the previous few days. Maximum temperature was not statistically different among moisture classes, although xeric sites had higher temperatures (175 °C) than the intermediate (150 °C) or mesic sites (147 °C) (fig. 3).

Animation of fire

The recorded information from the sensors located each 50m throughout the study area allowed us to evaluate and visualize some aspects of the fire behavior. Although the animation cannot be shown in this paper, the reader is encouraged to view it at the web site at: http://www.fs.fed.us/ne/delaware/4153/ffs/zaleski_burn.html.

This animation shows the fire being set from the east, along both north and south fire lines, as well as some internal firing. The simulation also shows a slower rate of spread in the valleys, with hotter, faster fires on the more xeric locations.

Light

A total of 112 hemispherical photographs were analyzed with the GLA software: 43 in 2000 (pre-thinning and burning) and 69 in 2001 (post treatments). There was a large increase in percentage open sky after thinning and burning, from 7.1 percent to 11.9 percent, on average (fig. 5). The percentage open sky varied by moisture regime, with the more mesic locations having a slightly more closed canopy

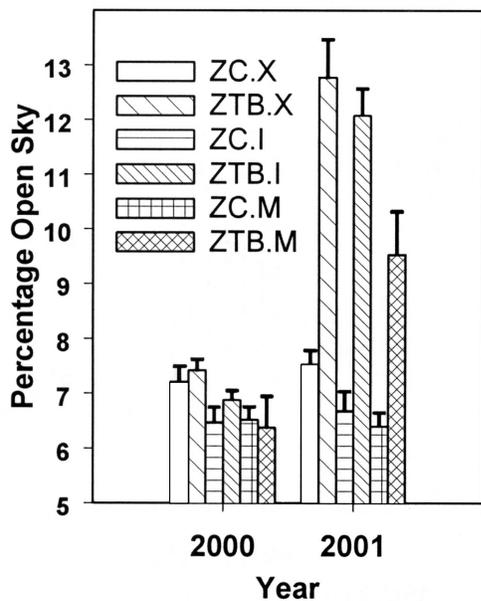


Figure 5—Percent open sky, 2000-2001 for Zaleski, as analyzed from hemispherical photographs and the GLA software. Legend: (1) site - Z=Zaleksi; (2) treatment - C=control, TB=Thin and Burn; (3) moisture class - X=xeric, I=intermediate, and M=mesic.

than xeric or intermediate. Even after thinning, the mesic locations had only 9.5 percent open sky as compared to over 12.1 percent for the other two treatments (fig. 5). The mesic sites, in addition to receiving less solar radiation, were more difficult to harvest because of longer skid distances and often steep topography.

Moisture

In general, the moisture levels decreased as the season progressed (fig. 6). The September 2001 data showed much drier conditions than the average values. Soil moisture variability was fairly high as expected from the field data. Many factors contribute to the detected moisture levels at a given location, including the amount of litter, green material, proximity to large tree roots, macro- and micro-topographic influences, drainage, microfissures in the soil, nearby animal activity, and errors associated with the technology.

Though not statistically significant, mean moisture levels were usually higher on the TB unit compared to C (fig. 6). We suggest that the removal of trees during thinning may have reduced substantially the amount of soil moisture transpired. The smaller plants, more abundant on the TB sites, transpire only a fraction of what larger trees do, so removal of overstory trees will substantially remove total leaf area and reduce transpiration. Transpiration per unit of land area has been shown to generally increase with greater leaf area index unless the canopy boundary layer resistance is so high that energy input controls evaporation (Landsberg 1986). In addition, the TB unit tended to have more green coverage at the herbaceous level, possibly providing a 'living mulch', which reduces solar radiation at the surface, perhaps to a level even lower than that on the C unit.

Moisture levels tended to increase from xeric to mesic IMI classes, though differences were not statistically significant.

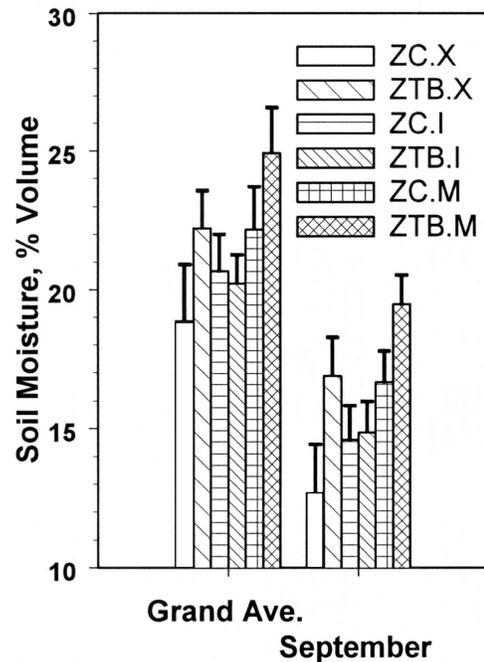


Figure 6—Percent soil moisture, by volume, for the Zaleski site during the 2001 growing season. Shown are the overall average values (eight sampling dates and three depths) and the last sampling date, from September 12-17, 2001. Legend: (1) site - Z=Zaleksi; (2) treatment - C=control, TB=Thin and Burn; (3) moisture class - X=xeric, I=intermediate, and M=mesic.

The higher moisture readings observed on the xeric TB unit can be traced to several outlier points which exist in complicated topographic settings not captured adequately in GIS using 30 m digital elevation model pixels. One would expect that it is more likely to find pockets of mesic conditions within an area classified as xeric (e.g., small drainages not detectable in 30 m grid cells), than vice versa.

Soil Temperature

Soil temperatures were recorded hourly from 13 April to 31 October, 2001, for each of the 105 points. There was a substantial treatment effect, with the TB unit having significantly higher ($P < 0.001$) soil temperatures than the C unit throughout most of the season (fig. 7). The greatest differential was in April, when the soil surface was blackened following the spring fires. At this time, the daily maximum temperature differentials were as much as 4 °C. In an earlier study, we found similar trends, with soil temperatures as much as 6.2 °C higher on burned vs. control sites in May (Iverson and Hutchinson 2002).

There were also significant ($P < 0.03$) temperature differences among moisture classes in all months except August ($P = 0.06$) and October ($P = 0.37$). In general, daily maximum temperatures were greatest on xeric and least on mesic areas (fig. 7). This pattern can be explained by increasing soil moisture content and associated thermodynamics (fig. 6), as well as decreasing solar radiation exposure (fig. 5) from the xeric to mesic moisture regimes.

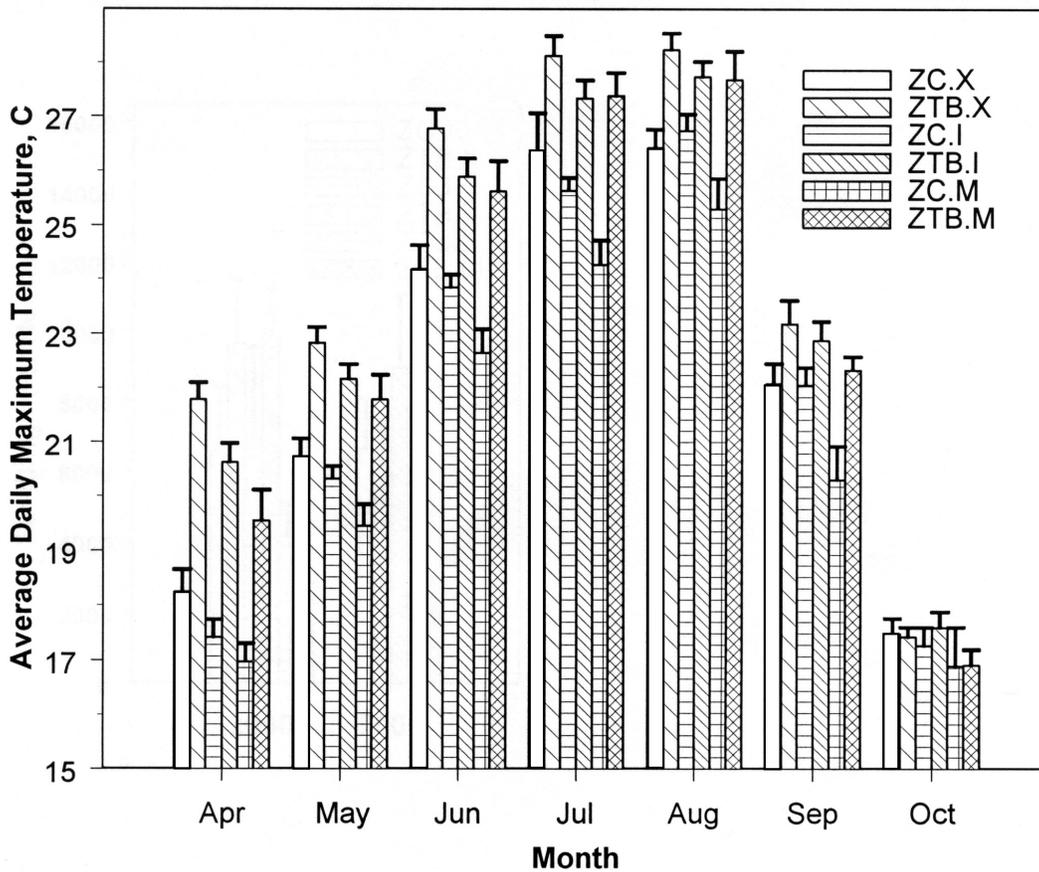


Figure 7—Daily maximum soil temperatures, averaged by month, for the Zaleski site during the 2001 growing season. Data were extracted from hourly data collect from 105 sensors. Legend: (1) site - Z=Zaleski; (2) treatment - C=control, TB=Thin and Burn; (3) moisture class - X=xeric, I=intermediate, and M=mesic.

Oak and Hickory Regeneration

There was an average of 8,060 oak or hickory seedlings/ha in 2000 and 6,390 seedlings/ha in 2001. There were very few oak or hickory saplings (>50 cm to 10 cm d.b.h.): 40 per ha in 2000 and 48 per ha in 2001. There were no significant differences in oak and hickory seedling or sapling densities between years using a pairwise t-test (N = 100 paired samples).

Oak and hickory seedling densities were significantly different among moisture classes (ANOVA, $P=0.02$), while treatment effect was nearly significant at the 5 percent level ($P = 0.06$), and year was not significant (fig. 8). No interaction effect was present. Fire and thinning treatments did not alter the number of oak or hickory seedlings in the first growing season following the spring fires: similar patterns existed before (2000) and after (2001) treatment. In both years, the TB unit had slightly more oak and hickory seedlings on the xeric and intermediate moisture classes, and slightly less on the mesic sites. Over both years and both treatments, the mesic sites had significantly fewer oak and hickory seedlings as compared to the other moisture classes. There were no significant differences in sapling densities among moisture classes, treatments, or years.

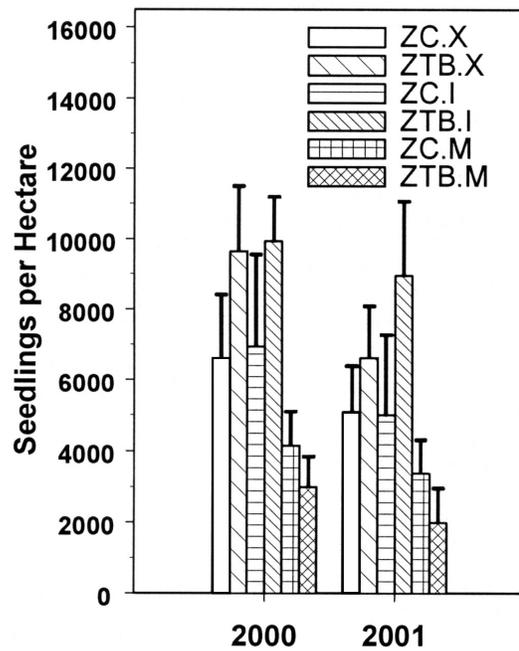


Figure 8—Oak and hickory seedling numbers per quadrat (2 m radius circle=12.87 m²) for Zaleski, 2000-2001. Legend: (1) site - Z=Zaleski; (2) treatment - C=control, TB=Thin and Burn; (3) moisture class - X=xeric, I=intermediate, and M=mesic.

CONCLUSIONS

We have demonstrated a method to capture some aspects of fire behavior during prescribed surface fires in eastern forests. Thermocouples and data recorders buried prior to the fires successfully logged temperatures every 2 seconds, which allowed analysis of maximum fire temperatures, duration, and heat index. With a spatial analysis of the data, a movie animation of the fire was created.

This study also provides a preliminary analysis of two primary factors related to landscape-level microclimate and vegetation: a human-controlled silvicultural regime of thinning and burning, and a topographically controlled moisture index. The thin-and-burn treatment, as compared to the control, resulted in higher seasonal soil temperatures. The blackened surface and the open canopy facilitated more absorption of solar radiation. The TB unit also increased soil moisture levels near the soil surface apparently because of reduced evapotranspiration. An evaluation of the thin-only and burn-only treatments (pending analysis of plot-level data) is needed to better assess these cumulative effects. In this first season after treatment, we did not detect a difference in oak and hickory regeneration between TB and C units.

The integrated moisture index also was related to the measured variables. The wetter sites had higher soil moisture, though there was a lot of variability associated with fine-scale features on the landscape. The IMI was based on a 30 m digital elevation model (DEM). If a finer-resolution DEM were available, perhaps the small ravines (less than 30 m wide) would be captured more accurately by the moisture index. Wetter sites also had lower fire temperatures and seasonal soil temperatures due to less incoming solar radiation. We also found lower light availability on the wetter zones. These sites tend to be the most difficult to harvest with poor accessibility. Finally, the wetter zones had significantly fewer oak and hickory seedlings and saplings. In fact, it was difficult to find a sapling on any site, but especially in the wetter zones. These data provide further evidence that these species regenerate poorly under closed-canopy, mesic conditions.

Though oak and hickory regeneration densities were unaffected by treatments, personal observation indicates that at least some of the resprouted oaks and hickories exhibit increased growth given adequate light and reduced competition from fire-sensitive species such as red maple. We are hopeful that over time, adequate oak and hickory advance reproduction will develop on the treated sites, thus improving the sustainability of forests that have been long dominated by oaks and hickories.

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OAK GROWTH AND RESPONSE TO THINNING

Stephen R. Shifley¹

Abstract—Oak growth and yield is simultaneously influenced by tree-, stand-, and landscape-scale factors. At the tree scale oak diameter growth varies by tree species (typically n. red oak >= scarlet oak > black oak > white oak > chestnut oak > chinkapin oak > post oak), but oak diameter growth is even more strongly influenced by crown class. Oak stands go through up to 5 stages of development that differ in tree size structure and stand dynamics. Knowing a stand's developmental stage helps guide the application of thinning practices and other silvicultural techniques. Periodic thinning beginning at age 30 in oak stands can double board foot yield over a rotation relative to unmanaged oak stands. This results from capturing volume that would otherwise be lost through mortality and from reallocating growing space to desirable trees. The greatest increases in yield occur when a series of periodic thinnings is started when the stand enters the stem exclusion stage of development. Stump sprouts require even earlier treatment to maximize growth. Estimating future growth and yield in even-aged stands is often facilitated by application of mathematical models; models are a necessity for growth estimation in uneven-aged stands and stands with a large non-oak component.

INTRODUCTION

Traditionally, interest in forest growth and yield has been associated with timber production. However, growth and yield is simply one aspect of the broader subject of stand dynamics that deals with changes in stand size structure and species composition over time. These changes can be related to timber yield, but they can also be related to yield in wildlife habitat, quantity of mast production, aesthetic qualities, or even ecological services such as storing carbon or maintaining species diversity. Like timber yield, yield of these other products and amenities changes over time and in response to management activities. Yield tables or growth models can aid in estimating future quantities of all these outputs.

Growth and yield can be evaluated and analyzed at different spatial resolutions. Stand growth and yield (per acre) is often of primary interest, but stand growth is the composite outcome of growth and survival of thousands of individual trees. Hence, growth of individual trees as affected by species, size, and competition is also often of interest, particularly for stands with mixed species and multiple age classes. Likewise, the composite growth and yield of multiple stands in a geographic region, their spatial arrangement, and their anticipated change over time can be important in forest planning, locating a new wood using facility, or dealing with insect or disease problems.

Major factors that affect growth and yield of oak trees and oak stands are presented in this paper. Particular emphasis is given to response to thinning, changes in stand structure, and changes in species composition over time.

OAK TREE GROWTH

There are clear differences among species in diameter growth rates (fig. 1). For example, mean growth rates for scarlet oak in Missouri are approximately twice those for post oaks of comparable diameter. Over several decades these differences can result in substantial differences in tree diameter (and often a tree's height and crown posi-

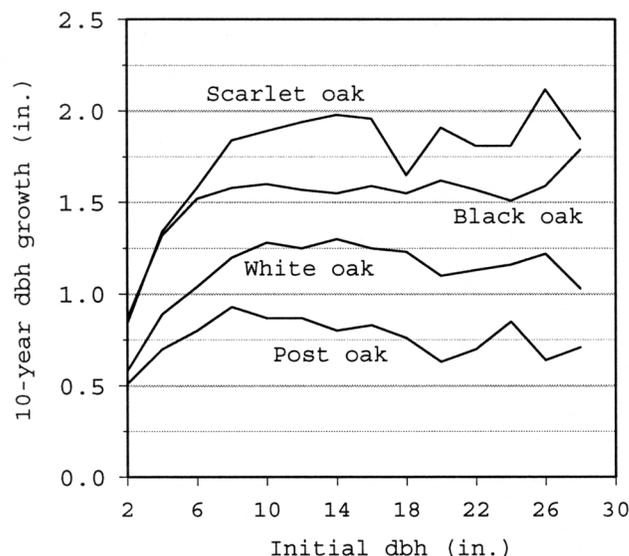


Figure 1—Mean periodic tree diameter-at-breast-height growth for black (*Quercus velutina* Lam.), scarlet (*Q. coccinea* Muenchh.), white (*Q. alba* L.), and post oaks (*Q. stellata* Wangenh.) in Missouri (based on Shifley and Smith 1982).

tion). However, tree longevity also plays a role, and over many decades the faster growing black and scarlet oaks are less likely to survive than white or post oaks, other factors being equal (Shifley and Smith 1982, Smith and Shifley 1984). Hence, in the long run, persistent oaks such as white oaks can often capture dominance from faster-growing, shorter-lived trees in the red oak group. We probably underestimate the influence of periodic droughts and other infrequent but severe external stressors in affecting longevity and species composition over the life of a stand. Such events may only occur once or twice during a rotation, but they can radically change stand species composition (e.g., the disproportionate loss of red and black oaks during drought-induced oak decline).

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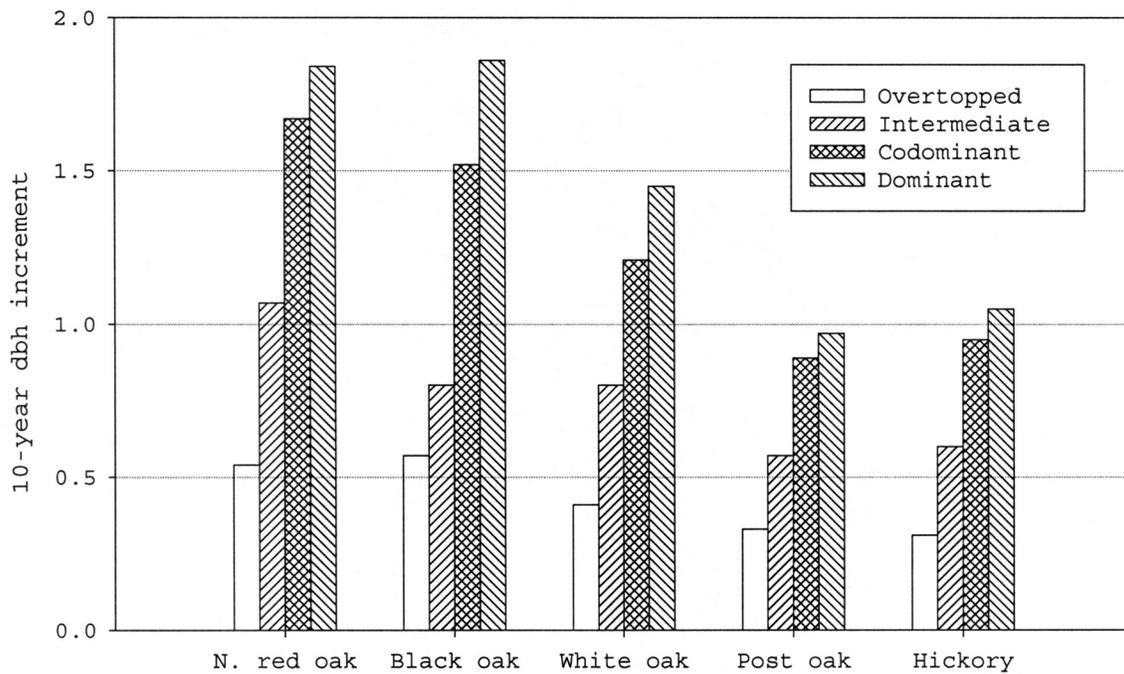


Figure 2—Effect of tree crown class on diameter growth for oaks and hickories in Missouri. The hickory group is a composite of all *Carya* spp. (based on Shifley and Smith 1982).

Crown position is even more influential than species in controlling diameter growth. A tree's crown class (dominant, codominant, intermediate or overtopped) can completely overshadow differences among species (fig. 2). Trimble (1969) stated that crown class is the single most important factor in tree diameter growth, and it is clear that a dominant or codominant oak of nearly any species will, on average, grow faster in diameter than an overtopped or intermediate oak of any other species.

Tree crown class is the result of the competitive sorting that takes place as trees increase in size and vie for a finite amount of growing space. The average annual diameter at breast height (d.b.h.) growth for a stand decreases as stand age and basal area increase, but those dominant and codominant trees that are well positioned in the canopy continue to grow rapidly at the expense of trees that have smaller or crowded crowns. Trees rarely improve their crown class over time unless a timber harvest or other significant stand disturbance occurs to release growing space. Thus, if a tree achieves a dominant or codominant crown class, it must maintain that canopy position or it will eventually lose out to competitors. Thinning manipulates crown classes and growing space to favor trees that satisfy management objectives.

Compared to diameter growth, the height growth of dominant and codominant trees is less affected by stand density. Hence, height growth of trees that have continuously remained in these two crown classes is used to measure site quality via site index. Previous studies have shown that on the same site the site index (i.e., height in feet at age 50) for scarlet oak is 3 feet greater than for black oak which is in turn 4 feet greater than for white oak (McQuilken 1974).

However, oaks have different height growth patterns. Scarlet and black oak get off to a rapid start but slow after 50 or 60 years. When the trees reach 100 years, white oaks in the upper canopy will often be 10 to 15 feet taller than black oaks (Carmean 1971). Tree height growth and site index are, of course, closely linked to volume growth of trees and stands.

In contrast to trees in the upper canopy, height growth of trees in subordinate crown classes is greatly affected by competitors, and oaks that fail to maintain a favorable crown position usually face an early demise, barring some disturbance to the overstory that increases available growing space. One of the few oak height models based on tree diameter and age (regardless of crown class) was published by Hilt and Dale (1982) as part of the OAKSIM model.

Over long periods of time, oaks that are persistent (e.g., through sprouting or through greater shade tolerance than competitors) are sometimes able to survive, despite the presence of faster growing competitors. For example, white oak (which is slower growing but longer lived and slightly more shade and drought tolerant than black, red, and scarlet oak) may eventually achieve dominance opportunistically. This may be the result of a designed timber harvest, or it may occur by chance when shorter lived species reach the end of their life span or when the droughts or other disturbances (that inevitably occur over the course of a long rotation) take their toll on other species. As the number of sites monitored continuously over many decades gradually increases, the importance of extreme events (e.g., drought, ice, fire, partial harvest) in triggering changes in species composition is increasingly apparent.

TREE RESPONSE TO THINNING

Controlling tree crown class through thinning is the single most important thing a manager can do to increase tree growth and stand yield over time. Studies in oak stands have demonstrated that dominant and codominant oaks will respond to increased thinning intensity with increased diameter growth across a wide range of diameters and ages, even if stand stocking is reduced to 30 percent or less (Dale 1972). Note, however, that oak management guides for timber production generally recommend keeping minimum stocking above 50 percent to avoid development of epicormic branching and to fully utilize the growing space per acre. At lower stocking levels, diameter growth of individual trees is increased, but stand growth is typically not maximized. Significant thinning effects have been reported for red, black and scarlet oaks up to 90 years old in Connecticut (Ward, 2002).

It often takes two years for tree diameter growth to achieve maximum response to thinning, and the effects of thinning on individual overstory trees may persist for as long as two decades. When trees are given a competitive advantage through thinning, they are often able to maintain that advantage by increasing their crown area and capturing growing space which allows them to maintain the faster growth rate for years. There are two general exceptions to this response to thinning. First, trees with small, poorly formed crowns (e.g., intermediate and overtopped crown classes) may not respond at all to thinning, or the response may be delayed by three to five years as tree crowns gradually enlarge to capture the growing space release by thinning. Second, oaks in stands less than 10-years old may not increase their diameter growth in response to thinning. In young stands crown classes are not firmly established, and the growing space released by the removal of a young tree is small relative to the ability of surrounding trees to expand and capture growing space. The rapid growth of vegetation relative to tree size in young stands means the effect of thinning is generally short-lived. Thus, the potential benefits of thinning in seedling/sapling stands can be quickly erased by crown expansion in residual trees and a flush of herbaceous growth. Consequently, diameter growth of dominant and codominant trees less than 10 years old has shown a variable response to thinning. When stands are very young, the intermediate and overtopped trees are actually more likely to respond to thinning with increased diameter growth than are larger trees. Herbicides applied to cut trees may increase the duration of the thinning effect in young stands (Johnson and others 2002).

Oaks often originate as stump sprouts, and sprouts present a different situation with respect to thinning young trees. Thinning has been demonstrated to be effective in increasing diameter growth on sprouts that were as old as 25 years, but the sooner sprout clumps are thinned to a single stem (down to 5 years of age), the greater the gain in diameter growth relative to unthinned clumps (Johnson and others 2002). Early thinning of stump sprouts to a single stem can double diameter growth relative to sprouts in unthinned clumps; diameter increases of 30 to 60 percent are common, depending on site index and initial tree size (Johnson and Rogers 1980). Although retaining the single largest sprout typically results in the largest future tree, smaller sprouts

released at an early age can perform nearly as well. Consequently, retaining sprouts based on form rather than tree size will result in relatively little loss in future size (Johnson and others 2002).

STAND GROWTH AND RESPONSE TO THINNING

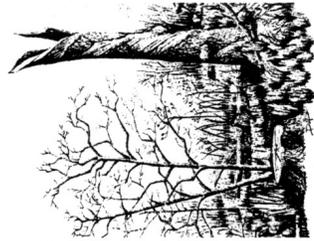
As even-aged oak stands develop over time they go through five stages of stand development: (1) stand initiation, (2) stem exclusion, (3) understory reinitiation, (4) complex, and (5) mixed stage (fig. 3) (Johnson and others 2002, Oliver and Larson 1996). These stages are defined by the population dynamics governing the tree community at each stage of development. For upland oaks in the Central Hardwood Region, the stages of development are associated with a characteristic range of stand ages. The stand dynamics at each stage govern the efficacy of thinning and the stand response to thinning. Thus, knowledge of a stand's stage of development is useful in understanding when, why, and how to thin.

Following a stand initiating disturbance (e.g., clearcut or stand-replacing fire) even-aged oak stands enter the stand initiation stage of development (fig. 3). New trees are added to the stand, tree crowns expand rapidly relative to their initial size, and trees compete intensely for growing space. Woody vegetation is often dense and "brushy". At this stage the growing space that is released by the death or removal of individual trees is rapidly occupied by the expanding crowns of surrounding trees. Consequently, thinning effects are short lived and highly variable. However, thinning stump sprouts is an exception. Because clumps of stump sprouts share the same growing space and the same root system, competition among them is much more intense than for seedlings or seedling sprouts with a single stem. Young sprout clumps respond with rapid growth when they are thinned to a single stem. In essence, clumps of stump sprouts begin life in the stem exclusion stage of development and stump sprout response to thinning is similar to that described below for stands in the stem exclusion stage of development.

As oak stands mature and move into the stem exclusion stage of development, the site is fully occupied and the number of trees in the stand naturally decreases as trees increase in size (fig. 4). Trees that are at a competitive disadvantage are eliminated from the stand. In the absence of a major disturbance, the number of trees per acre will decrease exponentially over time. This change can be expressed graphically as a function of age or in the format of a Gingrich-style stocking chart.

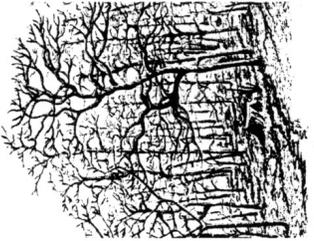
It is during the stem exclusion stage of development that managers can have the greatest impact on stand growth and yield. Thinning conducted during this stage of development can recover trees that will otherwise die and simultaneously reallocate growing space to the most desirable residual trees based on species, size, or form. Increased volume yield from thinning is the combined result of (1) utilizing trees that would otherwise die and (2) increasing the growth of selected residual trees (fig. 5). In his yield tables for thinned oak stands, Gingrich (1971a, 1971b) indicated that by thinning a stand early and often it is possible to double board foot volume yield relative to unthinned stands. The key is to

Stage of development



1. Stand initiation stage.
Typically age 0-20 years
Seedlings or saplings

Results from a stand initiating disturbance—typically timber harvest, wind or fire. Brushy mass of woody vegetation often with abundant herbaceous growth. Basal area and trees per acre are increasing.



2. Stem exclusion stage.
Typically age 10 to 70 years
Saplings to young sawtimber

Stand ceases to accumulate trees as the growing space is fully occupied. Stand develops overstory understorey and subcanopy layers. The number of trees decreases exponentially as trees become larger in size. Subcanopy is densely shaded and subcanopy vegetation is sparse. Shade tolerant trees may persist in subordinate canopy layers.



3. Understory reinitiation stage.
Typically age 50-100+ years;
Mature sawtimber

Increasing overstory tree size leads to larger canopy gaps when overstory trees die or are cut. Those gaps in combination with a rising canopy level and greater spacing among trees allows more light to reach the forest floor than during the stem exclusion stage. New trees become established. Regeneration often favors shade tolerant trees. In some ecosystems oak reproduction may persist and accumulate in the understorey by periodically dying back and resprouting.

Continue thinning.
Underplant or burn as needed to control species establishment.
Consider regeneration for stands under even-aged regimes.



4. Complex stage.
Typically age > 100 years.
Mature sawtimber or old growth. Regeneration in canopy gaps leads to uneven-aged stand.

Large canopy gaps are created by the loss of individual overstory trees. Gaps are too large to be completely filled through crown expansion of surrounding trees. New age cohorts (seedlings or advance reproduction) are established in the gaps and some new trees eventually reach the overstorey. Shade tolerant reproduction is favored in mesic ecosystems. Oak reproduction may succeed in more xeric ecosystems. Includes mature forests that are lightly thinned and mature, managed uneven-aged stands. Includes old-growth as a special case.

Regenerate or continue intermediate thinning for uneven-aged or long-rotation even-aged stands. Prescribed burning may increase species diversity or favor oak reproduction.



5. Mixed stage.
Typically age > 15 years (i.e., oldest cohorts are beyond stand initiation stage).

Results when a stand in the stem exclusion, understory reinitiation or complex stage is heavily disturbed, but not to the extent that an entirely new stand is regenerated. May be the consequence of wind, fire, insects, disease or harvest. Irregular age and tree size-class distribution. Over time the stand will move toward the complex stage of development.

Salvage, timber stand improvement, sanitation cut, release, regeneration harvest.

Typical thinning and regeneration practices to increase timber yield

Thin stump sprouts to maximize growth response. Other thinning or crop tree selection is often ineffective at this stage. Prescribed fire may favor oaks.

Begin periodic thinning for maximum growth response. Select crop trees. This is the earliest stage where stocking charts are relevant for prescriptions.

Figure 3—Stages of oak stand development with notes on thinning for increased timber production and on other management practices (based on Johnson and others 2002, illustrations by David Hamilton).

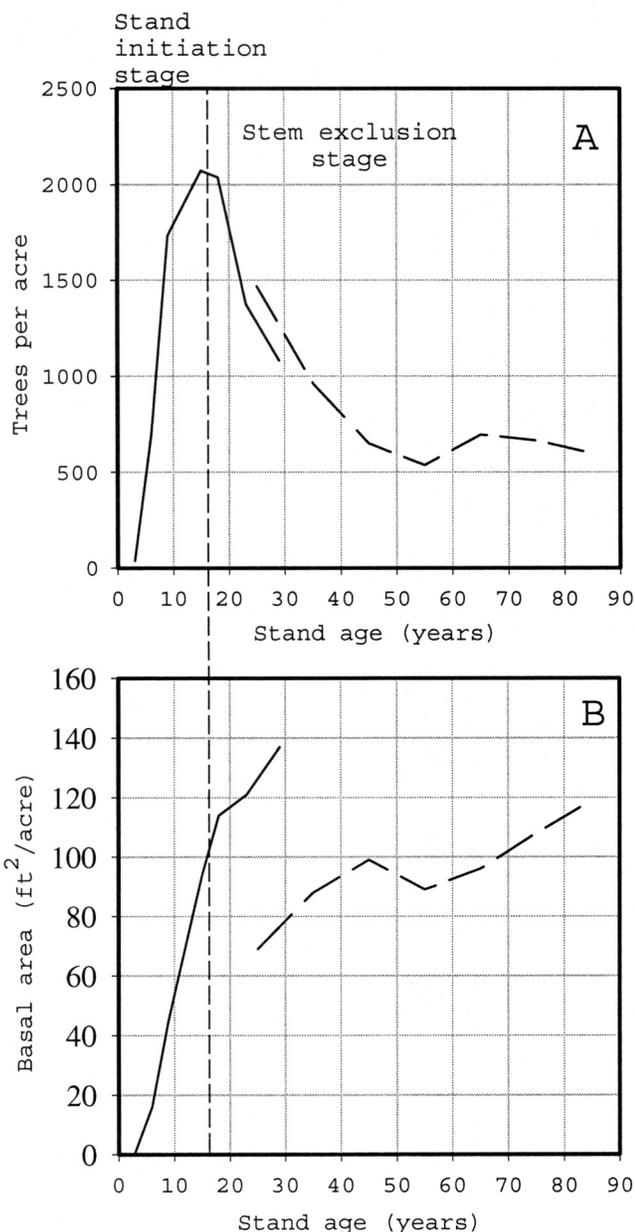


Figure 4—(A) The shift from the stand initiation stage to the stem exclusion stage of development is signaled by the change from increasing to decreasing trees per acre over time. This occurred at about age 17 in this example. (B) Basal area continues to increase. The solid line shows data for a bottomland sweetgum-red oak stand (Johnson and Krinard 1988) and the dashed line shows data for an upland oak-mixed hardwood stand in Connecticut (Ward and others 1999).

start thinning early in the stem-exclusion stage of development—approximately age 30 for eastern oak stands. The biggest net increases in total volume occur by thinning oak stands on excellent sites, but even on moderate and poor sites total yield can be doubled relative to unthinned stands.

During the understory reinitiation stage the stand is nearing economic maturity and silvicultural practices in oak stands generally concentrate on establishing desirable advance reproduction and maintaining tree quality. Thinning during

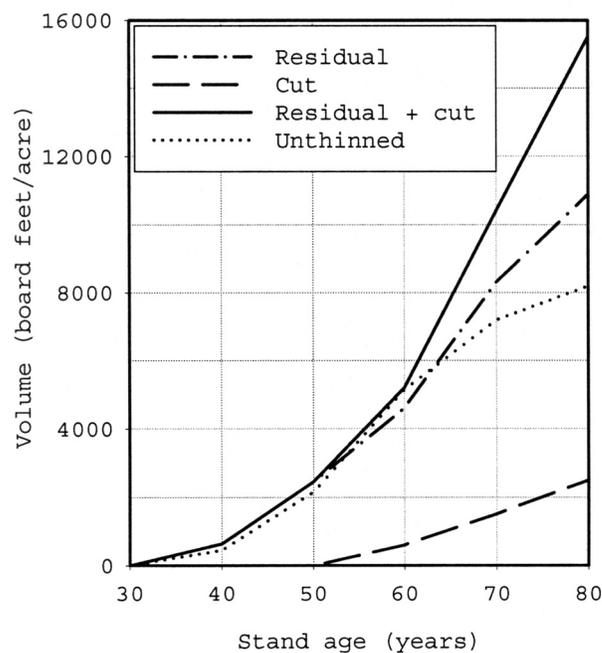


Figure 5—Yield of thinned and unthinned stands over time. With regular thinning, the combined yield of cut and residual trees can double the yield of an unmanaged stand (based on Gingrich 1971a).

this stage of development will result in faster growth of vigorous residual trees on good sites. Due to the relatively large tree crowns, removal of trees by thinning will also provide more light to the forest floor and canopy gaps will persist longer than at earlier stages of development. Economically the major concerns associated with thinning at this stage revolve around (1) minimizing epicormic branching, (2) minimizing mechanical damage of residual trees, (3) controlling future species composition, and (4) ensuring that thinning prior to overstory removal provides sufficient time (about a decade) to capture the response of residual trees. For oak stands that are to be managed on long rotations or to be converted to uneven-aged silviculture, commercial thinning through the stem exclusion stage of development will typically result in faster growth and greater total yield.

When a stand reaches the complex stage of development (fig. 3), it has become an uneven-aged stand because canopy gaps are sufficiently large to recruit new age cohorts. Thinning to promote overstory crop trees or thinning to promote the development of a balanced uneven-aged stand structure is warranted if the goal is uneven-aged management.

It is difficult to generalize about growth and yield for oak stands with mixed species and multiple age classes. Although the same basic principles apply with regard to how trees respond to stand density and crown class, the differential growth and survival rates among tree species and size classes can greatly affect the oak component of the stand. Estimating growth and yield for such stands requires the use of mathematical models. Mathematical models also facilitate exploring the outcome of alternative thinning practices on stand development. For example,

Table 1—Oak growth and yield models (excludes regeneration models)

Model type and name	Applicability	Notes
Yield Tables		
Upland oaks (Schnur 1937)	Well-stocked, even-aged, unmanaged upland oak stands; geographic range is bounded by New York, southern Michigan, Missouri, Tennessee, and western North Carolina	Comprehensive yield, composition, and size structure information by site index and age; the primary reference for upland oak yield in fully stocked, unmanaged, minimally disturbed stands; good baseline source of comparison for managed stands
Oak woodlots (Gevorkiantz and Scholz 1948)	Even-aged, mixed oak stands in western and south-central Wisconsin	Comprehensive volume yield by age and site quality; good baseline for comparison of managed stands
Managed upland central hardwoods (Gingrich 1971a, 1971b)	Central hardwood region, even-aged upland stands that are managed or where management is contemplated	Good guidance on the broad-scale effects of thinning on stand yield by age, and site index; thinning prescriptions are linked to Gingrich (1967) stocking guide and management guides by Roach and Gingrich (1962, 1968)
Stand-Level Models		
GROAK (Dale 1972, 1973)	Based on data from Ohio, Kentucky, Missouri, and Iowa; applicable to even-aged, upland mixed oaks stands	Predicts oak growth and yield as function of stand age, stand basal area, and site index; evaluates the effects of thinning on oak growth and yield; more versatile than yield tables for thinned oaks; models can be applied using spreadsheet software; also incorporated into the Northeast Decision Model (NED) (http://www.fs.fed.us/ne/burlington/ned/)
Upland oaks (Graney and Murphy 1994)	Boston Mountains region in northwest Arkansas	A recalibration and detailed evaluation of methodology used on GROAK as applied to the Boston Mountain region
Minnesota yield models (Walters and Ek 1993)	Oak-hickory forests in Minnesota	Predicts growth and yield as a function of stand age and stand basal area; based on statewide Forest Inventory and Analysis inventory data including stands with a wide variety of past disturbances; good indicator of regional “woods run” yields; part of a system of models for 14 Minnesota forest types
Appalachian hardwood multispecies model (Bowling and others 1989)	Appalachian hardwoods in the Blue Ridge ecoregion of North Carolina and Georgia	Predicts density, height, and volume for red oak, white oak, and other species groups, including d.b.h. frequency distribution by species
Individual-Tree Models		
OAKSIM (Hilt 1985a, 1985b)	Even-aged upland oak stands aged 3 to 120 years in southern Ohio and eastern Kentucky	Estimates growth and survival of individual trees with overall stand growth constrained to be consistent with Dale’s (1972) GROAK model; one of the few sources of oak height growth and taper equations (Hilt and Dale 1982); can be implemented using the NED http://www.fs.fed.us/ne/burlington/ned/
TWIGS Miner and others (1988), Bolton and Meldahl (1990a, 1990b), and Hilt and Teck (1989)	Even- and uneven-aged stands with pure or mixed species; four regional variants cover from Minnesota to Missouri to West Virginia to Maine, and Alabama, Georgia, and South Carolina	Software allows simulated thinning, volume estimation, and economic analysis; tree growth and survival models have been incorporated into FVS (see below) http://www.ncrs.fs.fed.us/pubs/Software
FVS (Forest Vegetation Simulator) http://www.fs.fed.us/fmcs/fvs/ .	Regional variants (21) are applicable to major forested regions of the United States; variants applicable with oaks include Lake States, Central States, Northeast, Southeast, South, Central Rockies, Klamath Mountains, Pacific Northwest Coast, Westside Cascades, and Westside Sierra Nevada	Good software support and excellent integration with data management, scenario evaluation, output, and display tools; nationally implemented and supported; can be user-calibrated with local inventory data; applicable to all major species groups within a region; includes models for some western oak species groups; models governing species dynamics are from a variety of sources including PROGNOSIS (Stage 1973), TWIGS (see above), and those developed specifically for FVS
GHAT Harrison and others (1986, updated 2000)	Even-aged Appalachian mixed hardwoods in Blue Ridge physiographic province of Virginia, North Carolina, Tennessee, and Georgia	Height growth, diameter growth, volume growth, and survival following thinning; designed specifically to address response to thinning in mixed species stands; includes equations for white, black, northern red, scarlet, and chestnut oaks http://www.cnr.vt.edu/g&y_coop/ghat.pdf

thinning or other cultural treatments that target particular tree species such as the oaks (favorably or adversely) can greatly alter future growth, yield, species composition and value. It often takes decades for the oak cohorts in a mixed species stand to succeed or fail, and models are the only practical tools available to address growth and yield for the infinite range of mixed stands that occur. Growth and yield models applicable to oaks and oak mixtures are summarized in table 1. Models accommodate a wide range of initial stand conditions, can evaluate alternative management regimes, produce repeatable results, and are increasingly used as a component of larger simulation and management systems. Examples include the Northeast Decision Model (NED) (<http://www.fs.fed.us/ne/burlington/ned/>), and national forest planning efforts based on the Forest Vegetation Simulator (FVS) (<http://www.fs.fed.us/fmcs/fvs/>).

ECONOMIC CONSIDERATIONS

Simulation models also facilitate economic analysis of thinning alternatives. Some models have integrated economic analysis capabilities. Predicted outcomes can also be analyzed in stand-alone economic analysis software which is widely available. Professional judgment and field experience are still required to evaluate potential effects of thinning on tree quality. In economic terms potential changes in tree grade can supercede the effects of total volume growth, and the available models have little or no capacity to predict changes in tree grade. Reported economic returns from thinning vary greatly depending upon the condition of the stand prior to thinning, growth response, and alternative rates of return (Johnson and others 2002). However, given the uniformly low alternative rates of return currently available, investment in hardwood thinning is as attractive an investment as at any time in the past several decades.

SUMMARY

Thinning has the potential to as much as double total yield over a rotation by capturing volume that would otherwise be lost to mortality. However, to maximize the effect, thinning should begin early in the stem exclusion stage of stand development and be repeated until one or two decades prior to a regeneration harvest. In addition to increasing total merchantable yield, thinning can increase tree quality and value. Tree conditions (species, crown class), stand conditions (stage of development, density, species mixture), and even landscape conditions (e.g., potential risk of disturbance by pathogens or fire) are all important considerations in thinning decisions. Perhaps most important is an understanding of the stand's stage of development. The stage of development (stand initiation, stem exclusion, understory reinitiation, complex, or mixed) provides important information on the stand's natural dynamic. Thinning is usually most effective when the silviculturist or resource manager works with, rather than against, the stand's natural dynamic (e.g., thinning to increase volume growth when the stand is in the stem exclusion stage, thinning to facilitate advance regeneration when the stand is in the understory reinitiation stage, etc.) Most effective thinning practices are designed to work in concert with the stand's natural dynamic and to accelerate change to meet ecological or economic objectives. A wide range of simulation models are available to explore alternatives for specific stand conditions.

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SUCCESS OF UNDERPLANTING NORTHERN RED OAKS

Martin A. Spetich, Daniel C. Dey, Paul S. Johnson, and David L. Graney¹

Abstract—We summarize results of the growth and survival of northern red oak (*Quercus rubra* L.) seedlings 11 years after planting in shelterwoods in the Boston Mountains of Arkansas. Shelterwood overstories were harvested 3 years after underplanting > 4,000 northern red oak seedlings. Woody vegetation that was competing with planted seedlings received two, one, or no competition control treatment(s). Results are expressed as the probability that a planted tree will live to attain a favorable competitive position at a specified year. These probabilities depend on initial seedling stem caliper before planting, site quality, weed control intensity, and shelterwood percent stocking. These probabilities of success increase with decreasing shelterwood stocking, decreasing site quality, increasing initial stem caliper, and increasing intensity of weed control. The reciprocals of the dominance probabilities provide silviculturally useful estimates of the numbers of trees that would need to be planted to obtain, on the average, one competitively successful tree in the future. Based on these results, we provide practical management methods to optimize success of underplanted northern red oak seedlings and to reach future stocking goals.

INTRODUCTION

Oaks are important to wildlife and, in turn, in forest energetics. Wildlife species that utilize oak mast include white-tailed deer (*Odocoileus virginianus*), black bear (*Ursus americanus*), turkey (*Meleagris gallopavo*), blue jays (*Cyanocitta cristata*), squirrels (*Tamiasciurus* spp., *Sciurus* spp., and others), and mice (*Peromyscus* spp.). For instance, a study by Harlow (1975) found that acorns made up an average of 76 percent of the diet of white-tailed deer during November and early December. Fluctuations in wildlife populations often follow fluctuations in oak mast production (McShea and Schwede 1993, Nixon and others 1975, Wentworth and others 1990). Major declines in the population of oaks could lead to similar declines in the populations of associated wildlife species where alternative resources are not available.

Over the last several years, oak decline has had a major impact throughout the Ozark Highlands. Mortality over large forest areas has led to the creation of shelterwood-like conditions. However, previously dense overstories have left many of these sites without oak regeneration or regeneration of sufficient size to survive competition from more shade-tolerant competitors. To address restoration of these sites, management methods are needed that can place oaks in a desirable position in relation to their interspecific competitors so that they may survive to become part of the future forest.

One option for restoring oak to these sites may be to plant oak seedlings under a shelterwood. For instance, Dey and Parker (1997) found that 99 percent of northern red oak seedlings were alive 2 years after underplanting in a shelterwood (50 percent crown cover) while only 90 percent survived in a closed-canopied undisturbed stand. Additionally, root volume, area, and dry mass were significantly greater for the shelterwood-planted seedlings. In a study comparing overstory density and understory competition, Teclaw and Isebrands (1993) found that underplanted

northern red oak performed better in shelterwoods with 25 percent crown cover than those with 50 percent crown cover. In this study we summarize the success of shelterwood-underplanted northern red oak (*Quercus rubra* L.) seedlings relative to interspecific competitors and provide management recommendations to optimize underplanting success.

The objectives of this paper are (1) to summarize the 11-year success of planting northern red oak seedlings under shelterwoods from which they were released 3 years after planting and (2) to recommend management methods to optimize successful underplanting of northern red oak based on these results.

SITES

The study sites were located in the Boston Mountains of Arkansas in the southern lobe of the Central Hardwood Region (Merritt 1980). The Boston Mountains are the highest and most southern member of the Ozark Plateau physiographic province. They form a band 30 to 40 miles wide and 200 miles long from north-central Arkansas westward into eastern Oklahoma. Elevations range from about 900 feet in the valley bottoms to 2,500 feet at the highest point. The plateau is sharply dissected; most ridges are flat to gently rolling and are generally < 0.5 mile wide. Mountainsides consist of alternating steep simple slopes and gently sloping benches.

Soils on mountaintops and slopes usually have shallow to medium depth and are represented by medium-textured members of the Hartsells, Linker, and Enders series (Typic Hapludults). They are derived from sandstone or shale residuum, and their productivity is medium to low. In contrast, soils on mountain benches are deep, well-drained members of the Nella and Leesburg series (Typic Paleudults). They developed from sandstone and shale colluvium, and their productivity is medium to high. Rocks in the area are

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alternating horizontal beds of Pennsylvanian shales and sandstones. Annual precipitation averages 46 to 48 inches; March, April, and May are the wettest months. Extended summer dry periods are common, and autumn is usually dry. The frost-free period is normally 180 to 200 days long.

METHODS

A total of 4,320 2-0 seedlings, undercut the first year in the nursery, were planted in early April 1987 at a 7.9- by 7.9-foot spacing in a split-split plot experimental design with five replicates (locations). The later loss of two main plots resulted in 4,128 seedlings being available for this study. Site index for red oaks (northern red and black oaks) ranged from 60 to 79 feet based on indirect estimation from soil and topographic factors (Graney 1977). Planted trees and competition were measured after the 1st, 3rd, 4th, 6th, 8th, and 11th growing seasons. This manuscript summarizes the 11th-year performance (8 years free of the shelterwood) of planted trees.

Designed study variables fall into two major categories: (1) those related to planting environment and (2) those related to nursery production. The former include shelterwood residual overstory density (40, 60, and 80 percent stocking) and three different competition control treatments

(no competition control, one competition control treatment, and two competition control treatments). Designed to control woody stems > 1 foot tall and ≤ 1.5 inches in diameter at breast height (d.b.h.), competition control treatments consisted of applying herbicide to cut stem surfaces. The latter designed study variables include time of lifting, shoot clipping, and four local seed sources (table 1).

In addition to the designed study variables, initial basal stem diameter (caliper) of each seedling was measured 0.8 inch above the root collar to 0.004 inch. Initial caliper averaged 0.43 inch and ranged from 0.16 to 0.89 inch. The height of the dominant woody competitor was measured on a 33.8-square-foot plot centered at every fourth planted tree location. The dominant competitor species, most abundant competitor species, and the density of all tree reproduction ≥ 11.8 inches tall also were recorded for each competition plot. More detailed methods can be found in Spetich and others (2002).

Through logistic regression, we were able to ascertain important environmental and management variables necessary to determine planted tree success. The logistic model allows us to integrate the combined effects of these variables into

Table 1—Designed study variables defined (independent variables)^a

Variable category	Independent variable name	Variable description
Planting environment	Preharvest overstory stocking—stocking after thinning from below (shelterwood creation)	Three levels: shelterwoods were thinned to 40, 60, or 80 percent stocking before planting. The overstory was removed 3 years after planting. ^b
	Competition control treatments ^c	Three levels: (1) control, ^d (2) one herbicide treatment (the winter before spring planting) plus mechanical weeding the winter before overstory removal, (3) two herbicide treatments. In both number 2 and 3 above, the first herbicide application (Tordon 101R or Roundup) was applied to cut stems the winter prior to planting. In number 3 above, the second herbicide application (Garlon-4) was applied to cut stems the winter before overstory removal. ^e
Nursery production	Shoot clipping treatments	Three levels: (1) shoots not clipped, (2) shoots clipped 8 inches above the root collar in the fall (November to December) before planting, and (3) shoots clipped 8 inches above the root collar in the spring (March) before planting.
	Time of lifting	Two levels: (1) seedlings lifted in November, and (2) seedlings lifted in March.
	Seed source	Four sources: collected from local stands distributed across the Buffalo Ranger District of the Ozark National Forest

^a The dependent variable is the success probability. The success probability is the likelihood that a planted tree will live to attain a favorable competitive position, i.e., at least 80 percent of the mean height of dominant competitors, at a specified year.

^b Overstory trees were defined as stems > 1.5 in. d.b.h. When harvests occurred, the cut surfaces of harvested trees were treated with an herbicide.

^c Competition control treatment refers to stems that were 1 foot tall or taller and ≤ 1.5 in. d.b.h.

^d Stems ≤ 1.5 in. d.b.h. not treated

^e Overstory shelterwood removal occurred during the winter of 1989–90.

a single expression. This expression not only indicates the likely success of a planted tree (where a successful tree is one that survives, plus attains and maintains at least 80 percent of the height of dominant competitors) under specific conditions, but its reciprocal is also a practical tool. Using these reciprocals, resource managers can determine the number of trees to plant to achieve a desired future stocking level of oak.

RESULTS AND DISCUSSION

Between year 6 and year 11, mortality of planted oaks increased by 21 percent. Overall, mortality was highest for oak seedlings with stems of 0.16 to 0.47 inch caliper. By year 11, the highest survival rate, 79 percent, was observed for seedlings with the largest initial caliper (0.67 to 0.87 inch). The survival rate was second highest (74 percent) for seedlings with calipers between 0.47 to 0.67 inch, and the lowest survival (67 percent) was recorded for seedlings in the 0.16- to 0.47-inch class.

We examined the field performance of individual planted trees and their competitors because competitive position in relation to surrounding vegetation is an important determinant of seedling survival. Rating of the most significant competitor results in a competition-centered approach to tree planting. More than 50 percent of the competition plots had dominant competitors represented by four species; sassafras (*Sassafras albidum* Nutt.), blackgum (*Nyssa sylvatica* Marsh.), red maple (*Acer rubrum* L.), and black cherry (*Prunus serotina* Ehrh.) were found in 16.6, 15.3,

12.5, and 10.8 percent of the plots, respectively. The four most abundant competitors were flowering dogwood (*Cornus florida* L.), blackgum, sassafras, and red maple, representing 23.2, 19.7, 12.7, and 10.7 percent of competitors, respectively (table 2). We further evaluated competitive success and variables important to that success using logistic regression.

Spetich and others (2002) found that planted tree success at year 11 increased with initial seedling stem caliper, decreasing site index, lower shelterwood stocking levels, increased woody vegetation competition control, and shoot clipping. Variables that increased success probabilities the most were percent shelterwood stocking, woody vegetation competition control, and initial caliper of seedlings. In figure 1A we show the relationship of initial caliper, site index, and success probability for two woody competition control treatments (based on models by Spetich and others 2002). Figure 1B illustrates decreased probability of seedling success when no woody competition control is applied. Figure 2 illustrates the relationship of percent shelterwood stocking and initial caliper, where larger caliper and lower stocking results in a higher probability of seedling success.

The reciprocals of success probabilities provide silviculturally useful estimates of the number of trees that would need to be planted to yield, on the average, one competitively successful tree in year 11. In table 3 we present these reciprocals as a practical tool to help managers make underplanting decisions.

Table 2—Percent of competition plots^a in which a given species occurred as the dominant competitor or most abundant competitor in 1997 (8 years after shelterwood overstory removal)

Species	Dominant competitor				Abundant competitor			
	Density ^b (%)			Total	Density ^b (%)			Total
	40	60	80		40	60	80	
----- percent -----								
Sassafras (<i>Sassafras albidum</i> Nutt.)	6.0	3.8	6.7	16.6	8.6	5.9	8.7	12.7
Blackgum (<i>Nyssa sylvatica</i> Marsh.)	3.8	5.6	5.8	15.3	3.9	7.5	8.3	19.7
Red maple (<i>Acer rubrum</i> L.)	3.9	4.9	3.7	12.5	4.8	3.0	4.9	10.7
Black cherry (<i>Prunus serotina</i> Ehrh.)	3.5	3.7	3.6	10.8	4.3	3.6	2.8	4.4
Flowering dogwood (<i>Cornus florida</i> L.)	2.4	2.1	3.2	7.8	1.9	2.2	1.2	23.2
Carolina buckthorn (<i>Rhamnus caroliniana</i> Walt.)	2.9	1.0	2.6	6.5	1.7	1.5	1.3	3.1
Oaks ^c (<i>Quercus</i> spp.)	2.6	2.3	1.2	6.1	1.9	0.7	0.9	5.4
Hickories (<i>Carya</i> spp.)	2.5	1.0	1.2	4.7	1.7	0.8	1.0	3.4
Eastern hophornbeam (<i>Ostrya virginiana</i> Mill.)	0.7	2.8	0.2	3.7	1.6	0.6	1.0	2.8
Sumac (<i>Rhus</i> spp.)	1.9	0.4	0.6	2.8	0.8	1.9	0.1	3.4
Sugar maple (<i>Acer saccharum</i> Marsh.)	0.4	0.6	1.3	2.2	0.3	0.6	1.3	2.1
Paw paw (<i>Asimina triloba</i> (L.) Dun.)	1.3	0.8	0.0	2.0	1.1	1.1	0.0	2.1
White ash (<i>Fraxinus Americana</i> L.)	0.3	1.0	0.7	1.9	0.4	1.3	0.4	2.0
Witch hazel (<i>Hamamelis virginiana</i> L.)	0.3	0.6	0.4	1.3	0.3	0.9	0.4	1.6
Other ^d	2.0	2.1	1.6	5.7	1.6	1.2	0.7	3.4

^a Based on 1,027 plots, 33.8-ft² in size where woody competitors occurred.

^b Represents percent stocking in the shelterwood phase.

^c Includes white oak, northern red oak, and black oaks.

^d Species that represent < 1.0 percent of the total and include American elm, American beech, black locust, serviceberry, wild plum, redbud, hackberry, mulberry, cucumber tree, Ozark chinkapin, black walnut, umbrella magnolia, eastern redcedar, and devils walkingstick.

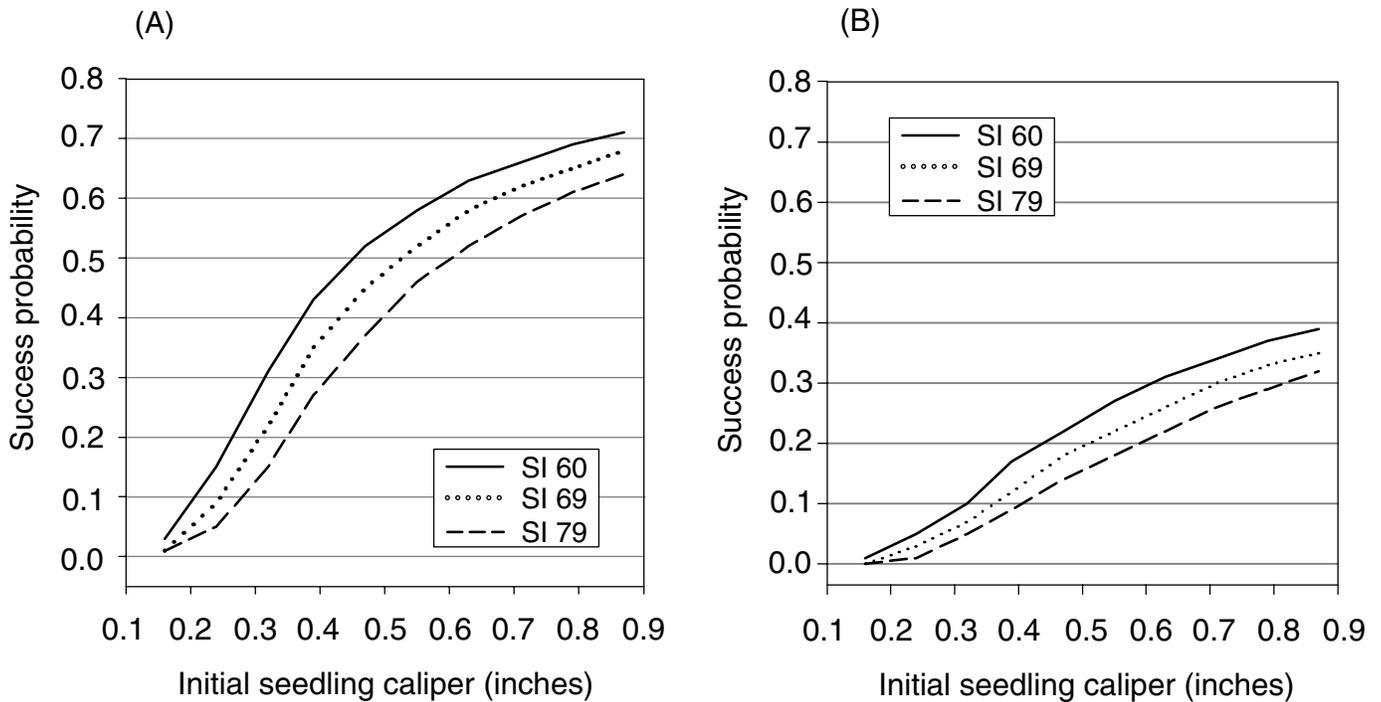


Figure 1—Success probability by initial seedling caliper and site index (SI) for top-clipped trees planted under shelterwoods with 40 to 60 percent stocking. (A) Two competition control treatments. (B) No competition control (based on Spetich and others 2002).

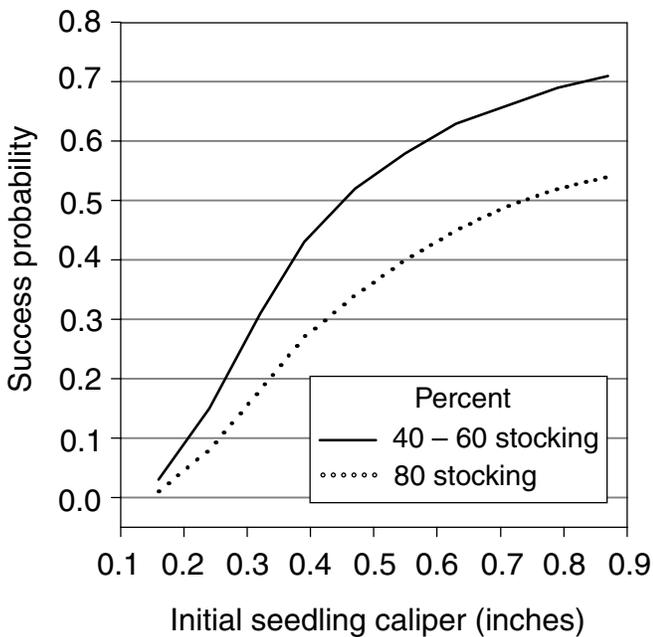


Figure 2—Success probability by initial seedling caliper and percent shelterwood stocking (based on Spetich and others 2002).

This study was not installed under oak decline conditions, so the recommendations below are best applied to healthy stands. However, reductions in stocking levels in stands affected by oak decline can approximate reductions in stocking imposed by a harvest. Following the recommendations below could result in similar oak underplanting success in these stands also.

RECOMMENDATIONS

To take maximum advantage of investments in site preparation, oaks could be planted at densities within treated areas that assure those areas are fully occupied at maturity, where “fully occupied” is the desired oak stocking at maturity necessary to meet management goals. Estimated dominance probabilities can facilitate decisions on an appropriate planting density. A reasonable goal might be at least 100 competitively successful trees per acre at stand age 11. This density would allow for some losses to mortality and suppression beyond 11 years, yet provide reasonable assurance that the oaks, by themselves, would ultimately occupy most of the growing space within treated areas. Using this method, the high per acre planting and site preparation costs associated with the planted area could be spread across the entire stand. For example, limiting planting to 20 percent of stand area would effectively reduce costs of \$400 per acre actually planted (nursery stock plus planting plus site preparation costs) to \$80 per acre prorated across the entire stand. Where possible, the unplanted portion of the stand (80 percent) could be regenerated naturally. Regeneration would be deemed successful if the

Table 3—Number of trees to plant in order to obtain one successful tree in year 11^a

Caliper ^e inches	Woody competition control ^b					
	None		Once ^c		Twice	
	Density ^d (percent)					
	40 – 60	80	40 – 60	80	40 – 60	80
Site index 60 feet						
0.16	126.0	259.8	67.7	139.1	33.9	69.1
0.24	21.9	44.3	12.2	24.1	6.5	12.4
0.32	9.6	18.7	5.6	10.4	3.3	5.7
0.39	6.0	11.4	3.7	6.5	2.3	3.7
0.47	4.5	8.2	2.9	4.9	1.9	2.9
0.55	3.7	6.6	2.4	4.0	1.7	2.5
0.63	3.2	5.6	2.2	3.5	1.6	2.2
0.71	2.9	5.0	2.0	3.1	1.5	2.1
0.79	2.7	4.5	1.9	2.9	1.5	1.9
0.87	2.6	4.2	1.8	2.7	1.4	1.8
Site index 69 feet						
0.16	306.5	633.7	164.0	338.6	81.4	167.5
0.24	38.9	79.6	21.2	42.9	11.0	21.7
0.32	14.4	28.7	8.1	15.8	4.5	8.3
0.39	8.2	15.8	4.8	8.9	2.9	4.9
0.47	5.7	10.8	3.5	6.2	2.2	3.6
0.55	4.5	8.2	2.9	4.9	1.9	2.9
0.63	3.8	6.8	2.5	4.1	1.7	2.5
0.71	3.4	5.9	2.3	3.6	1.6	2.3
0.79	3.0	5.2	2.1	3.3	1.5	2.1
0.87	2.8	4.8	2.0	3.0	1.5	2.0
Site index 79 feet						
0.16	748.0	1,547.9	399.6	826.5	197.6	408.1
0.24	69.9	143.6	37.7	77.1	19.1	38.5
0.32	21.9	44.3	12.2	24.1	6.5	12.4
0.39	11.2	22.2	6.5	12.3	3.7	6.6
0.47	7.3	14.1	4.4	8.0	2.7	4.5
0.55	5.5	10.4	3.4	6.0	2.2	3.5
0.63	4.5	8.2	2.9	4.9	1.9	2.9
0.71	3.9	6.9	2.5	4.2	1.8	2.6
0.79	3.4	6.1	2.3	3.7	1.6	2.3
0.87	3.1	5.4	2.1	3.4	1.6	2.2

^a (Eight years after shelterwood overstory removal): calculated by dividing 1 by the success probability. To determine the number of trees per acre to plant, multiply the number of trees per acre that you would like to have at year 11 (11 years after planting) by a number below. To locate this number use the one where your specific site index, competition control plans, and overstory density intersect with the caliper of trees you wish to plant.

^b In all three cases of none, competition control once and competition control twice: stems > 1.5 inches d.b.h. were cut with the overstory and treated with herbicide.

^c Includes a mechanical weeding before shelterwood removal.

^d Represents percent stocking in the shelterwood phase.

^e This is the initial basal stem diameter of seedlings measured 0.8 inches above the root collar.

Source: Spetich and others 2002.

combined planted and natural reproduction produces an adequate standwide representation of oak and other acceptable growing stock. Adequacy and acceptable growing stock would be defined by the management goals; e.g., wildlife hard mast needs, species diversity, forest restoration, maintenance of this keystone species, or any reasonable management objective. Specific steps to follow to optimize planted seedling success include:

1. Select upland sites within the site index range of 60 to 79 feet for red oaks.
2. Create a shelterwood by reducing overstory density to 40 to 60 percent stocking by thinning from below; i.e., concentrating removals on subcanopy trees down to 1.5 inches d.b.h. Treat the cut surface of cut stems of competitors with an effective herbicide.
3. Before planting, cut all competing woody plants 1 foot or taller and 1.5 inches or less d.b.h., then apply an effective herbicide to the cut surface.
4. Plant 2-year-old undercut seedlings with clipped tops that average at least 0.5 inch in caliper measured 0.8 inch above the root collar (seedlings should be grown from a local seed source).
5. Apply a second competition control treatment (herbicide) before shelterwood removal.
6. Remove the shelterwood three growing seasons after planting. Treat the cut surface of cut stems of competitors with an effective herbicide.

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This publication reports research involving herbicides. It does not contain recommendations for their use, nor does it imply that the uses discussed here have been registered. All uses of herbicides must be registered by appropriate State and/or Federal Agencies before they can be recommended.

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WOOD PRODUCTS BY SPECIES AND QUALITY IN UPLAND FORESTS

David W. Patterson¹

Abstract—Products that can be produced from an upland forest depend on the species and quality of the trees present. Quality depends on growth rate and tree form. These variables are discussed as well as the products that can be produced such as veneer and plywood, grade lumber, handle stock, pallet stock, cross ties, and industrial lumber.

INTRODUCTION

The wood products that can be produced from trees of the upland forest of Arkansas are discussed in this paper. These products depend on several factors such as species and quality. Therefore, the different types of wood that are present will be discussed as well as how growth rate affects the quality of each type. Also discussed will be how tree form affects wood quality. Finally, the different types of products will be presented.

WOOD TYPES

The upland forest is mainly a hardwood forest. Hardwoods can be classified into two types: ring-porous and diffuse-porous. Ring-porous woods include species such as the oaks, hickories, and ashes. These species are the most desirable in the forest. The diffuse-porous woods include red maple and blackgum. Diffuse-porous woods are usually less desirable and used in products of lesser value. Some of these woods are referred to as soft hardwoods and are used in place of southern pine in some products. There are some softwoods such as shortleaf pine on some south facing slopes and eastern red cedar present in the upland forests.

EFFECTS OF GROWTH RATE

The effect of growth rate on the quality of wood depends on the type of wood under consideration. With ring-porous woods, the quality improves as the growth rate increases. This is because of the structure of the growth rings. In ring-porous hardwoods, three to five rows (depending on species) of large pores or vessels are laid down at the beginning of the growing season and the remainder of the ring is made up of fibers and small vessels. No matter what the size of the growth ring is, the tree will always lay down the same number of rows of large vessels. Any extra growth or lack of growth will appear in the amount of fibers produced. Therefore, the faster the growth is, the stronger and the more appealing to the eye the wood is.

Back when the chip mills were operating in the Northwest part of the state, I was contacted by one mill manager to check the quality of their chips because the Japanese customers were refusing to pay the agreed upon price. The wood samples I examined had very small growth rings made up of mainly earlywood vessels and very few fibers. I told the manager that I could see why the Japanese were

saying that they were realizing twenty-five percent less pulp per ton of chips as compared to chips procured from east of the Mississippi. It is interesting to note that there were several groups that insisted that those trees should not be cut but allowed to grow larger. Once larger, they would provide high quality hardwood lumber. Sorry, but with the growing conditions that those trees were experiencing, they would never produce anything but very low quality wood.

With diffuse-porous hardwoods, the vessels are much smaller and located throughout the growth ring. Because of this, there is no correlation between growth rate and wood properties or quality for diffuse-porous woods. The wood is basically the same whether fast grown or slow grown.

Softwoods such as eastern red cedar, hemlock, spruce, fir, etc., show the same relationship as diffuse-porous hardwoods. Softwoods with abrupt latewood such as southern pine and Douglas-fir appear to have lower quality wood with an increase in growth rate. Some researchers believe that this is the effect of age, not growth rate.

EFFECTS OF TREE FORM

Besides the growth rate, a tree's form greatly affects the quantity and quality of the products that can be produced. It is desirable that each tree be straight. When the bole deviates from straight, solid wood products will have cross grain, which will result in warping and splitting when dried. The more severe the sweep (curve in the bole), the shorter the logs have to be cut to minimize the effects of cross grain. Trees with crook will have portions bucked out and left in the forest.

Leaning trees are most undesirable. All trees want to be upright. If hardwood trees are leaning, they will produce tension wood on the upper side of the bole, which will force the bole into an upright position. Tension wood is bad from the start. It causes problems with machining, drying, finishing, and pulping. The chemical composition and cell structure of tension wood is different from normal wood.

The best trees have circular cross sections with the pith in the center. When a tree has a tear drop or oval cross section, the pith is located toward the smaller side and the quality of the solid wood products it produces is lower. There are two main reasons for non-circular cross sections. First, tension wood will cause the tree to produce a wide

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growth ring on the upper side and a very narrow ring on the lower side. The undesirability of tension wood has already been mentioned. Second, when there is competition on two or three sides of the tree, the crown will grow toward the sunlight and the bole will grow more on that side.

Limbs result in knots in solid wood products manufactured from the tree. Knots are the single most important quality-limiting defect and they grow from the pith outward. The best quality trees self-prune early and quickly produce a clear surface for most of the bole's length. A downside with hardwoods is that in many species, if the sunlight reaches the bole, new limbs (epicormic branching) will form at the cambium. It is sad to see a prime grade tree suddenly sprouting new branches on its lower bole and thereby, substantially lowering the grade. Therefore, one must be careful not to cause epicormic branching when thinning a hardwood stand to increase growth rate.

The hardwood tree grades for factory grade lumber are an example of how tree form affects the quality. The first limiting factor is size: grade 1 trees must be at least 16 inches in diameter at breast height (d.b.h.), grade 2 trees must be 13 inches in d.b.h., and grade 3 trees must be 10 inches in d.b.h. The second limiting factor is the amount of clear material in the third best face. Defects such as limbs, bird pecks, whorls, bulges, cracks, etc. limit the clear spaces. The next limiting factor is the amount of sweep: nine percent for grade 1, 15 percent for grade 2, and 50 percent for grade 3 trees.

WOOD PRODUCTS

The most valuable product from the hardwood forest is veneer. Most hardwood veneers are sliced and not peeled. Grain orientation is critical to achieve the desired visual effect. The logs are sawn to produce flitches that have the desired grain orientation on their face. The flitch is attached to a veneer slicer that slices veneers with the same grain pattern. One can see that in order to obtain the desired veneer, the process must start with logs that are large, straight, circular in cross section, and clear of knots and other defects. Veneers from highly valued species are used in the production of decorative hardwood plywood, furniture, cabinets, paneling, etc. Veneers from lower valued species such as red maple, blackgum, sweetgum, and yellow-poplar are used for inner plies and back plies for products where only the face shows.

Some of the soft hardwoods are peeled and used with softwoods to make structural plywood. I have visited some plywood plants in North Carolina where red maple, sweetgum and yellow-poplar are used with southern pine to make plywood. Since defects and/or patches are permitted, the best quality logs are not required.

The most common use for quality logs is factory grade lumber. Since you do not need perfect logs to make solid wood parts, the price of factory grade logs is lower than for veneer grade logs. Many of the big sawmills do pay according to the log grade and not just by volume or weight. The price of the resulting lumber varies greatly by grade as well. The difference between the price of FAS (top grade) and No. 3 common (lowest grade) lumber could be a factor of

seven or eight for red oak and other valued species. Grade lumber can be used to make furniture, cabinets, paneling, flooring, mouldings, and architectural woodwork. It is easy to sell the high grade lumber but somewhat difficult to sell the low-grade lumber. All logs, regardless of grade, have some low-grade lumber in them.

Quality hickory and ash logs can be used to produce handle stock. Hickory is used for handles of striking tools such as hammers, picks, and axes while ash is used for long handles such as hoes, shovels, and rakes. Again, the faster the growth rate, the better the handles are from these species.

The number one user of hardwood lumber in the United States is the pallet industry. Approximately five billion board feet of hardwood lumber or almost 40 percent of the total hardwood production are used annually in the production of pallets. Here strength and stiffness are the deciding factors and not appearance. Sagging deck boards cause problems when inserting the forks of a forklift through the pallet.

Cross ties are another market for lower grade logs. These logs must be big enough so that there is no wane or other defects in the bearing plate area. The logs need to be straight so that the resulting ties will remain straight after drying.

Industrial lumber includes board road, sewer boards and dunnage. Board road is a 3-layer, reversing herringbone roadway for heavy equipment going in and out at an oil-drilling site. It minimizes the land disturbance. The law requires that any ditch over four feet deep must be bulk-headed before anyone can work in the ditch. Sewer boards are used for that purpose. Dunnage is used to insure that a cargo item does not shift or move while being transported by rail or ship.

In other parts of the country, soft hardwoods are used to make oriented strand board (OSB). The original OSB mills were in the Lake States using aspen. If the red oak borer does kill most of the oaks in the forest, red maple and other soft hardwoods may become the dominate species. But, OSB plants cost a lot of money.

The hardwood forest can also be used as a source of raw material for the pulp and paper industry. But even the pulp and paper industry requires a certain level of quality in its wood resource. Hardwood pulp is generally used to make high end paper such as coated and glossy paper used in magazines while softwood pulp is generally used for newsprint and paper bags.

Fuel is the number one use of wood in the world. Home fireplaces and stoves along with industrial energy uses can remove a lot of low-grade trees from the forest. Transportation costs may be the limiting factor in Arkansas.

The sale of products (wood, water, wildlife, etc.) offset the costs of forestry operations in the upland forest. This paper has discussed how the growth of the trees affects the quality and types of wood products that can be produced from the upland forests. This information should aid the forester in making management decisions on upland forests.

Oak Decline

OAK DECLINE AND RED OAK BORER IN THE INTERIOR HIGHLANDS OF ARKANSAS AND MISSOURI: NATURAL PHENOMENA, SEVERE OCCURRENCES

Dale A. Starkey, Forrest Oliveria, Alexander Mangini, and Manfred Mielke¹

Abstract—Oak decline is a complex disease resulting in dieback and mortality of oaks. A number of factors are involved and can be classified as predisposing, inciting, or contributing, according to their roles. Decline events have been noted repeatedly during the past century in the eastern U.S. A severe episode of oak decline is occurring in the Interior Highlands region of Arkansas and Missouri. It includes an unprecedented epidemic of red oak borer (*Enaphalodes rufulus* Haldeman). Mortality and dieback of northern red, (*Quercus rubra* L.), black, (*Q. velutina* Lam.), scarlet (*Q. coccinea* Muenchh.) and southern red (*Q. falcata* Michx.) oaks on thousands of acres of Interior Highland forest became evident in 1999 following 2 years of severe regional drought. A third year of drought in 2000 greatly exacerbated the problem and mortality and dieback have continued through 2002. Aerial sketch-map surveys of portions of the Ozark National Forest in Arkansas estimated that up to 300,000 acres are severely affected. Data from ground evaluations during 1999-2000 on the Ozark and Mark Twain National Forests (Missouri) showed an average of 15-28 percent of red oak basal area per acre is dead in affected stands. An additional 2-14 percent had severe dieback. Data from 2000 and 2002 plot re-measurements on the Ozark National Forest showed that mortality and dieback continued, especially in red oaks where an additional 16-20 percent of basal area per acre died over three years. However, many stands with high basal areas of red oaks have experienced nearly 100 percent mortality. Red oak borer attacks were noted only on red oak species. Greater than 10 old and new red oak borer attacks on the lower bole were noted on over 18 and 23 percent, respectively, of red oak basal area per acre in damaged stands on the Ozark National Forest in 1999. On the Mark Twain National Forest in 2000, 54 percent of the red oak basal area per acre had greater than 10 attacks.

INTRODUCTION

Oak decline is a complex disease with no single cause (Manion 1981, Wargo and others 1983). It is characterized primarily by progressive branch dieback and mortality of oaks growing in the overstory. Dieback and mortality are generally slow and can occur over several years. However, sudden mortality and rapid dieback can occur as well. A number of interacting factors contribute to decline—stand, site, abiotic and biotic factors (fig. 1). Oak decline is best conceptualized, according to Manion (1991), by categorizing factors into predisposing, inciting and contributing

groups (fig. 2). Stands are predisposed to decline by such factors as relatively advanced physiologic age (Hyink and Zedaker 1987, Oak and others 1996), shallow, rocky soils, ridgetop and upper slope locations, dense oak stocking, and previous climate (e.g., severe regional droughts during the 1950's, 1980's (Tainter and others 1990)). Decline is incited by factors such as short-term, acute drought or insect defoliation. Secondary insects and pathogens are contributing factors that further stress trees and ultimately lead to mortality. Some contributing factors are: armillaria root rot (*Armillaria* [Fr.:Fr.] spp.), two-lined chestnut borer (*Agilus*

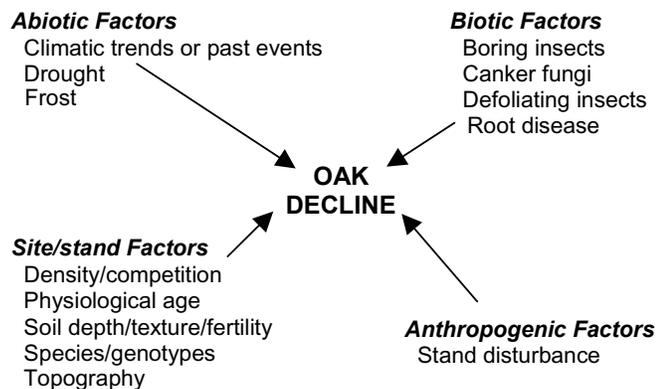


Figure 1—Causal factors of oak decline organized by type.

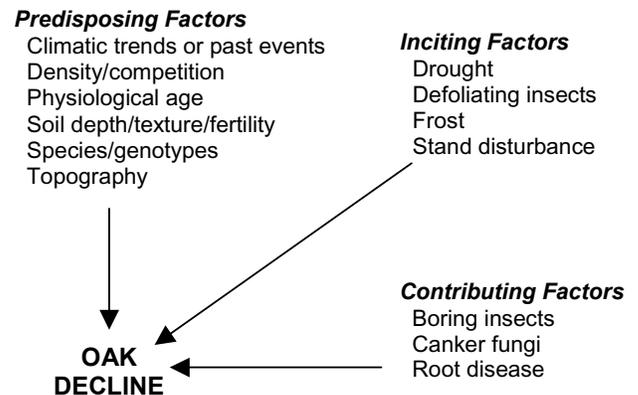


Figure 2—Causal factors of oak decline organized by their function in the decline syndrome.

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bilineatus Weber), red oak borer (ROB, *Enaphalodes rufulus* Haldeman) and hypoxylon canker (*Hypoxylon atropunctatum* [Schwein.:Fr.] Cooke). Species in the red oak group (northern red oak, *Quercus rubra* L.; black oak, *Q. velutina* Lam.; scarlet oak, *Q. coccinea* Muenchh.; and southern red oak, *Q. falcata* Michx.) are affected more quickly and severely than those in the white oak group (white oak, *Q. alba* L.; post oak, *Q. stellata* Wangenh.; chestnut oak, *Q. prinus* L.; Starkey and others 1989). Other species are affected as well, to varying degrees, but generally much less severely than oaks.

Oak decline or similar events have been described in most eastern states since the mid-1800's (Ammon and others 1989, Hopkins 1902, Millers and others 1988). Events have been documented in the Ozark Highlands of Arkansas and Missouri in the early and mid-1980's (Bassett and others 1982, Lewis 1981, Mistretta and others 1981, Rhodes and Tainter 1980, Starkey and others 1989, Yeiser and Burnett 1982). The Highlands area has an abundance of older oak-hickory forest types on sites of low to moderate productivity that are susceptible to decline. Stands with these characteristics seem particularly prevalent on national forests. In 1999, mortality and dieback of red oaks became abundant on the Ozark and Ouachita National Forests in Arkansas, and the Mark Twain National Forest in Missouri. Decline and mortality were accompanied by unusually heavy attacks by the ROB.

ROB's have generally been considered to cause degrade in red oaks due to the galleries they excavate in the wood (Donley and Acciavatti 1980, Solomon 1995) rather than causing tree mortality. They have a two-year life cycle with adult emergence mostly synchronous in odd-numbered years. Emergence peaks in mid-summer and adults lay eggs on red oak bark, particularly under lichens. After the eggs hatch, young larvae bore through the bark and begin to feed in the inner bark and eventually excavate a small

area, killing the cambium layer in an area usually not exceeding about 4 square inches. During the second season, larvae begin to bore into the wood of the tree and turn upward until the larvae reach mature size (about 0.5 inches in diameter). Frass and sawdust are ejected from the galleries as they are excavated and continually enlarged to accommodate the growing larvae. Borers pupate within the gallery and adults exit the same entrance hole they created, leaving an oval emergence hole. Casual tree examinations and dissections on the Ozark National Forest have documented high borer populations and adult emergence in 1999 and 2001. Most foresters, entomologists and pest management specialists who have viewed the problem indicate they have never before seen an outbreak of such magnitude. Preliminary, detailed tree dissections have documented hundreds of old and new attacks on individual red oaks (Personal communication. Dr. Fred Stephen. 2001. Professor, University of Arkansas, 317 Agriculture Bldg., Fayetteville, AR 72701), whereas the highest previously published rates are about 71 attacks per tree (Hay 1974).

Aerial sketch-map surveys were conducted to estimate the extent and severity of the problem, and to guide field survey work. Ground evaluations were conducted in Arkansas (Starkey and others 2000) and Missouri (Mielke and others 2000) to determine the extent, severity and cause of the recent dieback/mortality and to document its association with ROB attacks. Revisits to surveyed stands on the Ozark National Forest were made in 2000 and 2002 in order to monitor progress of the decline event.

METHODS/ACTIVITIES

An evaluation was conducted in late summer, 1999 on the Pleasant Hill Ranger District of the Ozark National Forest north of Clarksville, Arkansas (Starkey and others 2000). Ranger District personnel conducted an aerial sketch-map survey and delineated large areas of forest that fell into 3 strata of damage: severe (hardwood stands within the gross

Table 1—Data collected on trees in sample stands, Ozark and Mark Twain National Forests, 1999–2002

Variable	Description
Species	Appropriate species code
D.b.h.	Diameter at breast height to the nearest 0.1 inches
Crown class	4 = dominant, 3 = codominant, 2 = intermediate, 1 = suppressed
Crown condition	0 = healthy, normal crown 1 = slight dieback: <1/3 of crown 2 = moderate dieback: 1/3-2/3 of crown 3 = severe dieback: >2/3 of crown 4 = dead, died this year: fine twigs present, brown leaves may be present, little or no bark sloughing 5 = dead, died 2–4 years ago: no fine twigs present, bark sloughing, sapwood rot obvious 6 = dead, died 4 or more year ago: stubby branches, extensive bark sloughing, extensive sapwood rot
ROB-OLD	Red oak borer attacks from previous years; number of old attacks on the lower 8 feet of bole: 0 = none, 1 = 1–10, 2 = 11–20, 3 = 21–30, etc.
ROB-NEW	Red oak borer attacks from current year; number of new attacks on the lower 8 feet of bole: 0 = none, 1 = 1–10, 2 = 11–20, 3 = 21–30, etc.

ROB = red oak borer.

forest area with a visual estimate of 75+ percent of crown cover affected [mortality, dieback or dead foliage], moderate (50-75 percent of crown cover affected) and slight (<50 percent crown cover affected). Six sawtimber-sized oak-hickory stands with reasonably good road access were selected at random in each of the damage strata for ground survey. Sample stands were surveyed using 5 basal-area-factor 10 prism plots arrayed on a transect through the main part of the stand at a minimum spacing of 150-200 feet. For sample trees >4 inches in diameter at breast height (d.b.h.), data included species, d.b.h., crown class, crown condition, number of old ROB attacks and number of new ROB attacks (table 1). In each stand, plot 1 was marked and a GPS (global positioning system) reading taken. These plots were relocated and re-measured in 2000 and 2002 to monitor the long-term progress of decline/mortality.

A similar ground survey was done on the Potosi and Salem Ranger Districts of the Mark Twain National Forest in Missouri in 2000 (Mielke 2000). Five affected stands were sampled on the Potosi Ranger District and 6 on the Salem. Stands were sampled in the manner described above except that old and new ROB attacks were not differentiated.

A more extensive aerial sketchmapping survey was performed in 2001 over the entire main division of the Ozark National Forest (Boston Mountain, Pleasant Hill, Bayou, and Buffalo Ranger Districts) by Forest personnel. Areas with light, moderate, and severe activity were delineated as in 1999.

RESULTS

Aerial sketchmapping of the Pleasant Hill Ranger District in 1999 delineated approximately 19,000 acres (16 percent) as severely affected, 24,000 (20 percent) as moderately

affected and 75,000 acres (64 percent) as slightly affected. Ground sampling of the 54 plots yielded a sample tree population of 864 trees. Red oaks comprised 46 percent of the basal area, white oaks 28 percent, and other species 26 percent. Ground sampling confirmed the relative damage classification during aerial sketchmapping. Mortality and dieback of all species were most prevalent in the severe stratum where 24 percent of the basal area per acre had moderate to severe dieback or was dead (fig. 3). Damage was less in the moderate (12 percent) and light (8 percent) strata. Comparing species groups, red oaks were more severely affected across all strata than white oaks or other species—22 percent of basal area per acre with moderate to severe dieback or dead compared to 8 and 7 percent, respectively (fig. 4). Red oaks in the severe stratum had the most damage—35 percent of basal area per acre with moderate to severe dieback or dead and less in the moderate (19 percent) and light (9 percent) strata (fig. 5).

Enumeration and characterization of ROB attack sites on the lower 8 feet of bole represent just a rough (and probably very conservative) estimate of infestation levels since they are difficult to tally accurately and quickly. Nonetheless, they provide a useful picture of the relative extent and nature of borer attacks. ROB attacks (both old and new) were noted only on red oak species—54 percent of basal area per acre had 1 or more old attacks and 45 percent had 1 or more new attacks (fig. 6). Both old and new ROB attacks on red oaks were most prevalent in the severe stratum, followed by the moderate and slight strata (figs. 7 and 8). Old ROB attacks on red oaks were most prevalent on dead trees (fig. 9). New ROB attacks, however, were most prevalent on moderate/severe red oaks followed by dead, then healthy/slight red oaks (fig. 10).

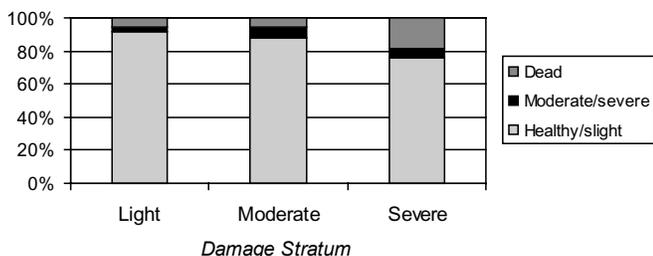


Figure 3—Percentage of basal area per acre by stratum and crown condition, Ozark National Forest, 1999.

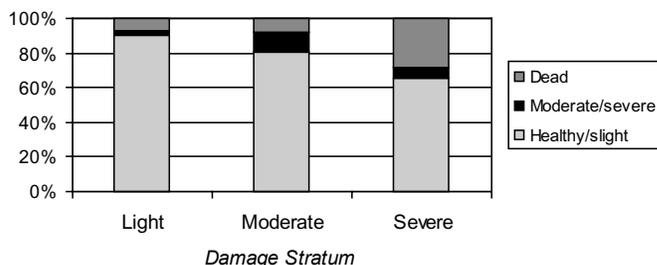


Figure 5—Percentage of basal area per acre of red oaks by stratum and crown condition, Ozark National Forest, 1999.

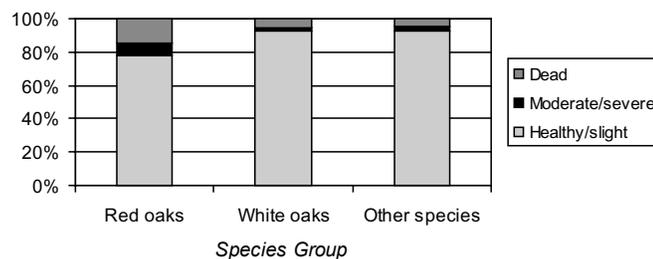


Figure 4—Percentage of basal area per acre by species group and crown condition, Ozark National Forest, 1999.

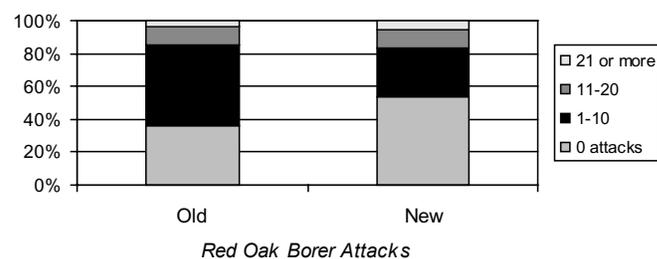


Figure 6—Percentage of red oak basal area per acre with old and new red oak borer attacks, Ozark National Forest, 1999.

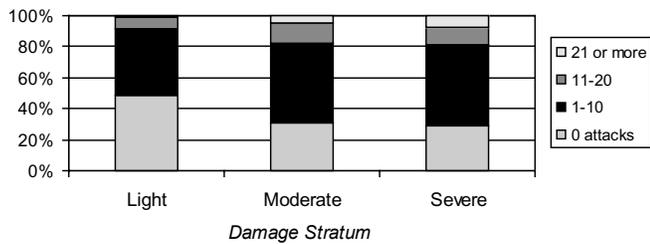


Figure 7—Percentage of red oak basal area per acre with old red oak borer attacks by stratum, Ozark National Forest, 1999.

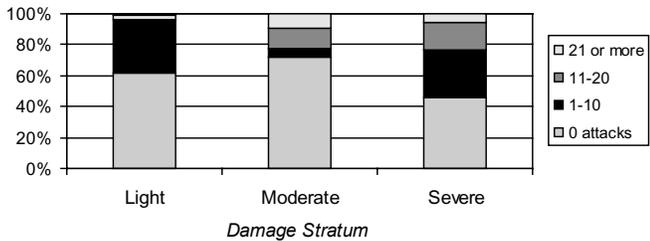


Figure 8—Percentage of red oak basal area per acre with new red oak borer attacks by stratum, Ozark National Forest, 1999.

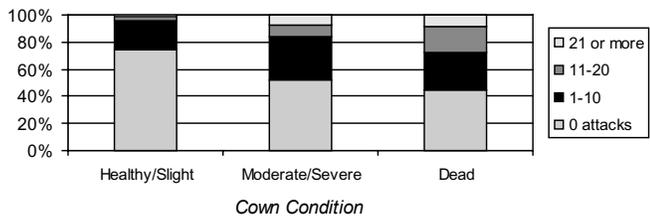


Figure 9—Percentage of red oak basal area per acre with old red oak borer attacks by crown condition, Ozark National Forest, 1999.

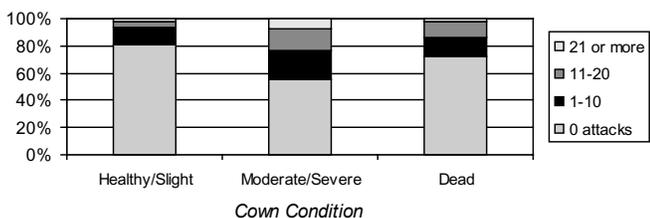


Figure 10—Percentage of red oak basal area per acre with new red oak borer attacks by crown condition, Ozark National Forest, 1999.

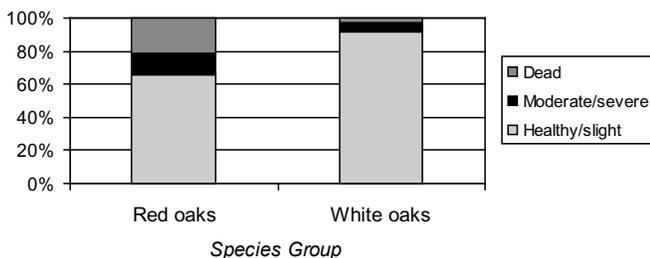


Figure 11—Percentage of basal area per acre by species group and crown condition for the Mark Twain National Forest.

Sampling on the Mark Twain National Forest in 2000 produced similar results with about 20 percent of scarlet and black oak basal area per acre dead, and 11 percent with moderate to severe decline (fig. 11). As on the Ozark National Forest, white oaks were much less affected. In addition, ROB attacks were present on most red oaks—almost 45 percent of basal area per acre had over 10 attacks (fig. 12).

Data from the re-measured plots on the Ozark National Forest showed that dieback and mortality continued in 2000 and 2002. In 2000, newly killed basal area accrued mostly in red oaks across all strata—an increase of 5-6 percent (table 2). Moderate/severe dieback increased most in white oaks in the light stratum (3.6 percent), but also increased in both white and red oaks in the light and moderate strata. In 2002 red oak mortality increased 11-14 percent in the moderate and severe strata (table 3). Thus, over the 3-year period, red oak mortality increased 7-20 percent while white oak and other species increases were only 2-7 percent and 2-8 percent (table 4).

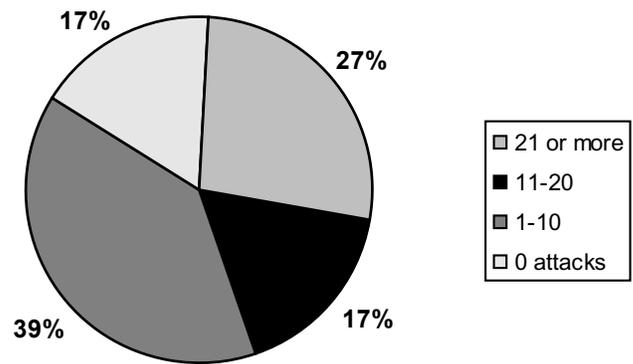


Figure 12—Percentage of red oak basal area per acre with red oak borer attacks on the Mark Twain National Forest.

Table 2—Estimated change (1999–2000) in percent of basal area per acre (trees >4 inches d.b.h.) by crown condition, species group, and damage strata on the Ozark National Forest

Crown condition	Stratum		
	Light	Moderate	Severe
Red oaks			
Healthy and slight	-7.3	-7.9	-5.4
Moderate and severe	+1.8	+1.5	0
Dead	+5.5	+6.3	+5.4
White oaks			
Healthy and slight	-5.4	-1.6	0
Moderate and severe	+3.6	+1.6	0
Dead	+1.8	0	0
Other species			
Healthy and slight	-1.8	0	0
Moderate and severe	+1.8	0	0
Dead	0	0	+1.8

Table 3—Estimated change (2000–2002) in percent of basal area per acre (trees >4 inches d.b.h.) by crown condition, species group, and damage strata on the Ozark National Forest

Crown condition	Stratum		
	Light	Moderate	Severe
Red oaks			
Healthy and slight	-1.8	-10.9	-8.9
Moderate and severe	0	-3.1	+0.5
Dead	+1.8	+14.0	+11.5
White oaks			
Healthy and slight	-1.8	-3.0	-0.5
Moderate and severe	-3.6	+1.5	0
Dead	+5.5	+1.5	+0.2
Other species			
Healthy and slight	0	0	-9.2
Moderate and severe	-1.8	0	0
Dead	-1.8	0	+6.4

Table 4—Estimated change (1999–2002) in percent of basal area per acre (trees >4 inches d.b.h.) by crown condition, species group, and damage strata on the Ozark National Forest

Crown condition	Stratum		
	Light	Moderate	Severe
Red oaks			
Healthy and slight	-9.1	-18.8	-14.3
Moderate and severe	+1.8	-1.6	+0.5
Dead	+7.3	+20.3	+16.9
White oaks			
Healthy and slight	-7.2	-4.6	-0.5
Moderate and severe	0	+3.1	0
Dead	+7.3	+1.5	+0.2
Other species			
Healthy and slight	-1.8	0	-11.0
Moderate and severe	0	0	0
Dead	+1.8	0	+8.2

The most recent (2001) aerial sketchmapping over the entire main division of the Ozark National Forest estimated that over 600,000 gross acres had moderate to severe damage from oak decline, with 300,000 of that in the severe category.

DISCUSSION

Clearly, the current oak decline episode in Arkansas and Missouri is severe and unique in relation to its association with such extremely high populations of ROB. The decline episode will run its course, probably abating with the return of more normal rainfall patterns. However, forest composition and structure will be severely impacted for years to come. Oaks generally, and the red oak group particularly, will be a smaller component of the new forest taking shape,

and given the prevailing low-disturbance/fire suppression regime, will most likely be replaced by shade-tolerant hardwood trees. The course of the ROB epidemic is uncertain. The reduction in host material will probably result in a return to a more historically normal population. The effects of these phenomena are currently being felt by the wood-using industry in the Ozark Highlands. Effects on wildlife, recreation, or other resources are no doubt occurring as well. These remain to be well documented.

ACKNOWLEDGMENTS

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BIOLOGY AND SAMPLING OF RED OAK BORER POPULATIONS IN THE OZARK MOUNTAINS OF ARKANSAS

Damon Crook, Fred Stephen, Melissa Fierke, Dana Kinney, and Vaughn Salisbury¹

ABSTRACT—A complex interaction of multiple factors has resulted in >75 percent mortality/decline of more than 1 million acres of red oak (*Quercus*, subgenus *Erythrobalanus*) on the Ozark-St. Francis National Forests. The most striking feature of this oak decline event is an unprecedented outbreak of red oak borer. A visual stand assessment method was devised for categorizing red oak borer infestation based on crown condition and number of adult emergence holes in the tree bark. An intensive sampling method was also developed to study borer populations at the within-tree level. Complete tree dissections revealed that red oak borer colonizes the entire tree bole. Emergence holes are the highest ever reported in the literature averaging 19.97/m² of bark despite high mortality during early larval stages.

INTRODUCTION

The red oak borer *Enaphalodes rufulus* (Haldeman) (Coleoptera: Cerambycidae), a normally endemic insect species of only minor importance, is currently undergoing a remarkable outbreak of unprecedented magnitude within the forests of the Ozark Mountains in Arkansas and Missouri (USA) (Stephen and others, in press).

Forests of the Ozark Mountains have been recently subject to stress from a widespread disease complex known as “oak decline” (Oak and others 1996). This complex is believed to result from a series of predisposing, inciting and contributing factors (Manion 1991). In the Ozark Mountains predisposing factors are tree age, prolonged drought, poor soils and low site quality. Inciting factors are thought to be short periods of severe drought stress (Starkey and others 2000). Data from the National Oceanic and Atmospheric Administration suggest there has been a drought of moderate consequence from 1998 until 2000, and two more serious droughts in the past 50 years (fig. 1). Whether these periods of drought have been sufficient to serve as an inciting factor for an oak decline event is speculation. Contributing factors have been postulated as being defoliating insects (walking sticks, *Diaperomera femorata* Say), root diseases (e.g., *Armillaria mellea* (Vahl: Fr.) Kumm., stem cankers (*Hypoxylon* species) along with secondary borers such as the two-lined chestnut borer, *Agryllis bilineatus* (Weber) and the red oak borer.

The red oak borer has an interesting two-year life cycle in the central US, with adults emerging synchronously, only in odd numbered years, around mid June (Hay 1972, Donley and Acciavatti 1983). Females oviposit eggs within bark crevices or under lichens (Donley 1978) which hatch within 14 days (Solomon 1995). Resulting larvae then chew into the bark and excavate a gallery in phloem tissue. After a winter-long quiescent period, larvae move from the phloem into the sapwood where in their second year they again overwinter before pupating around May. During the later feeding stages frass is ejected from entrance holes and can be seen at the base of infested trees. Preliminary estimates of red oak borer densities, made by our lab during 2001,

were striking. The number of early larval attack holes averaged 244/m². Density of mature (2nd year) larvae averaged 21.4/m² while emerging adult density averaged 18.5/m². The magnitude of the outbreak becomes clear when compared to Hay’s (1974) study that examined 480 trees but reported only 2.5 to 3.7 average attacks per tree (the highest being 71). Hay (1974) also trapped emerging adults and reported that the highest number of emerging adults on a tree was 15.

We present here a summary of our sampling methods. We also present an update on red oak borer biology and mortality, along with preliminary data on population levels at the within-tree level. The importance of red oak borer as the main contributing factor to current oak mortality will also be discussed.

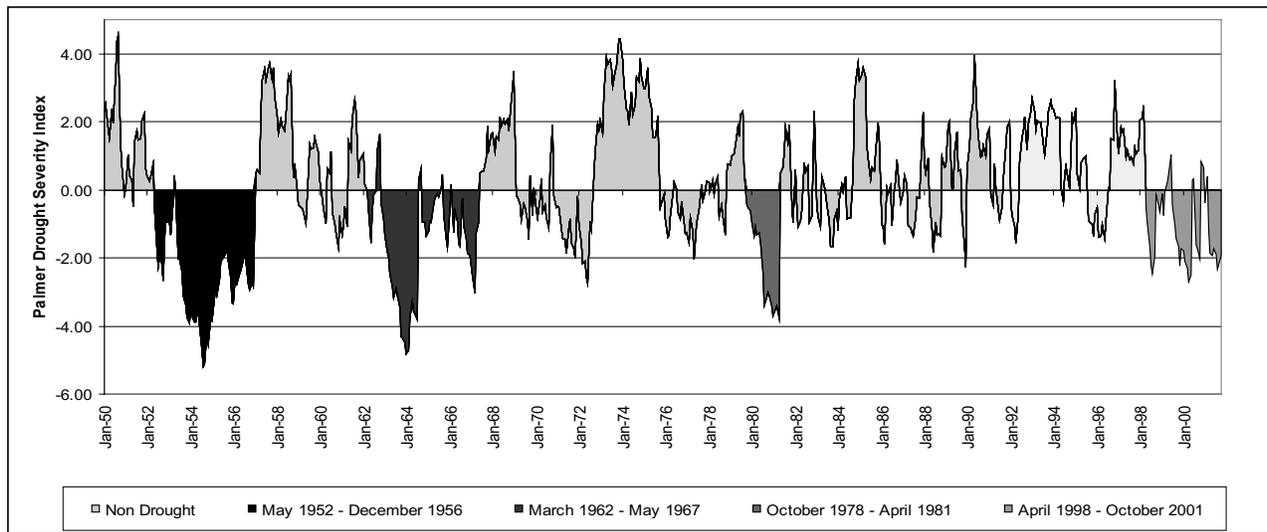
METHODS

A plot was selected within the “Fly Gap/Morgan Mountain” area of the Ozark-St. Francis National Forest so that it incorporated an appropriate representation of variation in site and stand conditions as well as red oak borer infestation density. All trees sampled within the plot were geo-spatially referenced using a GPS navigator unit (Garmin III+). Stand conditions were assessed in a 100 m x 30 m (3000 m² area) plot. Species and diameter at breast height (d.b.h., 1.3 m) was determined for all trees >10 cm. Crown condition and emergence hole density (from 0-2 m ht) were recorded as in table 1. Crown class, epicormic branching (shoots arising from latent buds of the tree bole), current year red oak borer attack and *Hypoxylon* presence were also recorded, as summarized in table 2.

Three trees were selected for felling using the rating system summarized in table 1. The three trees sampled were rated as emergence hole density classes of 1 low tree and 2 medium trees on the dates shown in table 3. Trees with a crown condition of 4 or 5 were not sampled as they were dead. Felled trees were cut into 0.5m sections; each log having the north-facing side marked with a line cut into the bark. Samples were then labeled, before being taken back to the laboratory for intensive sampling. Samples were

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Drought Number	Drought Period	Duration (months)	Peak monthly PDSI	Mean monthly PDSI	s.e. for mean PDSI
1	May 1952 – Dec 1956	56	-5.19	-2.93 (a)	0.16
2	Mar 1962 – May 1967	63	-4.81	-1.55 (b/c)	0.19
3	Oct 1978 – Apr 1981	19	-3.79	-2.21 (a/b)	0.29
4	Apr 1998 – Oct 2001	41	-2.69	-1.22 (c)	0.16



The Palmer Drought Severity Index (PDSI): An Index based on the principles of balance between moisture supply and demand, uses temperature and rainfall information to indicate the severity of a wet or dry spell. The above monthly values are averages of time-bias-corrected divisional temperature-precipitation-drought index data from Arkansas division 1, 2, 4 and 5 for the past 50 years obtained from National Oceanic and Atmospheric Administration

(<http://wf.ncdc.noaa.gov/oa/climate/onlineprod/drought/xmgr.html>)

The four droughts indicated above displayed extended periods of moderate to extreme drought.



Figure 1—Evidence for droughts in the Ozark Mountain region, from 1950 through 2000.

Table 1—Tree sampling categorization A

Crown condition	Emergence hole density classes
0 = No dieback	0 = None
1 = 1 – 33% dieback	1 – 5 = Light
2 = 33 – 66% dieback	
4 = Died this year	5 – 20 = Medium
(brown leaves in August)	>20 = Heavy
5 = Dead 2 – 4 years (no fine twigs)	
6 = Dead >4years	

kept in a refrigerated room at 2 °C to prevent larval development or migration within the tree. Chilling appeared to have no effect on larval mortality. Lichens and moss were cleaned off the bark surface with a 14 cm diameter wire wheel brush (drill-powered) after which attack and

emergence holes were mapped (ht versus circumference from north-facing line). The logs then had the surface layer of bark scraped off with a ten-inch ‘Ox-Head’ draw knife so that early larval galleries and larvae (dead and alive) could be counted and mapped. Older, deeper galleries were then traced down into the sapwood, using chisels, before being mapped.

RESULTS

Stand Description

Total live tree (>10 cm d.b.h.) density was 450 trees/ha and total basal area occupied by large trees was 24.3 m²/ha. Tree species richness (gamma diversity, Whittaker 1975) was 12 with red oaks being dominant (123 trees/ha and 11.3 m²/ha basal area). White oaks were the next dominant tree species (113 trees/ha and 7.0 m²/ha basal area). Other tree species totaled 214 trees/ha with a basal area of 6.32 m²/ha. Standing dead tree density was 107 trees/ha, 38 percent of which comprised of red oaks (50 percent of these red oaks died this year).

Table 2—Tree sampling categorization B

Crown class	Epicormic branching	Hypoxylon	Current year attack
1 = suppressed	Yes	Present	Brown ooze on bole
2 = intermediate	No	Absent	Frass at tree base
3 = codominant		Is it associated with ROB (Y/N)	Attack holes
4 = dominant			

ROB = red oak borer.

Table 3—Dates of tree felling 2002

Tree	Rating	Date
Tree 1	High	1-16-02
Tree 2	Low	3-12-02
Tree 3	Medium	4-4-02
Tree 4	Medium	4-5-02
Tree 5	Medium	6-28-02

Crown condition of the red oaks was generally poor with severe epicormic branching being apparent on trees with greater dieback. Twenty-two percent of live red oaks appeared to suffer no apparent dieback, 35 percent experienced 1-33 percent dieback, 27 percent had 34-66 percent dieback, and 16 percent had >67 percent crown dieback.

Emergence hole categories appear to be related to crown condition (fig 2). Of 21 trees sampled with 0-33 percent dieback, 20 had less than 5 emergence holes. All but one standing dead red oak tree with intact bark (n=9) had >5 emergence holes, indicating that they had undergone a longer 'history' of attack by previous generations of red oak borer.

Crown class of live red oaks showed that in this particular plot, trees were mainly dominant and co-dominant with respect to other tree species. Of the 37 live red oaks examined all showed signs that they had been attacked by the latest generation of larvae (July/August 2001). Dead trees and trees with very severe crown dieback tended not to show signs of recent attack. *Hypoxylon* was only observed on dead and dying trees.

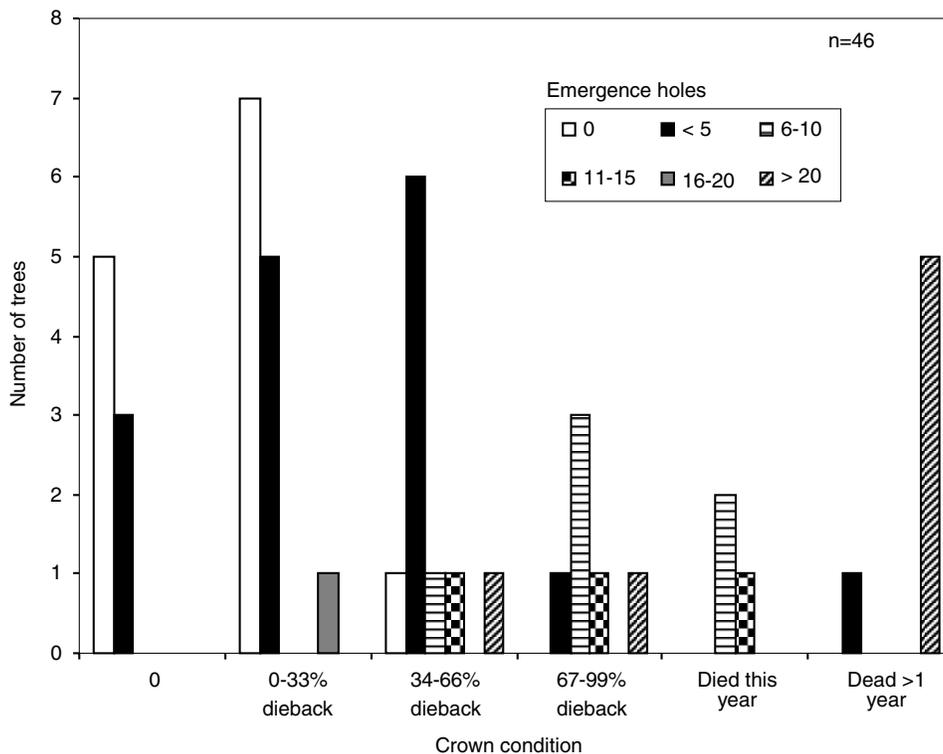


Figure 2—Red oak borer emergence hole category in relation to tree crown condition for the Fly Gap/Morgan mountain area of the Ozark National Forest.

TREE DISSECTIONS

Examination of infested log sections revealed some interesting facts from which several assumptions could be made about borer/tree interactions. First, after newly hatched larvae burrow into phloem tissue they form small, irregular, circle-shaped galleries of approximately 4 cm². When, around November, temperatures drop it appears larvae enter a quiescent period until the following May. Dissections revealed that cell tissue around these galleries became necrotic and blackened. It is uncertain when this necrotic tissue formed around the larvae but it appeared to occur once larval feeding stopped during winter.

During June 2002, dissections revealed that the surviving larvae had not yet moved out of the necrotic galleries. For all three trees sampled the mean number of attack holes/m² of bark was 179 (±16.4SE). The mean number of emergence holes/m² of bark for all three trees was 19.97 (±2.51SE).

Dissections revealed that borers attacked every section of the tree's main bole. Bark attack site density increased in number from the base of the tree to the middle, after which density decreased (fig. 3). Numbers appeared to dip slightly just before halfway up the infested bole. Late larval galleries and emergence site density also followed this general trend (figs. 4 and 5). Early larval galleries, however, appeared to gradually decrease in density from base to top of the tree (fig. 6).

Mortality was calculated for three time periods from July 2001 – Aug 2001

1. mortality from attacks of newly hatched larvae: from July 2001 until formation of early first year gallery by larvae (Aug-Nov 2001 approx) (n=82)

$$1 - \left(\frac{\text{total \#1st year galleries}}{\text{total \# bark attack sites}} \right) = 0.337 \pm 0.07 (SE)$$

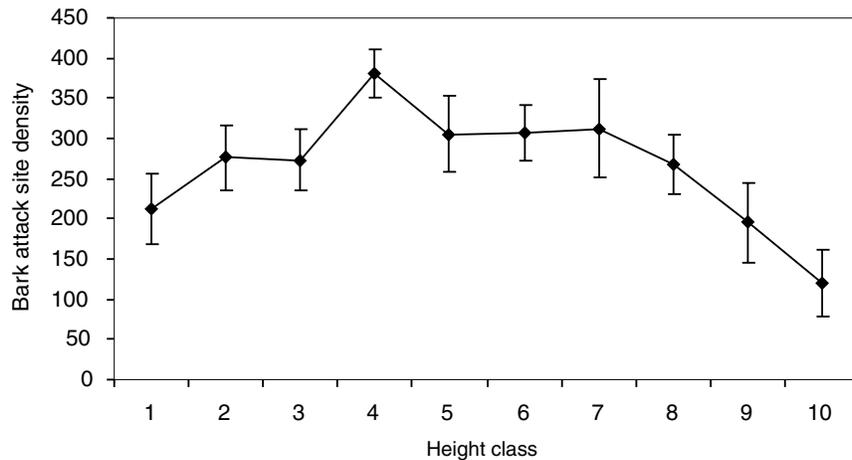


Figure 3—Distribution of bark attack densities (per 1 m²) of red oak borer larvae from the base (1) to the tip of the tree (10). n=3.

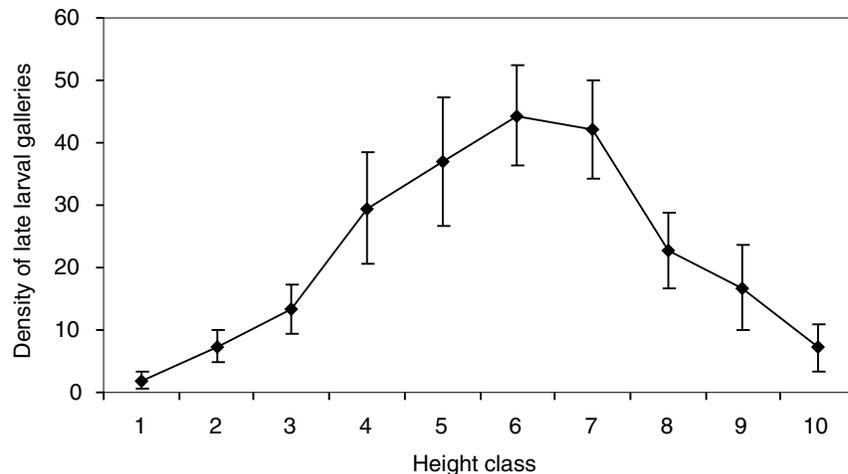


Figure 4—Distribution of late larval galleries (per 1 m²) from the base (1) to the tip of the tree (10). n=3.

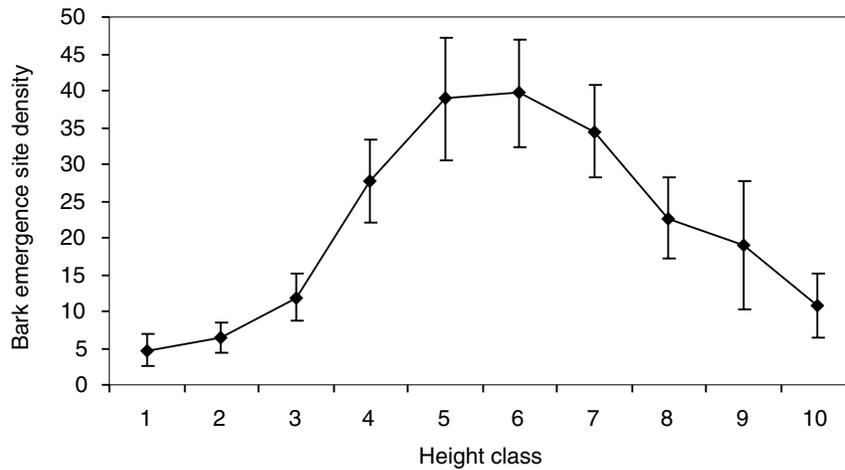


Figure 5—Distribution of bark emergence sites (per 1 m²) from the base (1) to the tip of the tree (10). n=3.

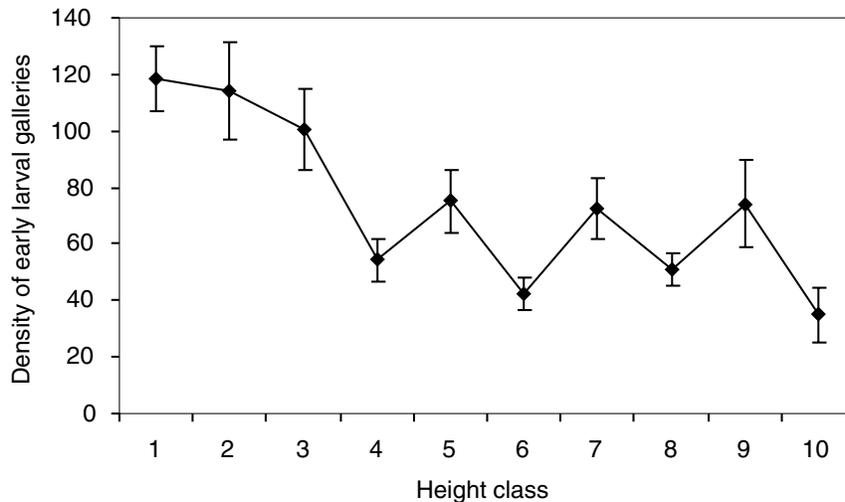


Figure 6—Distribution of live early larvae (per 1 m²) from the base (1) to the tip of the tree (10). n=3.

- mortality from live early larvae: larvae in galleries formed from Aug-Nov 2001 until live larvae were sampled in trees during Jan-May (n=82)

$$1 - \left(\frac{\text{total \# live early larvae}}{\text{total \# 1st year galleries}} \right) = 0.442 \pm 0.03 (SE)$$

- total mortality from attack of new larvae: from July 2001 until live larvae in necrotic gallery (sampled Jan-May 2002) (n=82)

$$1 - \left(\frac{\text{total \# live early larvae}}{\text{total \# bark attack sites}} \right) = 0.657 \pm 0.04 (SE)$$

It is important to note that these mortality estimates are not calculated from number of eggs oviposited on the bark surface, but from newly hatched larvae that are able to first bore into the bark surface. Mortality is expected to be low

when later stage larvae have burrowed into the sapwood of the tree (mainly due to protection offered by living in gallery so deep inside the bole).

DISCUSSION

It is clear from our preliminary results that red oak borer population densities are remarkably high and that trees within the Ozark National forest are undergoing severe levels of attack. Despite heavy larval mortality during the past year surviving larvae boring into the sapwood were still at incredibly high densities, especially when compared to Hay's results from 1974. The only other reported survey of red oak borer attack was done by Donley and Rast (1984) who reported that red oak borer adult emergence (from 421 red oaks) averaged 2.0 per tree in Pennsylvania and 3.6 in Indiana.

At present we cannot explain the apparent trend for population densities to dip near the center of the infested

boles. This may simply be an artifact. Further tree dissections will clarify whether the borer population has a uni- or bi-modal distribution within trees.

Although predisposing factors such as old tree age, shallow soils, periods of drought, low species diversity and fungal pathogens may be indicted as possible contributors to the current 'oak decline' event, it is clear that red oak borer populations are much higher than ever seen in recorded history and that they are the main factor responsible for tree death. If oak decline has reduced tree vigor in such a manner as to permit higher survival of red oak borers over several generations, it is perplexing to note that such high levels of red oak borer populations have never been reported with other oak decline events, despite the fact that this endemic insect species has been present in those forests. The consequences of the current outbreak in terms of changes to forest composition and structure are as yet unclear. It is predicted that changes to some groups, such as the complex of neotropical migrant birds, may be significant (Smith and Stephen, in press).

Mortality studies are continuing and it is hoped that by July/August 2003 partial life tables will be completed for an entire generation. Current sampling methods at the within-tree level are being refined to optimize number of tree sections needed to accurately estimate within tree population densities. This will enable more trees to be sampled from different areas and allow populations to be compared between stands of different conditions.

Our initial stand assessments show that crown condition and emergence hole density (from 0-2 m) give a quick and simple method of assessing red oak borer infestation. This method is presently being used by USDA Forest Service survey teams to assess red oak borer populations in stands over the entire Ozark-St. Francis National Forests. These surveys should be able to more precisely estimate the severity of the current epidemic.

ACKNOWLEDGMENTS

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OAK MORTALITY TRENDS ON THE INTERIOR HIGHLANDS OF ARKANSAS

James F. Rosson, Jr.¹

Abstract—Using data from the U.S. Department of Agriculture (USDA) Forest Service, Forest Inventory and Analysis program, I studied mortality trends of oak (*Quercus* spp.) across four physiographic sections of the Interior Highlands in Arkansas. Surveys for 1978, 1988, and 1995 showed oak mortality levels of 3.9, 8.9, and 5.5 percent, respectively. Increases in mortality were strongly correlated with a major drought event in 1980 (reflected in the 1988 survey). The highest recorded mortality (1988 survey) was in the Arkansas Valley section. Other strata examined included ownership and stand-size classes. The highest mortality by ownership was on forest industry lands; by stand-size class, it was highest where diameters averaged ≥ 12.0 inches. Six oak species accounted for 95 percent of mortality. A high population resilience rate was evidenced by the rapid increase and decrease in oak mortality before and after the 1980 drought event.

INTRODUCTION

A recent outbreak of the red oak borer (*Enaphalodes rufulus* Haldeman) in Arkansas has raised interest and concern about oak mortality. Data currently available are not suitable to quantify the extent of infestation or the number of trees killed. However, U.S. Department of Agriculture (USDA) Forest Service, Forest Inventory and Analysis (FIA) data, which span three survey measurement periods, are available to quantify mortality trends prior to the borer outbreak. Although the most recent survey (dated 1995) predates the red oak borer outbreak, valuable information can be derived from older surveys to describe oak mortality patterns on the Interior Highlands of northwest and west Arkansas. By providing baseline data of mortality dynamics, it may be easier to put into perspective the extent of infestation now occurring in the oak component. With a better understanding of mortality dynamics, resource managers may better use silvicultural techniques to prevent, retard, or cope with mortality incidents (Nyland 1996). Little information has been reported about oak mortality patterns by physiographic regions, ownership, size class, and species.

I considered an area that includes the Interior Highlands of Arkansas (Fenneman 1938), where the oak-hickory forest type predominates. Oaks (*Quercus*) were the species of interest. A drought event in Arkansas in the early 1980s provided the opportunity to correlate oak mortality with drought during three survey periods (1978, 1988, 1995). I compared, over time, total oak mortality among Physiographic Sections (Fenneman 1938), ownership classes, and stand-size classes. I also examined mortality trends for select oak species.

METHODS

The inclusive area of the study is the Interior Highlands Physiographic Division (Fenneman 1938). In Arkansas, this Division includes four physiographic sections in two provinces: The Springfield-Salem Plateaus and Boston Mountains sections in the Ozark Plateaus Province and the Arkansas Valley and Ouachita Mountains sections in the Ouachita Province (fig 1).

The data of surveys conducted in 1978, 1988, and 1995 came from the USDA Forest Service, Forest Inventory and Analysis (FIA). Using geographic information system (GIS) software, I digitally traced the physiographic boundary lines of the four physiographic sections over a layer of FIA plot locations, thereby establishing the baseline data file to define FIA plots by physiographic strata. The scale of the map used to outline the physiographic boundaries was 1:7,000,000 (adequate for regional analysis).

The sample design for the three surveys consisted of sample plots located on a 3-mile by 3-mile grid. Only trees ≥ 5.0 inches in diameter at breast height (d.b.h.) were used in this study. These trees were tallied using a 37.5 basal area factor (B.A.F.) prism on 10 points dispersed over an area of 1 acre (see Rosson 2002 for more details on sampling methods in Arkansas).

Several plot- and tree-level attributes were sampled on each sample unit. Tree attributes important to this study were species, d.b.h., and tree history. Of particular interest in this study was tree history, which was used to identify mortality.

Because sample plots were remeasured, trees could be tracked over time and their history noted whether they were new trees, survivor trees, cut (removed) trees, or mortality trees (dead and standing, dead and broken off, or dead and completely down). Use of remeasured plots is one of the best techniques available to track tree mortality over time (Bonham 1989).

Mortality estimates were generated from weighted density data. Trees per acre (t.p.a.) was the metric used. The weighting was derived from the area factor—the amount of land area each plot represented. When weighting was applied, the resulting metric was the total oak population expanded by plot by strata.

Although it would seem that a dead tree could be easily identified, errors can be made. Because FIA data are collected

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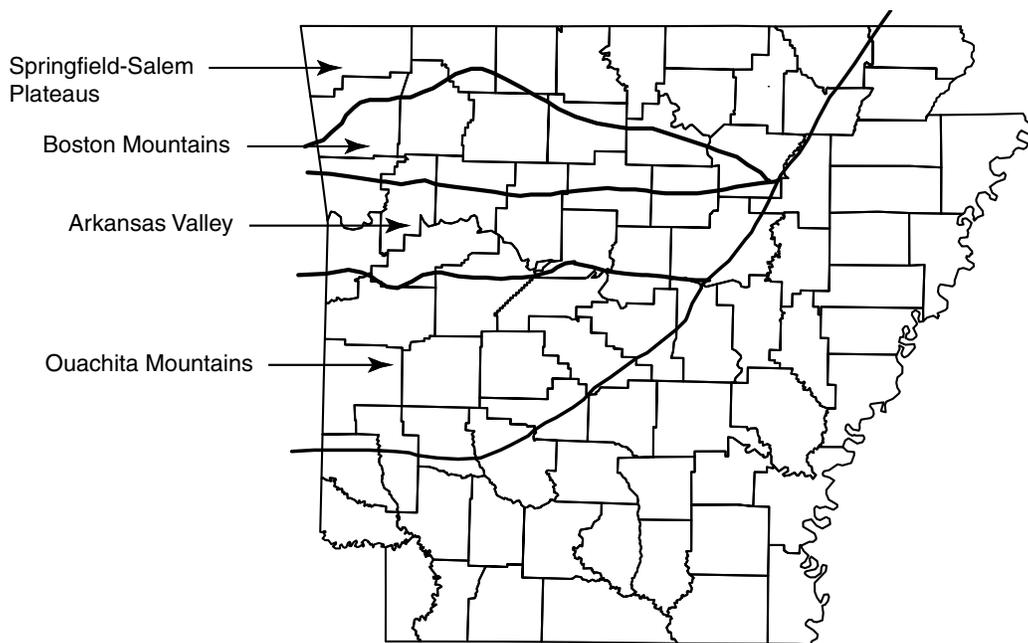


Figure 1—The four physiographic sections on the Interior Highlands of Arkansas (After Fenneman, 1938).

in all seasons, recently dead deciduous trees may escape detection from late fall through the end of winter. The assessment also may have missed trees that had died and were harvested between surveys; i.e., it was not possible to determine if a cut tree was dead or alive at the time of harvest. For these reasons, I chose not to include harvested trees in this study.

Tree measurement is another possible source of error. The d.b.h. of recently dead trees may be accurate, but those trees dead for a period of years may have fallen over, broken off, or the bole may be decayed to an extent that accurate measurement is not possible. In such cases, d.b.h. was derived from a model that estimates d.b.h. at the time of death. Time of death since the most recent survey was estimated in the field by the data collector. The d.b.h. model was only used to project from time of death the supposed growth of a living tree of the same size. This is important when sampling with variable radius plots because d.b.h. is used to determine tree density.

To evaluate changes in mortality, the average annual periodic mortality and annual periodic mortality rate were derived.

The average annual periodic mortality is,

$$AAPM = \left(\sum (N_d \times W_a / T) \right) / n \quad (1)$$

where

AAPM = the average annual periodic mortality

N_d = the number of dead trees per acre per plot (by strata or species)

W_a = the area factor per plot

T = the elapsed time (in years) per plot between plot measurements

n = the number of sample plots per strata.

The AAPM is an estimator of the number of trees that died per strata or species for each survey period.

The annual periodic mortality rate is,

$$APMR = (N_{ld} \times W_a / N_d \times W_a) / T \times 100.0 \quad (2)$$

where

APMR = the annual periodic mortality rate (in percent)

N_{ld} = the number of live and dead trees per acre per plot (by strata or species)

N_d = the number of dead trees per acre per plot (by strata or species)

W_a = the area factor

T = the elapsed time (in years) per plot between plot measurements.

The APMR is an estimator of the proportion of trees that died per strata or species.

Differences in oak mortality by physiographic type, ownership, and stand-size class were tested with a t-test procedure for the unplanned comparison of two means (Greig-Smith 1983, Kent and Coker 1992). This was derived by,

$$t_s = (\bar{y}_1 - \bar{y}_2) / \sqrt{SEM_1^2 + SEM_2^2} \quad (3)$$

where

t_s = the t-statistic value

\bar{y}_1 = the mean of mortality at time 1

\bar{y}_2 = the mean mortality at time 2

SEM_1 = the standard error of the mean at time 1

SEM_2 = the standard error of the mean at time 2.

The tests were done at the 0.05 probability level.

RESULTS AND DISCUSSION

The Interior Highlands comprise 16.5 million acres in west and northwest Arkansas (fig. 1). Forty-two counties are included; 29 of them totally within the Physiographic Province and the remaining 13 partially inside the southern and eastern boundary line. A total of 10.2 million acres of timberland occur within the Interior Highlands (table 1).

The largest physiographic section is the Ouachita, which has 5.1 million acres of land area and 3.8 million acres of timberland. The largest ownership class is in nonindustrial

Table 1—Timberland area by Fenneman's Physiographic Sections and by ownership classes on the Interior Highlands of Arkansas^a

Fenneman's Physiographic Section and Ownership Class	Total land area	Timberland area	n
- - - thousand acres - - -			
Ouachita			
National forest		1,308.1	230
Public		136.1	25
Forest industry		1,201.3	212
NIPF		1,115.1	192
Total	5,073.6	3,760.6	659
Arkansas Valley			
National forest		161.1	30
Public		129.7	20
Forest industry		90.0	15
NIPF		1,344.1	214
Total	3,532.3	1,724.9	279
Boston Mountains			
National forest		738.8	131
Public		23.1	4
Forest industry		113.2	19
NIPF		1,510.6	258
Total	3,130.5	2,385.7	412
Springfield-Salem Plateaus			
National forest		125.6	26
Public		94.7	15
Forest industry		—	—
NIPF		2,091.5	333
Total	4,746.0	2,311.8	374
Interior Highlands			
National forest		2,333.5	417
Public		383.6	64
Forest industry		1,404.4	246
NIPF		6,061.3	997
Total	16,482.3	10,182.9	1,724

n = the number of timberland sample plots in each physiographic and ownership strata; NIPF = nonindustrial private forest; — = no sample plot.

^aArea data is based upon plots measured in the 1995 survey.

private forest (NIPF), 6.1 million acres, followed by national forest, which is 2.3 million acres (table 1).

The average annual periodic mortality (AAPM) for all oaks sampled on the Interior Highlands increased from 1978 to 1988 and then fell to near the 1978 levels at the time of the 1995 survey (table 2). The largest increase in oak mortality was on the Arkansas Valley physiographic section, where the AAPM went from 954.1 to 5,306.7 trees per weighted plot, a highly significant change ($t_{0.05} = 6.60$). The other physiographic sections also had significant increases in AAPM between 1978 and 1988, 1,081.0 ($t_{0.05} = 3.68$), 2,499.5 ($t_{0.05} = 5.20$), and 1,425.4 trees per weighted plot ($t_{0.05} = 2.73$) for the Ouachita, Boston Mountains, and Springfield-Salem Plateaus sections, respectively.

The highest annual periodic mortality rate (APMR) was in the Arkansas Valley section in 1988, where 14.04 percent of all oaks died. The other sections also showed increases between 1978 and 1988, then returned to near their 1978 levels when the 1995 survey was conducted. There was no discernible pattern in the ranking of physiographic sections by APMR. The highest rankings by survey year were: the Springfield-Salem Plateau section, the Arkansas Valley, and the Boston Mountains for 1978, 1988, and 1995, respectively.

The patterns of AAPM by ownership and survey year were similar to those of the four physiographic sections. There was an increase between 1978 and 1988 followed by a decrease between 1988 and 1995 (table 3). There were no significant differences among ownerships in 1978. Specifically, there was no difference between national forest

timberland and public timberland ($t_{0.05} = 0.52$) nor was there a significant difference between forest industry and NIPF ($t_{0.05} = 1.17$).

Statistically significant differences were evident between ownerships in 1988. The AAPM on national forest land increased to 3,883.5 trees per weighted plot, the highest of any ownership in the 3 survey years. National forest lands were significantly different from other public lands; 3,883.5 and 1,984.7 trees per weighted plot, respectively ($t_{0.05} = 2.81$). There was a statistically significant difference between forest industry and NIPF lands, 2,071.4 and 3,766.4 trees per weighted plot ($t_{0.05} = 3.61$). The 1995 survey showed that the AAPM had declined somewhat. Changes in AAPM by ownership between 1988 and 1995 were only significant for national forest ($t_{0.05} = 2.18$) and NIPF timberland ($t_{0.05} = 4.30$); other public and forest industry lands were not significantly different, $t_{0.05} = 1.11$ and $t_{0.05} = 1.81$, respectively. When comparing AAPM among ownerships within the 1995 survey, I found no difference between national forest and other public lands ($t_{0.05} = 0.36$) but the difference between forest industry and NIPF was statistically significant ($t_{0.05} = 3.74$). Additionally, there was no difference between national forest and NIPF lands in AAPM ($t_{0.05} = 0.94$) or between other public lands and NIPF ($t_{0.05} = 0.76$).

Stand-size classes were examined to discern differences among the size classes between years and within years (table 4). In 1978, there were no differences in the AAPM between the 5.0-7.9-inch and 8.0-11.9-inch classes ($t_{0.05} = 0.42$); nor was there a difference between the 8.0-11.9- and the 12.0-15.9-inch classes ($t_{0.05} = 0.50$) or the 12.0-15.9- and the ≥ 16.0 -inch classes ($t_{0.05} = 0.33$). As in the previous

Table 2—Average annual periodic mortality per plot and annual periodic mortality rate by year and Fenneman's Physiographic Sections^a

Year	Fenneman's Physiographic Sections	Average annual periodic mortality	Annual periodic mortality rate	Variance of average annual periodic mortality	n
			<i>percent</i>		
1978	Ouachita	1,122.9	3.64	23,755,817.8	613
	Arkansas Valley	954.1	2.61	8,483,027.0	167
	Boston Mountains	1,834.0	3.87	18,770,468.8	302
	Springfield-Salem Plateaus	2,054.5	4.96	23,372,541.0	180
1988	Ouachita	2,203.9	8.16	31,112,018.5	657
	Arkansas Valley	5,306.7	14.04	99,604,425.9	265
	Boston Mountains	4,333.5	8.49	71,044,389.8	421
	Springfield-Salem Plateaus	3,479.9	7.15	51,183,438.2	357
1995	Ouachita	1,724.1	4.88	27,125,931.2	659
	Arkansas Valley	2,119.6	5.62	29,964,393.3	279
	Boston Mountains	3,071.4	6.12	40,688,129.3	412
	Springfield-Salem Plateaus	2,919.4	5.68	40,196,162.5	374

n = the number of timberland sample plots in each physiographic strata.

^a The average annual periodic mortality is the number of trees per acre weighted by the area expansion factor each plot represents.

Table 3—Average annual periodic mortality per plot and annual periodic mortality rate by year and ownership class on the Interior Highlands^a

Year	Ownership class	Average annual periodic mortality	Annual periodic mortality rate	Variance of average annual periodic mortality	n
<i>percent</i>					
1978	National forest	1,505.5	3.45	17,264,299.1	387
	Public	1,245.2	4.23	8,333,702.2	40
	Forest industry	1,005.6	4.27	34,763,366.9	232
	NIPF	1,501.9	3.89	18,152,184.7	603
1988	National forest	3,883.5	9.04	69,280,316.1	416
	Public	1,984.7	5.67	17,147,416.7	59
	Forest industry	2,071.4	11.05	40,547,095.8	251
	NIPF	3,766.4	8.74	57,929,807.3	974
1995	National forest	2,775.2	5.81	37,901,590.2	417
	Public	3,101.7	7.07	46,059,335.8	64
	Forest industry	1,188.4	5.65	19,066,464.8	246
	NIPF	2,444.0	5.32	34,850,646.2	997

n = the number of timberland sample plots in each ownership strata; NIPF = nonindustrial private forest.

^a The average annual periodic mortality rate per plot is the number of trees per acre weighted by the area expansion factor each plot represents.

Table 4—Average annual periodic mortality per plot and annual periodic mortality rate by year and stand-size class on the Interior Highlands^a

Year	Stand-size class in inches at d.b.h.	Average annual periodic mortality	Annual periodic mortality rate	Variance of average annual periodic mortality	n
<i>percent</i>					
1978	<5.0	0.0	0.00	0.0	68
	5.0 – 7.9	1,324.5	2.90	39,913,321.3	250
	8.0 –11.9	1,501.9	3.90	16,594,270.2	862
	12.0 –15.9	1,817.5	7.45	21,333,720.0	73
	?16.0	1,438.4	10.97	9,514,229.2	9
1988	<5.0	55.7	0.27	367,409.0	248
	5.0 – 7.9	3,457.9	8.94	52,296,977.3	306
	8.0 –11.9	4,324.8	9.60	69,783,893.8	1,029
	12.0 –15.9	3,364.1	11.22	48,486,792.1	100
	?16.0	3,668.8	27.91	50,125,944.4	17
1995	<5.0	818.9	4.77	12,284,125.3	131
	5.0 – 7.9	1,201.1	3.88	17,616,440.5	270
	8.0 –11.9	2,687.9	5.43	37,734,153.9	1,187
	12.0 –15.9	3,472.2	10.18	47,316,184.3	123
	?16.0	2,744.6	18.95	57,227,065.9	13

D.b.h. = diameter at breast height; n = the number of timberland sample plots in each stand-size strata. Note that some trees ?5.0 inches in d.b.h. may occur in the <5.0 inch stand-size class because the class is the average of all trees on the sample plot.

^a The average annual periodic mortality rate per plot is the number of trees per acre weighted by the area expansion factor each plot represents.

physiographic and ownership tests, the 1988 survey showed a large increase in AAPM for all the stand-size classes, although no statistically different averages occurred among any of the classes. By 1995, the AAPM was still significantly different from what it had been in 1978 for the 8.0-11.9-inch stand-size class ($t_{0.05} = 4.02$). The remaining size classes were not significantly different.

The APMR was highest for the largest stand-size class (≥ 16.0 inches d.b.h.). This class averaged 11, 28, and 19 percent mortality for 1978, 1988, and 1995, respectively; but the inferences were not as strong because of the small sample size (table 4). However, the magnitude of the APMR for this size class does support the notion that mortality rates will be higher in older stands when conditions of stress exist (Oliver and Larson 1990).

Six oak species accounted for 96 percent of the total oak density (trees ≥ 5.0 inches d.b.h.) on the Interior Highlands. The relative ranking of these oaks was *Quercus alba* (35 percent), *Q. stellata* (24 percent), *Q. velutina* (14 percent), *Q. rubra* (11 percent), *Q. falcata* (7 percent), and *Q. marilandica* (5 percent), and it remained the same throughout the three survey periods despite increases and decreases in mortality.

These six oaks also accounted for 95 percent of the total oak mortality (AAPM) for the three survey periods, although their ranking did shift somewhat between surveys. *Quercus alba* had the most trees die in 1978, accounting for 28 percent of total oak mortality. Following were *Q. velutina*, *Q. stellata*, *Q. rubra*, *Q. marilandica*, and *Q. falcata*, accounting for 20, 19, 12, 9, and 7 percent of total oak mortality. By

1988, the proportion of *Q. alba* mortality had decreased to 24 percent while *Q. velutina* increased to 24 percent. *Quercus velutina* led in the proportion of oak mortality in 1995 (23 percent) while *Q. alba* had declined even more (down to 18 percent), third in rank behind *Q. velutina* and *Q. stellata*.

There were shifts among species rankings depending on whether AAPM or APMR were used when estimating mortality. The AAPM provided information about the total number of trees that died, while the APMR revealed the proportion of a stratum or species that died. With regard to the latter, most oak death recorded in the 1988 survey occurred in *Q. alba*, although the proportion of that species' population to have died was only 6 percent (table 5).

The ranking of the six important oaks by APMR in 1978 was *Q. marilandica*, *Q. velutina*, *Q. rubra*, *Q. falcata*, *Q. alba*, and *Q. stellata* (table 5). *Quercus marilandica* led in all three surveys with 8, 21, and 15 percent APMR for 1978, 1988, and 1995, respectively.

Damage due to the 1980 drought was most apparent in the 1988 survey, but only a slight shift in species ranking occurred. *Quercus falcata* surpassed *Q. rubra*, 12 percent versus 8 percent, respectively. By 1995, the ranking was the same as in 1978 except that *Q. stellata* surpassed *Q. alba* (5 percent versus 3 percent, respectively).

Empirical data have depicted *Quercus* species mortality trends on the Interior Highlands of Arkansas since 1969. The data were analyzed by physiographic section, ownership, stand-size class, and species. There were significant

Table 5—Annual periodic mortality rate (percent) of select *Quercus* species on the Interior Highlands of Arkansas by survey year^a

Species	1978	n	1988	n	1995	n
	%		%		%	
<i>Quercus alba</i> L.	3.03	70	6.48	205	2.90	92
<i>Q. falcata</i> Michx.	4.02	20	11.68	63	5.18	34
<i>Q. falcata</i> var. <i>pagodifolia</i> Ell.	3.59	3	18.64	9	13.61	5
<i>Q. lyrata</i> Walt.	12.51	3	4.88	3	3.24	4
<i>Q. marilandica</i> Muenchh.	7.67	29	20.86	91	14.72	66
<i>Q. michauxii</i> Nutt.	0.00	0	0.00	0	4.92	1
<i>Q. muehlenbergii</i> Engelm.	0.77	3	1.00	1	4.69	8
<i>Q. nigra</i> L.	2.52	1	5.19	11	7.36	6
<i>Q. nuttallii</i> Palmer	4.78	2	3.93	7	15.51	1
<i>Q. palustris</i> Muenchh.	0.00	0	6.90	3	0.00	0
<i>Q. phellos</i> L.	5.50	6	14.44	14	8.98	11
<i>Q. rubra</i> L.	4.07	50	8.28	112	7.18	105
<i>Q. shumardii</i> Buckl.	7.29	4	6.52	4	1.48	3
<i>Q. stellata</i> Wangenh.	2.99	56	6.40	133	4.62	106
<i>Q. velutina</i> Lam.	5.48	62	13.05	179	8.59	153

n = the number of sample plots where mortality was recorded for at least one *Quercus* species ≥ 5.0 inches in d.b.h.

^a Only *Quercus* species that occurred (live or dead) on at least five sample plots in any of the three survey years were included. Total n was 1,262 for 1978, 1,700 for 1988, and 1,724 for 1995.

differences among surveys for all categories. The most logical cause for these differences was the 1980 drought, which significantly increased tree mortality.

Despite increases in mortality in 1988, the *Quercus* population (trees ≥ 5.0 inches d.b.h.) increased across the Interior Highlands by 1995. Only one species of the highest ranking six oaks decreased—*Q. marilandica*. The highest AAPM by physiographic section was on the Arkansas Valley; the highest AAPM by ownership was on forest industry land; and the highest AAPM by stand size was in classes ≥ 12.0 inches, all in 1988. Overall, across the Interior Highlands, the *Quercus* APMR was 3.9 percent in 1978, 8.9 percent in 1988, and 5.5 percent in 1995.

Although FIA data cannot be used to test cause and effect hypotheses, correlation inferences between natural or man-induced disturbance events, and supporting data, can be quite strong. In this mortality study, strong, statistically significant increases in oak mortality were evident for the 1988 survey. Trees measured in 1988 reflected responses that occurred between 1978 and 1988. A period of drought occurred around 1980, early in the 1988 survey period. This left enough time for stressed trees to respond (death or survival). If the event had occurred closer to the end of the survey period, the response may not have been evident by the time of measurement and thus would not have been detected until the following survey measurement. This is one type of situation that makes strong cause-and-effect inferences difficult to interpret when using survey data.

Because mortality increased between 1978 and 1988 but had declined by 1995, it can be assumed that the drought, directly or indirectly, caused the increase in oak mortality reflected in the 1988 survey period. However, it is not known

what constitutes a normal AAPM or APMR for oak on the Interior Highlands. If it can be assumed that the mortality levels for the 1978 survey period (years 1969 to 1978) are close to normal, then this study shows an increase in mortality in the 1988 survey followed by a fairly quick return to mortality levels reflected in the 1978 survey. This may indicate a high rate of population resilience to short-term stress when viewed at the macro scale of sampling (Begon and others 1986, Kimmins 1997).

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ASSESSING OAK DECLINE INCIDENCE AND DISTRIBUTION IN THE SOUTHERN U.S. USING FOREST INVENTORY AND ANALYSIS DATA

Steven W. Oak, James R. Steinman, Dale A. Starkey, and Edwin K. Yockey¹

Abstract—Forest Inventory and Analysis data for twelve southern states were used to evaluate regional oak decline status. Total host type, vulnerable host type, and affected areas were determined. The attributes used for classification were forest type, predominant stem size class, oak basal area percent, and dieback damage coding. Host type totaled 104.7 million acres in the most recent inventory cycle (1991-1997), of which 41.6 percent were classified as vulnerable. Oak decline affected over 4.4 million acres, or 10.1 percent of the vulnerable host type. This was a slight incidence increase over the previous inventory cycle (1984-1989). Two-thirds of the decline-affected area was contained in 4 states—Virginia, North Carolina, Arkansas, and Tennessee in decreasing rank order. Large increases in incidence occurred in Arkansas and North Carolina, while incidence decreased markedly in Tennessee. Oak decline incidence in Virginia remained unchanged between inventory cycles.

INTRODUCTION

Hardwoods dominate forest cover in the thirteen states of the southern region, with about two-thirds of the area in upland hardwood, bottomland hardwood, or oak-pine mixtures. Upland hardwood is by far the largest forest type group, accounting for about 37 percent of the forested area (Sheffield and Dickson 1998). Oaks dominate the growing stock volume in upland hardwood stands, comprising 47 percent of the total region wide. The next most abundant species is yellow poplar, which makes up only 12.6 percent (Hansen and others 1992).

Oak species are economically and ecologically important in the southern region as valuable timber species and indispensable habitat components for wildlife feeding on hard mast. However, oak decline is a widely distributed change agent that is altering species composition and forest structure in upland hardwood and mixed oak-pine forests. Oak decline is a disease complex resulting from the interaction of three groups of factors as described by Manion (1991). Physiologic age, soil depth and texture, oak species composition, and oak density are the main long-term predisposing factors. Common inciting factors include prolonged acute drought, spring defoliating insects like fall cankerworm and gypsy moth, and late spring frost. The biotic agents most often identified as contributing factors include *Armillaria* root disease, *Hypoxylon* canker and insect pests of opportunity like twolined chestnut borer and red oak borer. The symptom separating oak decline from other diseases of oak is slow, progressive dieback from the top downward and the outside inward in upper canopy trees (i.e., dominants and codominants). This symptom reflects aboveground the condition of the root system underground. The time scale of disease progression from inception to the death of susceptible trees is typically measured in years or decades, but tree mortality after a relatively short period of dieback sometimes occurs.

Oak decline is not a new phenomenon. Forest workers reported occurrences as early as the mid 1800's (Beal 1926, Balch 1927) and in every decade since the 1950's (Millers and others 1988). An apparent increase in incidence and severity in the early 1980's and continuing through the 1990's led to an intensification of survey and monitoring activities (Bassett and others 1982, Starkey and others 1989, Stringer and others 1989, Oak and others 1990, Starkey and others 2000), but most were relatively limited in geographic scale. Periodic multi-resource inventories conducted by the U.S.D.A Forest Service Southern Research Station Forest Inventory and Analysis work unit (FIA) afford the opportunity for regional assessments of oak decline. The results for two inventory cycles— 1984 through 1989 and 1991 through 1997 are reported in this paper.

METHODS

Permanent inventory plots are distributed over the land area of each state and visited at approximately six to eight year intervals by FIA field crews. Detailed accounts of data collection procedures can be found in field instruction manuals (U.S.D.A Forest Service 1984, 1985). Included among these procedures is coding for tree damages. The standard code that correlates most closely with oak decline is dieback, when it occurs in dominant and codominant oak trees. The geographic limit of this analysis was determined by the twelve southern states using common damage coding. These states are Virginia, North Carolina, South Carolina, Tennessee, Georgia, Florida, Alabama, Mississippi, Louisiana, Arkansas, Oklahoma, and Texas.

The host type population in these states included plots where oaks dominate tree species composition (table 1). These plots represent the area eligible for oak decline. Other forest types may also contain relatively small numbers of oaks subject to decline, but such plots were excluded because resource damage from this disease is unlikely.

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Table 1—Forest Inventory and Analysis forest types and forest-type groups included in host type for oak decline analysis

Physiographic type	Forest-type group	Forest type
Upland	Oak-hickory	Post oak-black oak-bear oak Chestnut oak White oak-red oak-hickory Northern red oak Yellow-poplar-white oak-northern red oak Southern scrub oak Mixed hardwoods
	Oak-pine	White pine-northern red oak-white ash Eastern redcedar-hardwood Longleaf pine-scrub oak Shortleaf pine-oak Virginia pine-southern red oak Loblolly pine-hardwood Slash pine-hardwood Other oak-pine
	Oak-gum-cypress	Swamp chestnut oak-cherrybark oak Sweetgum-Nuttall oak-willow oak Overcup oak-pine

The vulnerable host type population was defined as the subset of host type plots where the predominant size class was pole- or sawtimber, and oaks comprised 30 percent or more of total stand basal area. Plots with these combinations of forest type, size class, and oak density represent the highest risk for oak decline occurrence and resource damage. Affected plots were the subset of vulnerable host type plots where one or more dominant or codominant oaks had dieback recorded as a damage code.

Subjective evaluation of dieback was considered the greatest potential source of error in decline classification. Quality assurance procedures for a similar FIA assessment of oak decline in western Virginia revealed that field crews were proficient at identifying decline symptoms. Field checks of 10 percent of plots classified as decline-affected showed they were correctly diagnosed in 92 percent of the cases (Oak and others 1991). However, all plots in the western Virginia assessment were classified as decline-affected and were inventoried during the growing season when decline symptoms are easier to diagnose. We established the reliability of individual tree coding and decline classification in this assessment by field checking 102 plots in North Carolina and Tennessee. These plots represented both affected and unaffected plots diagnosed in the dormant and growing seasons (table 2). These states were selected because the inventories were the most recently completed at the time of validation and, therefore, least likely to have changed condition over time. Field checks were conducted during the growing season after the statewide inventories were completed (approximately 2-10 months).

Table 2—Number of plots in Tennessee and North Carolina used for dieback and oak decline validation, by initial inventory season and decline status

Inventory season	Decline	Unaffected
- - - number of plots - - -		
Growing	37	29
Dormant	14	22
Combined	51	51

RESULTS

Validation

Individual tree coding by FIA field crews for presence or absence of dieback was correct for 89 percent of the cases (table 3). Accuracy was highest for unaffected trees than for affected overall, with no errors found for unaffected trees diagnosed in the dormant season. Affected trees evaluated in the dormant season were the most difficult for field crews to diagnose, though some of these apparent errors of omission could have been due to dieback that developed between the initial inventory and the validation effort. It is less likely for dieback symptoms to have been lost or masked in the short time between the initial inventory and validation.

Table 3—Validation of dieback and decline status of Forest Inventory and Analysis plots in Tennessee and North Carolina

Season of inventory	Decline plots	Unaffected plots	Both
----- percent correct -----			
Individual tree dieback coding			
Growing	84	93	88
Dormant	79	100	92
Combined	83	96	89
Stand decline classification			
Growing	84	83	83
Dormant	86	77	81
Combined	84	80	82

1984-1989 Survey Period

The total area of host type was 114.7 million acres in the twelve surveyed states (table 4). Alabama led the region with 13 million acres, but there were six others with more than 11 million acres each (Georgia, Arkansas, North Carolina, Virginia, Tennessee, and Mississippi in decreasing rank order). While the total host type acreage in the remaining states was no higher than 7 million acres (Florida), the differences in host type acreage among states was probably due more to differences in total state land area, than to density of host type plots.

Vulnerable host type totaled about 40 million acres. The geographic distribution of these plots show more dense concentrations in the Southern Appalachian Mountains of Virginia, North Carolina, Tennessee, South Carolina, and

Georgia; along the eastern and western highland rim of middle Tennessee; and in the Ozark-Ouachita highlands of Arkansas and eastern Oklahoma (fig. 1). The regional distribution map showing plot locations is not one snapshot in time, but rather a mosaic of snapshots due to the varying inventory dates for each state.

The total area affected by oak decline was 3.6 million acres during this survey cycle (table 4). Virginia had the largest area (1.1 million acres). About 60 percent of the total affected area was located in Virginia, Tennessee, and North Carolina. Sampling error for affected area varied from 0.89 to 16.82 percent for all States, but was < 2 percent for each of the top three.

Regional incidence (percent of vulnerable host type area affected by decline) averaged 9.13 percent, but this was highly variable among states. Virginia and Florida had incidence approaching 20 percent, though Virginia had nearly 4 times the vulnerable host type acreage of Florida. Tennessee and North Carolina had incidence of about 12 and 10 percent, respectively, while Mississippi, Alabama, Oklahoma, and Louisiana had incidence of 3 percent or less. Relatively high densities of affected plots are located in northern Virginia, western North Carolina, the western highland rim of middle Tennessee, and in the northern Arkansas highlands (fig. 2.)

1990-1997 Survey Period

Host type area totaled 104.7 million acres during this period (table 5), a decrease of over 10 million acres since the earlier inventories. Florida experienced the greatest loss (3 million acres), but Georgia, North Carolina, and South Carolina each lost in excess of 1 million acres. Loss of host type could be due to diversion of former timberland to non-forest uses, such as urbanization; or change from oak dominated forest to a different forest type through management actions or natural forest dynamics (i.e., succession).

Table 4—Area and incidence of oak forest type affected by oak decline, 1984–89

State	Host type		Vulnerable host type		Affected		Incidence	Inventory year	
	acres	no. plots	acres	no. plots	acres	no. plots	percent		
Alabama	13,032.5	2,244	4,169.9	718	138.1	24	3.31	1984	
Arkansas	12,219.6	2,162	4,758.9	836	289.5	51	6.08	1988	
Florida	7,306.4	2,711	1,522.0	568	296.0	114	19.45	1987	
Georgia	12,526.3	3,501	4,058.7	1,250	341.2	69	8.41	1989	
Louisiana	6,363.2	1,088	1,140.0	195	16.3	3	1.43	1984	
Mississippi	11,112.2	1,917	2,465.3	422	93.7	16	3.80	1987	
North Carolina	11,913.9	3,510	4,259.7	1,135	422.6	100	9.92	1984	
Oklahoma	3,581.0	600	2,005.2	331	29.6	5	1.48	1986	
South Carolina	6,606.5	2,378	2,133.8	730	139.9	51	6.56	1986	
Tennessee	11,328.4	1,944	5,596.8	963	651.0	114	11.63	1989	
Texas	6,843.0	1,137	1,873.3	308	99.2	16	5.30	1986	
Virginia	11,887.3	3,327	5,802.3	1,515	1,114.4	272	19.21	1986	
Total	114,720.3	26,907	39,785.9	8,852	3,631.5	871			
Overall incidence								9.13	

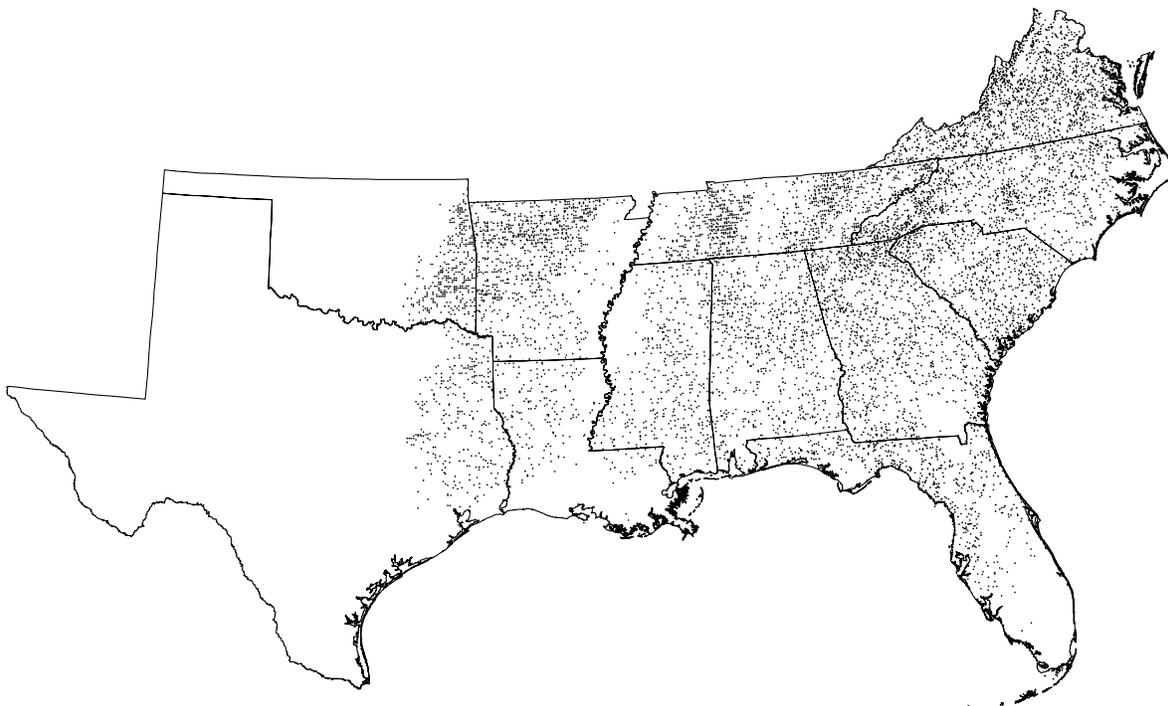


Figure 1—Geographic distribution of vulnerable host type plots for 12 Southern States, 1984-1989.

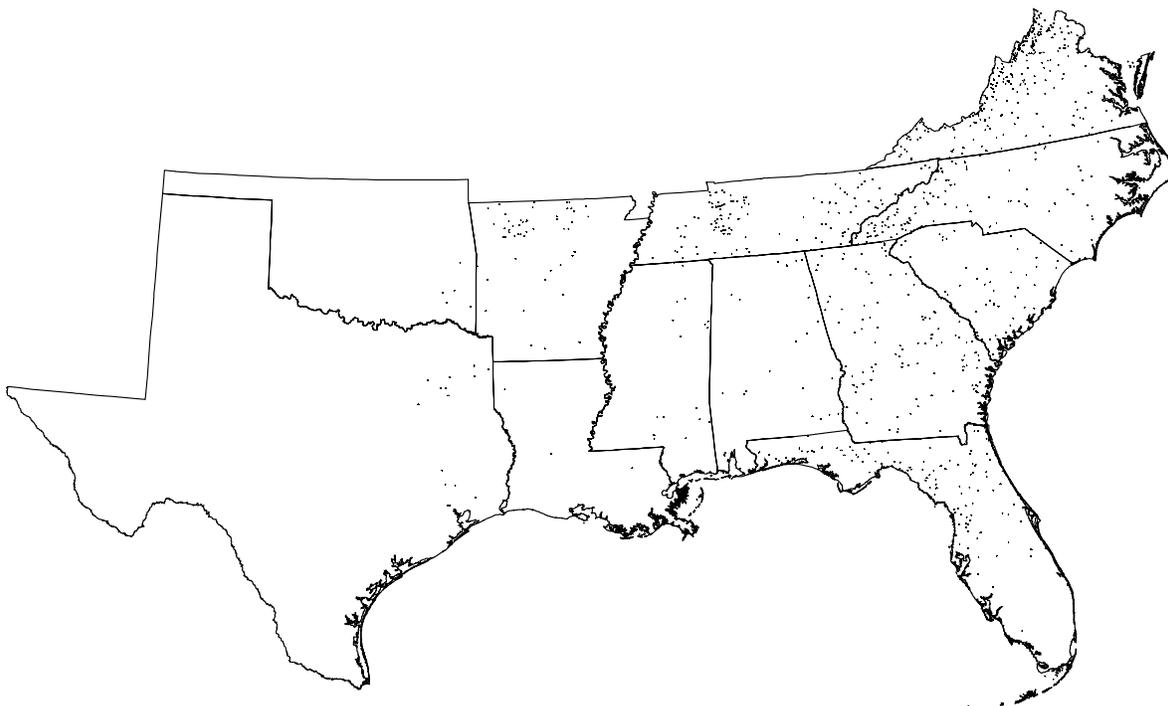


Figure 2—Geographic distribution of affected plots for 12 Southern States, 1984-1989.

Despite the loss of host type, vulnerable host type increased by 3.7 million acres regionwide. Arkansas registered the largest increase among the 12 states, almost 2 million acres, and led the region in total vulnerable host type area with 6.7 million acres. Virginia, Tennessee, and Alabama

each had more than 4 million acres of vulnerable host type, but other large increases were noted in Mississippi, Louisiana, and Texas (1.4, 1.0, and 0.9 million acres, respectively). Geographic patterns similar to those observed in the earlier inventory were also seen during this period (fig. 3).

Table 5—Area and incidence of oak forest type affected by oak decline, 1990–97

State	Host type		Vulnerable host type		Affected		Incidence	Inventory year	
	<i>acres</i>	<i>no. plots</i>	<i>acres</i>	<i>no. plots</i>	<i>acres</i>	<i>no. plots</i>	<i>percent</i>		
Alabama	13,402.9	2,835	4,272.1	756	260.5	47	6.10	1990	
Arkansas	12,252.4	2,081	6,734.2	1,145	707.0	121	10.50	1995	
Florida	4,271.8	1,621	1,601.8	595	211.7	80	13.22	1995	
Georgia	9,797.3	3,501	3,747.1	1,250	250.7	69	6.69	1997	
Louisiana	6,317.3	1,106	2,174.4	385	167.0	31	7.68	1991	
Mississippi	11,381.5	1,930	3,900.6	659	203.4	37	5.21	1994	
North Carolina	9,280.8	2,711	3,861.3	1,040	754.3	178	19.53	1990	
Oklahoma	3,602.1	593	1,960.9	321	135.5	21	6.91	1992	
South Carolina	5,106.6	1,798	1,809.8	611	164.0	55	9.06	1993	
Tennessee	11,343.3	2,672	5,176.6	1,126	357.5	74	6.91	1997	
Texas	6,962.7	1,197	2,763.4	476	105.8	19	3.83	1992	
Virginia	10,945.6	2,960	5,510.1	1,413	1,090.5	268	19.79	1992	
Total	104,664.3	24,555	43,512.3	9,777	4,407.9	1,000			
Overall incidence								10.13	

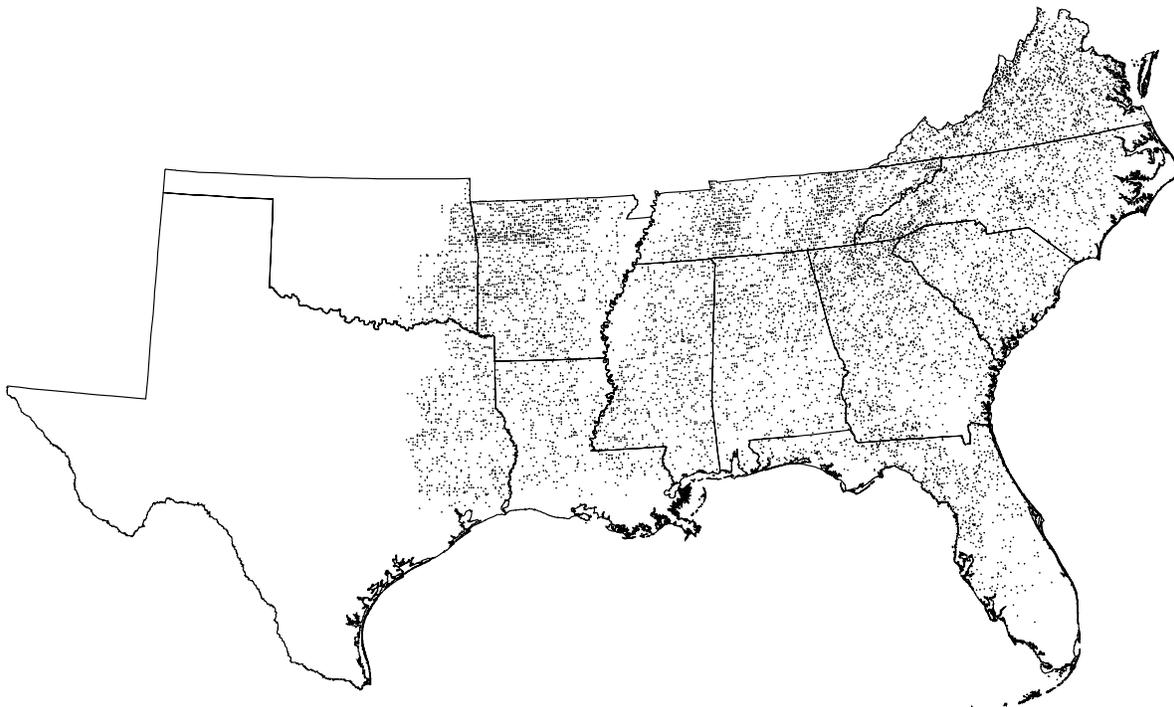


Figure 3—Geographic distribution of vulnerable host type plots for 12 Southern States, 1990-1997.

Area affected by oak decline totaled 4.4 million acres, up 0.8 million acres since the previous inventory. Virginia affected area remained almost the same (1.1 million acres in both inventories), but large changes occurred in North Carolina, Arkansas, and Tennessee. Despite a decrease in vulnerable host type in North Carolina, affected area nearly doubled to 0.8 million acres. In Arkansas, the large increase in vulnerable host type was mirrored by an increase in affected area of more than double, while in Tennessee, vulnerable host type remained the same and affected area

decreased to half the area reported for the earlier inventory period. As for the earlier survey period, sampling error was low for the top three States in affected area.

Regional incidence increased slightly to 10.13 percent. Incidence in Virginia remained close to 20 percent, while incidence in North Carolina almost doubled to a similar figure. As in the earlier inventory, about 60 percent of the total affected area was represented by three states, with Arkansas replacing Tennessee and joining Virginia and

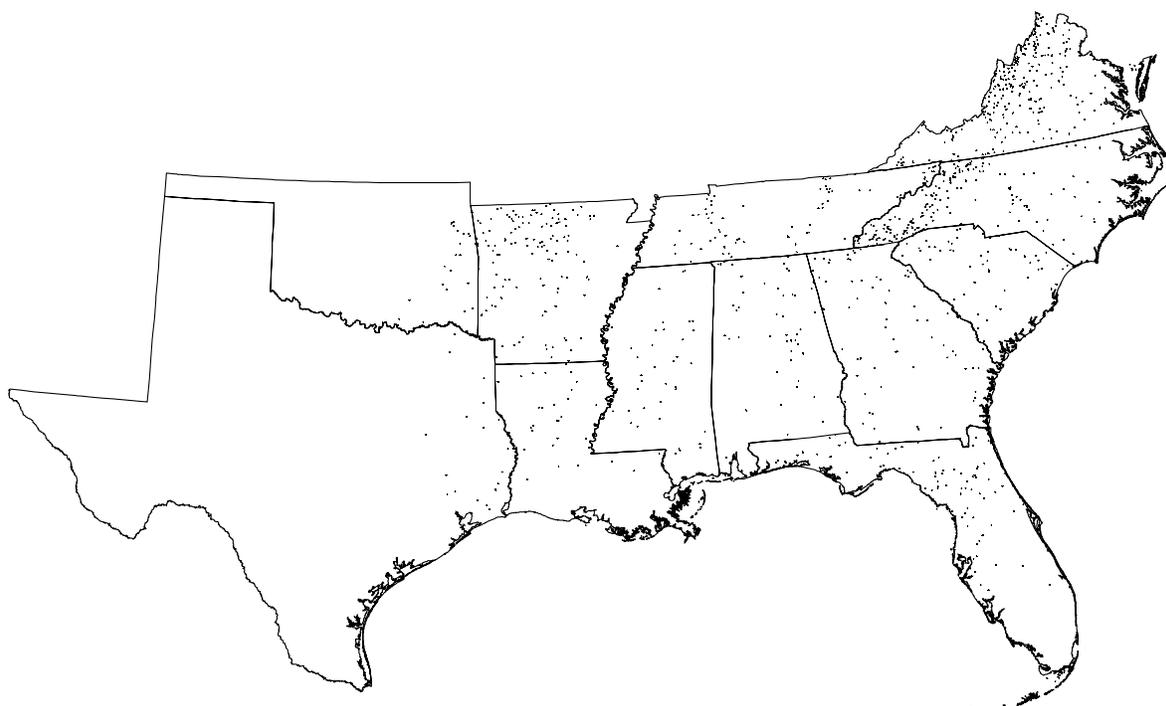


Figure 4—Geographic distribution of affected plots for 12 Southern States, 1990-1997.

North Carolina in the more recent inventory. Florida had high incidence in both inventories, but relatively low host type, vulnerable, and affected areas. The density of affected plots remained high in northern Virginia, but appeared to have intensified between inventory periods in western North Carolina and the Ozark-Ouachita highlands of Arkansas and Oklahoma. By contrast, affected plot density appeared to decrease in eastern Tennessee and the western highland rim (fig. 4).

DISCUSSION

Virginia, North Carolina, and Tennessee had consistently large oak decline affected area in the inventories conducted between 1984 and 1997, ranking in the top four among the 12 states in both inventories. Together they accounted for about 60 percent of the total affected area in the region. Florida had among the highest oak decline incidence during the period, but this was applied against vulnerable host type area that was the smallest among the states evaluated.

The aging and growth of upland hardwood forests in Arkansas resulted in large increases in vulnerable host type, and affected area over the inventory period. Vulnerable host type increased about 1.5 times between 1988 and 1995, while affected area increased about 2.5 times from 290,000 acres to 707,000 acres. This change captured by the 1995 inventory represents the beginning of the current unprecedented oak decline episode in the Ozark-Ouachita highlands. The earliest reports of the current episode were not made until about four years later in 1999 (Starkey and others 2000).

FIA inventories are useful for evaluating oak decline incidence and distribution. Other conditions can result in dieback

that does not constitute oak decline. However, the presence of dieback symptoms in dominant and codominant oak trees in combination with the forest types, predominant tree size classes, and oak densities we recognized reliably represented oak decline. Future work will present finer spatial resolution of these data by breaking out individual survey units within states and by application of nearest neighbor statistical tools to individual plots.

Changes in methods instituted since the 1997 inventory cycle have made future analysis by these methods obsolete. New procedures will have to be developed for use with the new sampling designs. As long as the dieback symptom is recognized and recorded, oak decline analyses with FIA data sets will be possible.

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BIRDS OF UPLAND OAK FORESTS IN THE ARKANSAS OZARKS: PRESENT COMMUNITY STRUCTURE AND POTENTIAL IMPACTS OF BURNING, BORERS, AND FORESTRY PRACTICES

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Abstract—Based on published works, our own research, and the U.S. Forest Service's R8 Bird database, we characterize breeding bird communities in mesic and xeric upland hardwood forests of the Arkansas Ozarks. Although 59 species have been recorded as breeding, typical breeding assemblages in mesic forests are 20-25 species, with only 5 species commonly found in xeric forests. Due to changes in forest composition, the breeding assemblages of today were probably rare or absent from the Ozarks 150 years ago. Any forestry practice that opens the closed canopy increases the number of species in upland hardwood forests. Development of a shrub-layer allows a different suite of birds to occupy the forest, which typically would be unsuitable habitat for them. Relatively few birds occur in upland forest in fall migration and especially winter, but many migrants use this habitat in spring. The recent decline in oaks due to the borer infestation may dramatically change the avifauna of this upland habitat. Prescribed burning in deciduous forests may also have positive and negative effects, which need further investigation. Cowbirds do not occur in upland forests, and their spread should be limited by the lack of feeding sites.

INTRODUCTION

The forested Ozarks are generally believed to represent as a source region for Neotropical migrants compared to fragmented areas to the east and north that have become population sinks (Donovan and others 1995, Robinson and others 1995, Howell and others 2000), with higher reproductive success among the more common Neotropical migratory species (> 50 percent, Li 1994). Relatively few studies have been conducted on breeding birds in undisturbed, upland hardwood forests of Arkansas (e.g., James 1971, Shugart and James 1973, Smith 1977) and almost no studies have examined birds in migration or during winter (James and others 1981, Rodewald 1995). More commonly, studies have been conducted on avian responses to forestry practices (e.g., Thompson and others 1992, Annand and Thompson 1997, Rodewald and Smith 1998), fragmentation (e.g., Donovan and others 1995), or insect outbreaks (Williams and others 1993, Nagy and Smith 1997, Smith and Stephen, in press).

The Ozark Mountains and Oak/Hickory Forest Ecosystem

Braun (1950) first coined the term "Interior Highlands" in referring to the forested Ozark and Ouachita mountains. Whereas the Ouachita Mountains are primarily forested with pines mixed with hardwoods, the Ozark Mountains are the western edge of the eastern deciduous forest (Braun 1950), having compositional affinities with forests stretching east through Ohio, Pennsylvania, and into southern New England (Whitney 1994: fig. 4.3).

The pre-settlement forest in some parts of the Ozarks was nearly a monoculture of majestic white oaks (*Quercus alba*), with canopies barely touching, first branches 3-5 m

from the ground, and a grass understory (see Braun 1950, Beilman and Brenner 1951). Other forested habitats included bottomland hardwoods in river drainages and cedar glades in drier areas, with significant amounts of pine in southeastern Missouri (Widmann 1907). Both red (subgenus *Erythrobalanus*) and white (*Leucobalanus*) oaks were common in the Arkansas Ozarks at the time of settlement (Foti and Heitzman, in press). However, the Ozarks were clear-cut in the period 1880-1900, primarily for railroad ties for the western United States (reviewed in Smith and Petit 1988). The resulting forest today is a nearly even-aged mixture of oaks, hickories, maples, and other deciduous species with some pine in the southern portions. Given the even-aged closed canopy, there generally is little or no shrub layer development and the ground cover is predominately poison ivy (*Rhus radicans*). Shelford (1963:59) referred to the Missouri and Arkansas Ozarks as the largest forest of oak and hickory without pine in North America and the Ozarks currently have the highest density of oaks in the United States (McWilliams and others 2002).

The Arkansas Ozarks are over 90 percent forested today, and about 75 percent of the forest is composed of a variety of oak-dominated habitats (Smith and others 1998). Based on slope and aspect, it is sometimes useful to separate north-facing slopes into mesic upland and south-facing slopes into xeric upland forests (e.g., James 1971, Smith 1977). According to a U.S. Department of Agriculture, Forest Service 1995 Forest Survey, red oaks (subgenus *Erythrobalanus*) comprise 46 percent of the live-tree volume, 42 percent of growing stock volume, and 35 percent of sawtimber volume of Arkansas timberland (J.M. Guldin, F. Oliveria, and M. Spetich. 2001. Research considerations in the red oak borer epidemic of 2001—suggested research strategy. Unpublished report. On file

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Citation for proceedings: Spetich, Martin A., ed. 2004. Upland oak ecology symposium: history, current conditions, and sustainability. Gen. Tech. Rep. SRS-73. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 311 p.

with: U.S. Department Of Agriculture, Forest Service, Hot Springs, AR 71901). Thus, much of the Arkansas Ozarks are covered with oaks, and red oaks, the more numerous subgenus, are of great commercial value to the economy of the state. Currently, however, the forests of the Ozark Mountains in Arkansas and Missouri are experiencing a remarkable outbreak of a native, normally endemic insect species, the red oak borer, *Enaphalodes rufulus* (Haldeman) (Coleoptera: Cerambycidae). By the end of 2001, the U.S. Forest Service estimated > 400,000 ha of forest in the Ozark Mountains were being impacted by this outbreak.

In this paper, we first characterize the breeding bird communities of the xeric and mesic upland hardwood forests of the Arkansas Ozarks, and present some data on birds present in spring and fall migration and during winter. We then present results of our research on effects of various forestry practices on breeding bird communities. Based on those results, we speculate on the effects of the current red oak borer outbreak on bird community structure. Potential impacts on bird communities from other sources, such as prescribed burning and cowbirds, are also discussed.

METHODS

Data reported here were compiled from four primary sources: two studies conducted by the authors that examined effects of various forest practices on bird community structure, data collected by the U.S. Forest Service on the Ozark National Forest in conjunction with their R8Bbird monitoring program, and theses, dissertations, and published works by graduate students at the University of Arkansas over the last 30 years.

Fleming Creek

In 1982 and 1983, the U.S. Forest Service's Silviculture and Hydrology Laboratories, at the time located in Fayetteville, AR, began a study of the impacts of 3 forest management practices on hydrology of 4 watersheds (one was a control) that drain into Fleming Creek, in north central Franklin County, AR, just south of the Madison County line.

One watershed (FC1, 11.3 ha) was a "conversion to pine" treatment. Both loblolly (*Pinus palustris* Mill.) and shortleaf (*P. echinata* Mill.) pine seedlings were planted in February and March of 1982 prior to herbicide application. Loblolly pines were planted on sites with more northerly aspects while shortleaf pines were planted on southerly aspects. No harvesting was done in this watershed, but existing hardwoods were killed via Velpar application (liquid squirted on 1.2 x 1.2 m spacing) in 1982 and Tordon 101 injection in 1983 and left standing.

Another watershed (FC3, 5.9 ha) was a shelterwood harvest, in which the existing stand was thinned to 56-60 percent of original basal area in 1982. Merchantable hardwood trees were cut during thinning and remaining, undesirable hardwoods (e.g., dogwoods, redbuds) were injected with Tordon 101. All work was completed in 1982.

The third watershed (FC4, 6.9 ha) was clearcut and all merchantable timber was removed, smaller trees of desirable species (e.g., oaks, hickories) were severed close the ground to promote sprout regeneration, and undesirable trees were injected with Tordon 101. All work was completed in 1982.

A fourth watershed (FC2, 13.3 ha) was designated as a control. No disturbance of any kind occurred in this watershed.

Monthly bird censusing began in all 4 watersheds in October 1983 and continued through September of 1984, with additional censuses in November 1984 and February, March, April, May, July and September of 1985, for a total of 18 censuses. Due to the small size of watersheds, a circular trail was established in each watershed and each census lasted approximately 1 hr, during which the observer would record all birds seen or heard on the plot while walking the trail, care being taken not to count individuals more than once. On each census day, two observers randomly chose 2 plots each and the direction to walk on the trail (i.e., clockwise or counter-clockwise). Censuses were begun at 10:00 and the 2 censuses by each observer were usually completed by 12:30. Data were grouped by season: spring (April – May, n = 4), summer (June – August, n = 3), fall (September – November, n = 5), and winter (December – March, n = 6).

Ozark National Forest Study

In 1993, a long-term project was initiated to study the effects of various management practices in oak-hickory forests within the Ozark National Forest. During 1993, two study areas were established (Williams Hollow and Gulf Branch) in anticipation of future harvesting, and an additional 3 study areas (Swain, Barberry, and Junction) were established in 1994.

Since 1993, 10-minute fixed-radius point-counts (Hutto and others 1986) have been conducted 4 times each summer at each study area during early June through early July. All species seen or heard within a 50-m radius of the center of the plot were recorded. Points were at least 150 m apart. All censuses were conducted by M. Mlodinow, who attempted to census plots on nearly the same days each year. However, censuses have not been performed on rainy or windy days.

Williams Hollow—Censusing began in summer of 1993 on sixteen 50-m radius circles. During fall of 1993, harvesting, which consisted of group selection cutting, was completed at the site by November of that year. Fourteen of the 16 circles were within the harvested area; two circles were approximately 75 m from the edge of the cut area, but were included in the analysis because they probably were influenced by the harvesting operation. Most of the uncut area was thinned between the 1998 and 1999 field seasons.

Gulf Branch—Censusing began during summer of 1993 on twelve 50-m radius circles. Between 17 and 24 June 1994, a logging road was established in the study area, possibly directly affecting one circle. Prior to censusing in 1995, logging, which consisted of shelterwood harvesting, was begun and was completed during fall of 1995. No logging activities were observed during censusing in summer of 1995. Prior to the 1997 field season, site preparation activities were completed, during which most of the understory was cut, creating scattered brushpiles. Six circles were within the area receiving all treatments and 6 circles were at least 100 m outside the treatment area.

Junction—Censusing began in 1994 on eight 50-m circles. During summer of 1996, group selection harvesting was

begun in mid-June prior to the last census and was completed in fall of 1996. Site preparation was 50 percent completed by March 1997.

Swain and Barberry—Censusing began in 1994 at Swain on six 50-m circles. This area was harvested in a group selection cut between the 1999 and 2000 field seasons, so we considered data collected between 1994 through 1999 as undisturbed forest. Censusing began in 1994 at Barberry on six 50-m circles. This area has not been sold for harvest and serves as a control for the other plots.

University of Arkansas Studies

The first seminal work done on habitat selection of birds in the Arkansas Ozarks was by Francis James (1971). Not only did this reveal important habitat relationships of birds in the Arkansas Ozarks, it introduced the use of multivariate statistics to the ornithological world. Hank Shugart (Shugart and James 1973) conducted thesis research examining changes in bird community structure along a successional gradient at the Pea Ridge National Monument, Benton County, AR. Unfortunately, his mesic upland forest plot was only 2.8 ha in size, limiting the usefulness of those data. Kimberly Smith (1977) conducted his thesis research in Leatherwood Cove, Newton County, AR, comparing the distribution of species along a moisture gradient on north- and south-facing slopes in what was then a part of the Buffalo National River. Douglas James led an NSF-funded undergraduate research project on the fauna of the Buffalo National River during summer of 1977 and winter of 1978 (James and others 1981). Pingjun Li (1994) examined reproductive ecology of 11 species of forest birds in the Ozark National Forest in Franklin County as part of his doctoral research. Paul Rodewald (Rodewald 1995, Rodewald and Smith 1998) examined effects of understory removal and selective cutting of the canopy on 26 species of birds in the eastern part of the Ozark National Forest (northern Pope and southern Newton cos.). Smith and long-time collaborator Frederick Stephen (Smith and Stephen In press) speculate on the impact of the current red oak borer on bird community structure in the Arkansas Ozarks.

U.S. Forest Service R8 Bird Data

Beginning in 1996, the Ozark-St. Francis National Forest implemented a landbird monitoring program within the Ozark National Forest. A total of 61 mesic upland hardwood plots, corresponding to habitats 53,54,55,69 and 81 in Hamel (1991) and 20 xeric upland hardwood plots, corresponding to habitats 51, 57, and 99 in Hamel (1991), were established throughout the national forest. Between 1997 and 2001, point counts (Hamel and others 1996) were conducted primarily by John Andre, Steve Duzan, Wayne King, Steve Osborne, Frank Palmer, and Glen Thomas. The resulting 11,630 records of individual birds during those 5 years are available in the R8Bird database (Trani and Belcher 2002).

Species Occurrence and Analysis

Birds were characterized as common, rare, or present by the following criteria. All species studied by James (1971) were by definition "common." Shugart and James (1973) presented densities of males per 40-ha and noted the presence of other species. Birds with densities of 5 or fewer

males per 40-ha were considered rare and those over 5 males per 40-ha were considered common. Smith (1977) presented a discriminant function analysis that ordinated samples along a moisture gradient. Birds at Fleming Creek were considered common if more than 5 sightings occurred on the 3 censuses. Species were present if seen once and rare if seen 2 to 5 times. Birds at Swain and Barberry were common if seen each year, rare if not seen every year, and present if only seen one or two years. Species in the R8Bird database were considered common if more than 20 individuals were recorded, rare if more than 5 but fewer than 20 individuals were recorded, and present if 4 or fewer individuals were recorded.

For the Fleming Creek watersheds, we compared richness, species diversity (H), and equitability (J) for all time periods and for the breeding season, using PROC GLM and Duncan's multiple range test in SAS (SAS Institute, Inc., Cary, NC). Overall similarity of the watersheds was calculated using the method described by Wolda (1981).

RESULTS

Breeding Bird Community Structure

A total of 59 species have been reported as breeding in upland hardwood forests in the Arkansas Ozarks (table 1), including Sharp-shinned Hawk (*Accipiter striatus*), Eastern Screech-Owl (*Otus asio*) and Whip-poor-will (*Caprimulgus vociferous*) reported by Rodewald (1995). A total of 25 species are permanent residents and 34 are migrants, but most species are either rare or present. Common resident species in mesic upland forests include Downy Woodpecker, Pileated Woodpecker, Tufted Titmouse, and White-breasted Nuthatch and possibly Red-bellied Woodpecker, Blue Jay, and American Crow. Common breeding migrants include Yellow-billed Cuckoo, Eastern Wood-Pewee, Acadian Flycatcher, Red-eyed Vireo, Blue-gray Gnatcatcher, Wood Thrush, Black-and-white Warbler, Worm-eating Warbler, Ovenbird, Hooded Warbler, and Scarlet Tanager. Thus, the typical avian breeding assemblage in a mesic upland forest in the Arkansas Ozarks is around 20-25 species (Shugart and James 1973, James and others 1981, Rodewald and Smith 1998). Only 5 species, Red-eyed Vireo, Tufted Titmouse, Blue-gray Gnatcatcher, Ovenbird, and Indigo Bunting, commonly occur in xeric upland hardwood forests in the Arkansas Ozarks during summer.

Winter Bird Community Structure

Upland hardwood forests are nearly birdless during winter. Of the 10 species seen during winter at Fleming Creek, 8 were seen only once or twice – Cooper's Hawk (*Accipiter cooperii*), Red-tailed Hawk, American Crow, Carolina Chickadee, Downy Woodpecker, Red-bellied Woodpecker, White-breasted Nuthatch, and Yellow-rumped Warbler. Pileated Woodpeckers were seen 4 times and 15 American Goldfinches were counted.

Migration in Upland Hardwood Forests

Rodewald (1995) reported 32 species of non-breeding migrants during spring (late April-May) of 1993 and 1994 on his study sites in eastern Ozark National Forest (table 2). Only 8 non-breeding migrants were seen on the control watershed at Fleming Creek during spring migration (table 2).

Table 1—Birds reported in relatively undisturbed upland hardwood forests during the breeding season in the Arkansas Ozarks

Species	Scientific name	James (1971)		Shugart and James (1973)		Smith (1977)		Fleming Creek		Swain/Barberry		Forest Service R8.bird	
		Mesic	Xeric	Mesic	Xeric	Mesic	Xeric	Mesic	Xeric	Mesic	Xeric	Mesic	Xeric
Turkey vulture*	<i>Cathartes aura</i>											P	P
Red-shouldered hawk*	<i>Buteo lineatus</i>											P	P
Broad-winged hawk	<i>B. platypterus</i>											P	P
Red-tailed hawk*	<i>B. jamaicensis</i>							P				P	P
Wildturkey*	<i>Megeagrís gallopavo</i>											P	P
Mourning dove*	<i>Zenaidura macroura</i>		R									P	P
Yellow-billed cuckoo	<i>Coccyzus americanus</i>	C						P		C		R	C
Great horned owl*	<i>Bubo virginianus</i>		P		P							P	
Barred owl*	<i>Strix varia</i>												P
Common nighthawk	<i>Chordeiles minor</i>		P		P								
Chuck-will's-widow	<i>Caprimulgus carolinensis</i>		P		P								
Chimney swift	<i>Chaetura pelagica</i>							P					P
Ruby-throated hummingbird	<i>Archilochus colubris</i>							R		P		P	P
Red-bellied woodpecker*	<i>Melanerpes carolinus</i>	C	R							R		R	R
Downy woodpecker*	<i>Picoides pubescens</i>	C					R	C		R		R	C
Hairy woodpecker*	<i>P. villosus</i>		R		R					R		P	R
Northern flicker*	<i>Colaptes auratus</i>		R		R							P	P
Pileated woodpecker*	<i>Dryocopus pileatus</i>				P			R		C		C	C
Eastern wood-pewee	<i>Contopus virens</i>	C			C			C		C		C	C
Acadian flycatcher	<i>Empidonax virescens</i>	C			C		C	C		C		P	C
Eastern phoebe	<i>Sayornis phoebe</i>									P			P
Great crested flycatcher	<i>Myiarchus crinitus</i>	C	R		C							P	P
White-eyed vireo	<i>Vireo griseus</i>				C							P	
Yellow-throated vireo	<i>V. flavifrons</i>	C			C					R			R
Red-eyed vireo	<i>V. olivaceus</i>	C	R		C		C	C		C		C	C
Blue jay*	<i>Cyanocitta cristata</i>				C			P		C		R	C
American crow*	<i>Corvus brachyrhynchos</i>				C					R		C	C
Fish crow*	<i>C. ossifragus</i>											C	P
Carolina chickadee*	<i>Poecile carolinensis</i>									C		R	R
Tufted titmouse*	<i>Baeolophus bicolor</i>	C	C		C		C			C		R	C
White-breasted nuthatch*	<i>Sitta carolinensis</i>	C	R		R		R	R		C		R	C
Carolina wren*	<i>Thryothorus ludovicianus</i>	C			C					R		P	R
Blue-gray gnatcatcher	<i>Poliophtila caerulea</i>	C			C		R	R		R		C	C
Wood thrush	<i>Hylocichla mustelina</i>	C			C			R		R		C	C
Gray catbird	<i>Dumetella carolinensis</i>				C			R		R		P	
Northern parula	<i>Parula americana</i>	C			C								R
Black-throated green warbler	<i>Dendroica virens</i>				C								R
Yellow-throated warbler	<i>D. dominica</i>												P

continued

Table 1—Birds reported in relatively undisturbed upland hardwood forests during the breeding season in the Arkansas Ozarks (continued)

Species	Scientific name	James (1971)		Shugart and James (1973)		Smith (1977)		Fleming Creek		Swain/Barberry		Forest Service R8.bird	
		Mesic	Xeric	Mesic	Xeric	Mesic	Xeric	Mesic	Xeric	Mesic	Xeric	Mesic	Xeric
Pine warbler*	<i>D. pinus</i>									P		P	P
Cerulean warbler	<i>D. cerulea</i>											R	
Black-and-white warbler	<i>Mniotilta varia</i>	C	C					R		C		R	C
American redstart	<i>Setophaga ruticilla</i>											R	C
Worm-eating warbler	<i>Helminthos vermivorus</i>									P		R	C
Ovenbird	<i>Seiurus aurocapillus</i>	C								C		C	C
Louisiana waterthrush	<i>S. motacilla</i>										P		P
Kentucky warbler	<i>Oporornis formosus</i>										R		R
Commonyellowthroat	<i>Geothlypis trichas</i>												P
Hooded warbler	<i>Wilsonia citrina</i>												C
Yellow-breasted chat	<i>Icteria virens</i>												R
Summer tanager	<i>Piranga rubra</i>												P
Scarlet tanager	<i>P. olivacea</i>												P
Eastern towhee*	<i>Pipilo erythrophthalmus</i>	C											C
Northern cardinal*	<i>Cardinalis cardinalis</i>												P
Indigo bunting	<i>Passerina cyanea</i>												R
Brown-headed cowbird*	<i>Molothrus ater</i>												C
American goldfinch*	<i>Carduelis tristis</i>												P

C = more common species; R = rarer species; P = species present on study site at least once (see text for full explanation).

Names followed by * are permanent resident species.

Where possible, the distinction is made between xeric and mesic upland forests. Data from Fleming Creek are from the control watershed during June and July. Data from Swain are from 1994 through 1999; data from Barberry are from 1994 through 2002; data from R8.bird are from 1997 through 2001.

Very little is known about use of upland hardwood forests during fall migration. Only 10 species were seen at Fleming Creek during fall and 8 of them were permanent resident species. One Ovenbird was observed along with 2 Brown Creepers (*Certhia americana*).

Combining all seasons, there were no differences in richness or species diversity among the 4 watersheds at Fleming Creek, but there was a significant difference in equitability (or evenness), species being less evenly distributed in the clear-cut ($J = 0.80$) than in the other 3 watersheds ($J > 0.90$ for all three) ($F = 4.61$, $df = 3, 59$, $P = 0.006$). During summer, species diversity and average species richness were significantly higher in the selective-cut ($H = 2.90$, average number of species per census = 22.0) compared to the other 3 watersheds ($F = 8.65$, $df = 3, 8$, $P = 0.007$ and $F = 11.25$, $df = 3, 8$, $P = 0.003$). Overall similarity (Wolda 1981) of the 4 watersheds at Fleming Creek for all censuses was 26 percent, suggesting that the plots are not very similar in species composition.

Effects of Various Forest Practices on Breeding Birds

Almost any forestry practice that disturbs the closed canopy of an upland hardwood forest in the Arkansas Ozarks increases the number of species present during the breeding season. At Fleming Creek, 21 species were found in the control, but 24 were found in the clearcut, 29 in the selective cut, and 30 in the pine conversion. At Gulf Branch, there were 32 species during the 3 years pre-cut and a total of 36 species present in the 7 years post-cut. At Williams Hollow, there were 28 species the first year (pre-cut) and a total of 39 species during the 9 years post-cut. At Junction, there were 29 species in the 3 years pre-cut and a total of 38 species in the 6 years of post-cut.

While several permanent resident species and some migrants remained common (table 3), a new suite of birds became common in the forests that had been subject to harvest. These included Indigo Bunting, Carolina Wren, Hooded Warbler, Kentucky Warbler, Northern Cardinal,

Table 2—Migrant species observed during spring on the control at Fleming Creek and in the eastern part of the Ozark National Forest

Species	Scientific name	Fleming Creek	Eastern ONF
Black-billed cuckoo	<i>Coccyzus erythrophthalmus</i>		X
Red-headed woodpecker	<i>Melanerpes erythrocephalus</i>		X
Least flycatcher	<i>Empidonax minimus</i>		X
“Trails” flycatcher	<i>E. traillii/alnorum</i>		X
Yellow-bellied flycatcher	<i>E. flaviventris</i>		X
Ruby-crowned kinglet	<i>Regulus calendula</i>		X
Veery	<i>Catharus fuscescens</i>		X
Swainson’s thrush	<i>C. ustalatus</i>	X	X
Gray-cheeked thrush	<i>C. minimus</i>	X	X
Solitary vireo	<i>Vireo solitarius</i>		X
Warbling vireo	<i>V. gilvus</i>		X
Philadelphia vireo	<i>V. philadelphicus</i>		X
Blue-winged warbler	<i>Vermivora pinus</i>	X	X
Golden-winged warbler	<i>V. chrysoptera</i>		X
Tennessee warbler	<i>V. peregrina</i>	X	X
Orange-crowned warbler	<i>V. celata</i>		X
Nashville warbler	<i>V. ruficapilla</i>		X
Blackburnian warbler	<i>Dendroica fusca</i>	X	X
Cape May warbler	<i>D. tigrina</i>		X
Magnolia warbler	<i>D. magnolia</i>		X
Yellow-rumped warbler	<i>D. coronata</i>	X	X
Bay-breasted warbler	<i>D. castanea</i>		X
Blackpoll warbler	<i>D. striata</i>		X
Yellow warbler	<i>D. petechia</i>		X
Mourning warbler	<i>Oporornis philadelphia</i>		X
Canada warbler	<i>Wilsonia canadensis</i>		X
Wilson’s warbler	<i>W. pusilla</i>		X
American redstart	<i>Setophaga ruticilla</i>	X	X
Rose-breasted grosbeak	<i>Pheucticus ludovicianus</i>		X
Dickcissel	<i>Spiza americana</i>		X
Bobolink	<i>Dolichonyx oryzivorus</i>		X
Orchard oriole	<i>Icterus spurius</i>		X
Baltimore oriole	<i>I. galbula</i>	X	X

ONF = Ozark National Forest.
Source: Rodewald (1995).

Table 3—Birds reported in disturbed upland forests that have been subjected to herbicides and the planting of pines (pine conversion), clearcutting, and shelterwood and group-selection harvesting regimes^a

Species	Pine conversion	Clearcut Fleming	Shelterwood		Group selection		
	Fleming		Fleming	Gulf Branch	William's Hollow	Junction	Swain
Turkey vulture*	P						
Wild turkey*				P			
Northern bobwhite*				P			
Yellow-billed cuckoo	P		P	C	C	C	R
Chuck-will's-widow	R						
Chimney swift		P					
Ruby-throated hummingbird	C	C	C	R	R	R	R
Red-bellied woodpecker*			R	R	R	R	R
Downy woodpecker*	R	R	C	C	C	C	C
Hairy woodpecker*		R	R	R	C	R	R
Pileated woodpecker*		P	R	C	C	R	P
Eastern wood-pewee	C	C	R	C	C	C	C
Acadian flycatcher	R		R		C	R	C
Eastern phoebe	C	R		P	P		
Great crested flycatcher	P				P		
White-eyed vireo	P			P	C	C	
Yellow-throated vireo	P		C	R	R	R	R
Red-eyed vireo	C		C	C	C	C	C
Blue jay*	R		R	R	C	C	R
American crow*				C	C	R	R
Carolina chickadee*	P	R	R	C	C	C	C
Tufted titmouse*		R	R	C	C	C	C
White-breasted nuthatch*			R	C	C	C	C
Carolina wren*		P	R	C	C	C	C
House wren		P					
Blue-gray gnatcatcher	R	P	C	C	C	C	
Eastern bluebird*		R	P	R	P	P	
Wood thrush				P	R	R	R
American robin*				P	P		
Cedar waxwing*	P		P				
Blue-winged warbler						R	
Northern parula	P		R				
Chestnut-sided warbler						R	
Pine warbler*				R	R		
Cerulean warbler						P	
Black-and-white warbler	P		C	C	C	C	R
Worm-eating warbler	P	R	C		R	R	
Ovenbird	P		R	C	C	C	C
Louisiana waterthrush	P				P		P
Kentucky warbler	C	R	R	R	C	C	R
Common yellowthroat	P						
Hooded warbler	C	R	C	C	C	C	C
Yellow-breasted chat	R	C			R	R	
Summer tanager				P	R	R	
Scarlet tanager	R	R	C	C	C	C	C
Eastern towhee*	C	C	R	C	C	C	P
Field sparrow						P	
Northern cardinal*		P	R	C	C	C	R
Blue grosbeak	R	R			P	P	
Indigo bunting	C	C	C	C	C	C	C
Brown-headed cowbird*	P	P	R	P	R	P	
American goldfinch*	C	C	C	R	R	R	R

C = more common species; R = rarer species; P = species present on study site at least once (see text for full explanation).

Names followed by * are permanent resident species.

^a All these studies have occurred in rather mesic situations. The Fleming Creek data are based on three censuses conducted in June and July of 1984 and 1985; the Gulf Branch data are based on point-counts done each summer from 1996 through 2002; the William's Hollow data are based on point-counts from 194 through 2002; the Junction data are from point-counts conducted from 1997 through 2002; and the Swain data are from point-counts conducted from 2000 through 2002.

Eastern Towhee, Eastern Wood-Pewee, and White-eyed Vireo. Other species not normally associated with mature forests also appeared in small numbers: Blue Grosbeak (*Vermivora pinus*), Chestnut-sided warbler (*Dendroica pensylvanica*), Blue-winged Warbler, Yellow-breasted Chat, and Eastern Bluebird (*Sialia sialis*). Brown-headed Cowbirds have a greater presence in disturbed forest (table 3) compared to undisturbed forests (table 1).

DISCUSSION

The breeding birds found in upland deciduous forest of the Arkansas Ozarks form a distinct group (James 1971), composed of obligate mesic forest species, such as Acadian Flycatcher, Wood Thrush, Worm-eating Warbler, Cerulean Warbler, Ovenbird, Black-and-white Warbler, and Scarlet Tanager, and other more wide-ranging species, mostly permanent residents that tend to have higher population densities (Shugart and James 1973, Smith 1977, Rodewald and Smith 1998). Members of that later group would include Carolina Chickadee, Tufted Titmouse, Pileated and Downy woodpeckers, and White-breasted Nuthatch. No introduced or exotic species have invaded this particular habitat.

In a typical upland hardwood forest in the Arkansas Ozarks, most migratory breeders and permanent resident species nest in the canopy or in tree trunks, a few migratory species nest on the ground (e.g., Ovenbird and Black-and-white, Kentucky, and Worm-eating warblers) and only one species nests in shrubs (Hooded Warbler). Given the relatively even-age structure of those upland forests, the canopy is closed and there is very little development of a shrub layer. For example, Acadian Flycatchers commonly sally for insects between the bottom of the canopy and above the forest floor within the forests of the Ozarks (Smith 1977). However, opening the canopy and allowing light to penetrate to the forest floor quickly (i.e., with 1 or 2 years) allows for development of a shrub layer (Rodewald and Smith 1998), which becomes an almost impenetrable thicket within 5 to 10 years. Even relatively small openings may have an impact on forest birds (Annand and Thompson 1997) and development of the shrub layer may attract new species (e. g., White-eyed Vireo, Blue Grosbeak, Indigo Bunting) not normally associated with mature forested habitats (Thompson and others 1992, Annand and Thompson 1997, Rodewald and Smith 1998). Opening of the forest canopy either immediately (Kendeigh 1982) or eventually (Rabenold and others 1998) allowed early successional bird species to colonize new areas that previously were unsuitable habitats (see also Thompson and others 1992). Rodewald and Smith (1998) concluded that removal of understory vegetation could negatively affect some ground-nesting and shrub-nesting forest interior species, whereas edge species might react positively. Similarly, Gram and others (2001) recently documented short-term changes in bird community structure in the Missouri Ozarks with an estimated change of only < 10 percent of the canopy structure. Fragmented forests in Missouri actually have more species than contiguous forests, but the abundance of Neotropical migrants that breed in mature forests is greatly reduced in the fragmented forests (Howell and others 2000).

Xeric upland hardwood forests had fewer breeding species than did mesic upland forests (table 1). At Pea Ridge National Monument, densities in xeric forest were about 100 males per 40-ha compared to nearly 400 males per-40 ha (Shugart and James 1973). Upland hardwood forests contain very few species in winter and our data suggest that fall migration may be meager in that habitat. It would appear that upland hardwood forests in the Arkansas Ozarks have a substantial migration in spring, which warrants further study. Rodewald (personal communication) also felt that numbers of birds in spring migration were higher on his study plots in the eastern Ozarks than in the western edge around Fayetteville.

Given the descriptions of the pre-settlement forests of the Ozarks (Braun 1950, Beilman and Brenner 1951, contra Steyermark 1959), these upland assemblages must be of recent origin, commonly occurring together in these forests for maybe only the last 150 years. The recent expansion of these upland forest types in the Ozarks may explain why fewer species breed here than in areas further to the east. Indeed it would appear that xeric upland hardwood forests in the Ozarks have the least number of breeding species than any other forest type in the eastern deciduous forest. Smith (1977) suggested that the recent appearance of the xeric upland forest may explain the low number of breeding species. The recent expansion of the Black-throated Green Warbler (Rodewald 1997), and possibly of Cooper's and Sharp-shinned (*Accipiter striatus*) hawks, would suggest that new species are still being added to the avifauna of the Arkansas Ozarks.

Impact of Elimination of Red Oaks by Red Oak Borers

Many forest insect species that have become unique and distinctly significant disturbance factors in relatively unmanaged native forests are exotics. The red oak borer, however, is a native insect species in eastern North America (Donley and Acciavatti 1980) that attacks living oak trees. Population levels of the epidemic magnitude currently being reported in the Ozark Mountains have never been witnessed within the range of this species. Typically red oak borer infestations have been local and they previously have been considered as an unimportant insect pest in oak forests (Oak 2002).

As reviewed in Smith and Stephen (In press), factors involved with the current outbreak include advanced age of stands (70-100 years); xeric conditions associated with shallow rocky soils, exacerbated by three years of drought; and appearance of two fungi, one attacking roots and one attacking above ground, all of which weaken the trees' resistance to attack by red oak borers. Coincident with that opinion is the idea that the logging history of the region, which consisted of continuous high grading of the forests during the early 1900s, resulted in stands that are frequently dominated by red oaks of similar age structure (Ozark-St. Francis National Forests 1978).

Based on research presented here and other published works, Smith and Stephen (in press) predicted that populations of 10 of 20 migratory species (Yellow-billed Cuckoo, Acadian Flycatcher, Red-eyed Vireo, Wood Thrush, Black-

throated Green Warbler, Cerulean Warbler, Worm-eating Warbler, Ovenbird, Louisiana Waterthrush, Scarlet Tanager) will decline, and only 6 forest species were predicted to increase (Eastern Wood-Pewee, Blue-gray Gnatcatcher, Chestnut-sided Warbler, Hooded Warbler, Kentucky Warbler, Summer Tanager). At least 5 early successional species currently found in the Arkansas Ozarks (e.g., White-eyed Vireo, Blue Grosbeak, Blue-winged Warbler, Indigo Bunting, Yellow-breasted Chat), which are rare or absent from upland hardwood forests, should increase with the development of a scrub layer as the canopy opens. Possibly new species currently absent from the Arkansas Ozarks, such as Prairie Warbler (*Dendroica discolor*), will appear as a breeding species (see Annand and Thompson 1997). Cerulean Warbler, a species of conservation concern, is currently a relatively common wide-spread breeder in the Arkansas Ozarks (James and others 2001), but it will probably be extirpated with the demise of large oak trees (see Rodewald and Smith 1998). Populations of Black-throated Green Warblers, which recently colonized the Arkansas Ozarks (Rodewald 1997), will likely also be greatly reduced, as will most wood-warblers that breed in mature forests. In the short-term, populations of Chestnut-sided Warblers, another new breeder in the Ozarks (Rodewald 1997), will probably increase (Rabenold and others 1998). In other studies where tree species disappeared, canopy foraging species were negatively impacted by the elimination of live trees in the canopy, and ground and low-foraging species were not (Kendeigh 1982, Rabenold and other 1998). Thus, the red oak borer infestation has the potential to greatly alter the composition of the avifauna of the Ozarks, which may have far-reaching implications for many species of Neotropical migratory bird species. Elimination of oaks from the Ozarks could potentially reverse the source-sink relationship rather quickly, such that the Ozarks also may become unsuitable for sustained reproductive success for many species.

Prescribed Burning

Although historically prescribed burning has been rare in deciduous forests (Rotenberry and others 1995), there currently is interest in having more prescribed burns in upland hardwood forests. Dechant (1996) had the opportunity to census a plot of deciduous forest that had been burned the previous winter in the Erbie Historic Area in north Newton County, AR, and compare it with an adjacent plot of forest that did not burn. Although her sample sizes are small, she found an increase in Acadian Flycatcher and Blue-gray Gnatcatcher on the burned plot, and Eastern Wood-Pewee, Yellow-throated Vireo, and Summer and Scarlet tanagers on the burned plot, but not on the control. Black-and-white Warbler, Carolina Wren, and White-eyed Vireo occurred on the control but not the burned plot. As others have found, this suggests that flycatchers and birds that sally for food respond positively to burns, whereas the ground- and shrub-nesting layer may be adversely affected, at least in the short term. More research is needed in upland deciduous forest on the effects of fire on bird populations. For example, Burke and Nol (1998) recently demonstrated that female Ovenbirds are more sensitive to changes in soil invertebrate densities, which could be affected by fire, than are male Ovenbirds.

Brown-headed Cowbirds in the Arkansas Ozarks

With forest fragmentation due to red oak borers, one might expect that parasitism by Brown-headed Cowbirds would increase (e.g., Donovan and others 1995, Howell and others 2000). Donovan and others (1995) and Howell and others (2000) found that cowbirds were more common in fragmented forests in the Missouri Ozarks than in contiguous forests. Although cowbird nest parasitism is almost zero in upland forests of the Arkansas Ozarks today (table 1, Li 1994), cowbirds are more numerous in forests that have had some alterations (table 2). However, even though individuals may travel long distances to breed (Thompson 1994), presence of cowbirds in the forests of the Arkansas Ozarks will be severely limited by the availability of suitable feeding sites (Thompson 1994).

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IMPACTS OF POTENTIAL OAK FOREST CHANGE ON BREEDING BIRDS IN NORTHWESTERN ARKANSAS

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Abstract—Birds found on existing census routes in the Ozark region of northwestern Arkansas were used to predict avifaunal changes that could occur in the area due to oak-hickory forest degradation caused by red oak borer beetle infestations. The two census routes used passed through high elevation forests where red oaks thrive the best. Analysis showed that 21 bird species would decrease, 38 would increase, and 6 would remain unchanged in abundance in the event of forest thinning.

INTRODUCTION

Widespread death of oaks (*Quercus*) due to attacks by red oak borer beetles, *Enaphalodes rufulus* (Haldeman), is well documented (Spencer 2001). Resulting thinning and opening of the upland oak-hickory forests has been described for the Ozark Plateaus region of Arkansas (Spencer 2001). The change in forest structure before recovery would produce intervening rather open canopy stands with dense understory compared to pre-infestation conditions. Particularly in areas of dense oak stands, such as at high elevations in the Ozark National Forest, areas of forest are being completely removed.

This phenomenon will affect avifaunal composition in impacted areas. As a resource for predicting the nature of these changes there are 44 years (1967 to 2000) of data available from two roadside bird censuses in the region of concern. These censuses, two routes from the Breeding Bird Survey (Robbins 1986), are situated at high elevations where northern red oak (*Quercus rubra* L.), of northern affinity, thrives the best. This oak is the primary host of the red oak borer. These two Breeding Bird Surveys are also the only ones in Arkansas that have high numbers of two bird species of northern affinity, Scarlet Tanager and Ovenbird. (Scientific names of birds are in the tables, and authorities for these names are found in the A.O.U. Check-list of North American birds, 7th ed.)

Both the census routes pass through mature forest with a few pasture openings at high elevation around 2000 ft, and dip down to extensive areas of pasture lands and farm residences around 1000 ft elevation. Therefore, both forest birds and open country birds have been found over the years on the routes. The objective of this study is to identify the avian species already present that will increase or decrease with the opening of the forest due to oak borer infestation.

STUDY AREAS

The Compton and Lurton routes were the Arkansas routes of the Breeding Bird Survey (Robbins 1986) used to analyze the effects of forest change on the avifauna in the Ozarks. Both routes are in Newton County. The Compton route begins near the town of Compton on the ridge top, follows

highway 43 into the Buffalo River Valley joining highway 21 for a ways and then up to the ridge top again on a rural road. The Lurton route follows rural roads starting near Lurton on road 123 continuing north to Mt. Judea, then swinging south again on a road toward Cowell. Both routes are 24.5 miles long and at around 2000 ft elevation at each end dominated by forest, with river valleys in the middle at around 1000 ft or below dominated by pastures and farm yards.

METHODS

The Breeding Bird Survey (Robbins 1986) is a roadside bird census comprising 50 stops along 24.5 miles of road, the starting point randomly selected. Precisely the same stops on the same routes are visited annually every June. The census starts one-half hour before local sunrise at the route starting point. The observer records at each stop all the birds seen and heard there in a three-minute period. Then the observer drives one-half mile to the next three-minute stop, repeating until all 50 stops are covered. This has been repeated annually since 1967 at the Compton and Lurton routes. The data presented here are for 44 years from 1967 to year 2000. Results are expressed in number of individuals per bird species for each route averaged over the 44 years.

RESULTS

In order to evaluate which species will increase and which will decrease with the opening of the forest, studies of birds and their habitats must be consulted. Useful compilations of this information exist. One publication covers Arkansas (James and Neal 1986) another includes Arkansas and the rest of the southeastern United States (Hamel and others 1992), three cover nearby Missouri Ozarks (Clawson 1982, Evans and Kirkman 1981, Jacobs 1997), and one pertains to the forest lands of the southeastern Atlantic coast states (Hamel and others 1982). These sources were used collectively in making avian habitat determinations, supplemented by the author's own familiarity with Arkansas birds from field studies over the past 50 years.

Among all the birds found on the routes only species associated with upland forest and open uplands were evaluated. This eliminated water birds, one introduced species (pigeon), nocturnal birds (routes are covered in daytime when owls

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and goatsuckers are roosting), rare birds, species at the edge of their range, and species such as vultures that fly over several habitats. The birds that are expected to decrease with the opening of the forest due to oak borer damage are included in table 1, the ones that would increase are in table 2, and shown in table 3 those that should remain unchanged in abundance.

Three hawks occur along the routes: Red-shouldered Hawk, Broad-winged Hawk, and Red-tailed Hawk. The open country Red-tailed Hawk will increase in areas where extensive tracts of forest are destroyed, the other two are forest birds and will decrease except where forest damage is slight.

The two upland game birds are Wild Turkey and Northern Bobwhite. The Turkey thrives where there are small forest openings but does not tolerate extensive forest loss. Also, acorns are a major winter food. Therefore, turkeys would decrease following extensive oak forest thinning from red oak borer damage. The bobwhite is an open country and shrubby thicket bird. It will increase with the loss of forest canopy.

Table 1—Summer birds found on the Compton and Lurton Breeding Bird Surveys in the Arkansas Ozarks: species that would decrease if forest stands become more open

Species	Birds per route	
	Compton	Lurton
Red-shouldered Hawk (<i>Buteo lineatus</i>)	0.56	0.44
Broad-winged Hawk (<i>B. platypterus</i>)	0.11	0.44
Wild Turkey (<i>Meleagris gallopavo</i>)	0.22	0.22
Red-bellied Woodpecker (<i>Melanerpes carolinus</i>)	6.56	2.89
Downy Woodpecker (<i>Picoides pubescens</i>)	3.56	3.56
Hairy Woodpecker (<i>P. villosus</i>)	1.44	0.67
Pileated Woodpecker (<i>Dryocopus pileatus</i>)	6.78	7.11
Eastern Wood-Pewee (<i>Contopus virens</i>)	11.00	12.33
Acadian Flycatcher (<i>Empidonax virens</i>)	2.22	4.56
Yellow-throated Vireo (<i>Vireo flavifrons</i>)	2.44	0.67
Red-eyed Vireo (<i>V. olivaceus</i>)	37.89	54.89
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	3.78	9.44
Wood Thrush (<i>Hylocichla mustelina</i>)	5.78	6.00
Cerulean Warbler (<i>Dendroica cerulea</i>)	0.67	0.56
Black and White Warbler (<i>Mniotilta varia</i>)	5.89	7.44
Worm-eating Warbler (<i>Helminthos vermivorus</i>)	1.44	2.89
Ovenbird (<i>Seiurus aurocapillus</i>)	9.89	33.67
Louisiana Waterthrush (<i>S. motacilla</i>)	1.33	0.56
Kentucky Warbler (<i>Oporornis formosus</i>)	9.00	5.78
Hooded Warbler (<i>Wilsonia citrina</i>)	2.89	5.22
Scarlet Tanager (<i>Piranga olivacea</i>)	6.89	9.00

Table 2—Summer birds found on the Compton and Lurton Breeding Bird Surveys in the Arkansas Ozarks: species that would increase if forest stands become more open

Species	Birds per route	
	Compton	Lurton
Red-tailed Hawk (<i>Buteo jamaicensis</i>)	0.22	0.33
Northern Bobwhite (<i>Colinus virginianus</i>)	6.00	1.22
Yellow-billed Cuckoo (<i>Coccyzus americanus</i>)	8.56	12.67
Ruby-throated Hummingbird (<i>Archilocus colubris</i>)	2.00	2.22
Red-headed Woodpecker (<i>Melanerpes erythrocephalus</i>)	0.00	0.00
Northern Flicker (<i>Colaptes auratus</i>)	0.22	0.00
Eastern Phoebe (<i>Sayornis phoebe</i>)	4.22	3.00
Great-crested Flycatcher (<i>Myiarchus crinitis</i>)	3.44	2.67
Eastern Kingbird (<i>Tyrannus tyrannus</i>)	1.89	1.33
Scissor-tailed Flycatcher (<i>T. forficatus</i>)	0.44	0.11
White-eyed Vireo (<i>Vireo griseus</i>)	6.56	4.22
American Crow (<i>Corvus brachyrhynchos</i>)	32.11	30.00
Purple Martin (<i>Progne subis</i>)	6.89	6.22
Barn Swallow (<i>Hirundo rustica</i>)	6.78	1.56
Carolina Wren (<i>Thryothorus ludovicianus</i>)	15.56	7.78
Blue-gray Gnatcatcher (<i>Poliophtila caerulea</i>)	13.44	13.11
Eastern Bluebird (<i>Sialia sialis</i>)	12.44	4.78
American Robin (<i>Turdus migratorius</i>)	7.78	3.33
Gray Catbird (<i>Dumetella carolinensis</i>)	0.22	1.22
Northern Mockingbird (<i>Mimus polyglottos</i>)	0.44	0.56
Brown Thrasher (<i>Toxostoma rufum</i>)	2.67	0.33
European Starling (<i>Sturnus vulgaris</i>)	1.00	2.78
Blue-winged Warbler (<i>Vermivora pinus</i>)	0.56	0.33
Yellow Warbler (<i>Dendroica petechia</i>)	1.00	0.00
Prairie Warbler (<i>Dendroica discolor</i>)	0.00	0.11
Common Yellowthroat (<i>Geothlypis trichas</i>)	2.56	0.78
Yellow-breasted Chat (<i>Icteria virens</i>)	6.22	7.56
Summer Tanager (<i>Piranga rubra</i>)	7.33	6.33
Eastern Towhee (<i>Pipilo erythrophthalmus</i>)	12.11	7.89
Chipping Sparrow (<i>Spizella passerina</i>)	13.56	12.56
Field Sparrow (<i>S. pusilla</i>)	15.33	6.89
Northern Cardinal (<i>Cardinalis cardinalis</i>)	17.67	15.00
Blue Grosbeak (<i>Guiraca caerulea</i>)	15.11	3.33
Indigo Bunting (<i>Passerina cyanea</i>)	39.89	51.22
Common Grackle (<i>Quiscalus quiscula</i>)	1.56	3.33
Brown-headed Cowbird (<i>Molothrus ater</i>)	11.89	6.33
Orchard Oriole (<i>Icterus spurius</i>)	6.00	2.56
American Goldfinch (<i>Carduelis tristis</i>)	5.56	1.89

Table 3—Summer birds found on the Compton and Lurton Breeding Bird Surveys in the Arkansas Ozarks: species that would not change in abundance if forest stands become more open

Species	Birds per route	
	Compton	Lurton
Blue Jay (<i>Cyanocitta christata</i>)	8.89	8.67
Carolina Chickadee (<i>Poecile carolinensis</i>)	9.89	13.67
Tufted Titmouse (<i>Baeolophus bicolor</i>)	16.78	9.67
Dickcissel (<i>Spiza americana</i>)	2.00	1.11
Eastern Meadowlark (<i>Sturnella magna</i>)	10.89	2.89
House Sparrow (<i>Passer domesticus</i>)	1.44	2.44

Yellow-billed Cuckoo, which is very abundant on both routes (table 2), seeks more open than dense forest and will only increase with forest thinning. Ruby-throated Hummingbird is an open country bird. It too will increase when forest openings are created.

Obviously most of the woodpeckers will decrease when the forest is degraded. For a brief period dead trees and wood boring insects will be an attraction followed by overall woodpecker decrease. The decreasing ones are Red-bellied Woodpecker, Downy Woodpecker, Hairy Woodpecker, and Pileated Woodpecker. The Red-headed Woodpecker is very responsive to standing dead trees and is expected to show a spectacular influx, even though none have been present on either route. It is a nomadic species that quickly finds new suitable areas. However, it also stores acorns for winter food. The loss of oaks will have a negative effect. Northern Flicker inhabits open lands where it feeds on the ground on ants. It will increase.

There were six species in the flycatcher family on the two census routes. Four will increase with forest degradation: Eastern Phoebe, Great-crested Flycatcher, Eastern Kingbird, Scissor-tailed Flycatcher. The Great-crested Flycatcher will increase if forest thinning is not too severe. The change in Phoebe abundance depends too on availability of its unique nesting site. The kingbird and Scissor-tailed Flycatcher, uncommon on the routes (table 2), occur in extensive open country. Two other flycatchers are both forest dependent and will decrease with disappearance of forest. Acadian Flycatcher seeks thickets in dense mature woods. Eastern Wood-Pewee, very abundant on the routes (table 1), will increase some with initial forest canopy opening but will decrease with further degradation.

Of the vireos on the routes, White-eyed Vireo is a denizen of dense thickets in forest edge habitat and will increase with forest opening. The other two, Yellow-throated Vireo and Red-eyed Vireo, are forest birds and will decrease. Notice that the Red-eyed Vireo along with the Indigo Bunting (tables 1 and 2) are the most common birds on both routes. These two top abundances are typical of bird populations in Arkansas (James and Neal 1986, p. 48) and the eastern United States.

American Crows, Purple Martins and Barn Swallows all will increase with forest degradation. The Blue Jay is an interesting case. The large wintering migratory population (James and Neal 1986) will dwindle because jays feed on acorns in winter. The birds counted on the survey routes are nesting birds not dependent on acorns in summer. However, they are also year around residents, so their winter survival will suffer from acorn deficits causing population decline. The thinning of the forest would have the opposite effect producing more jay habitat because jays occupy broken forest, not dense closed canopy stands. Counterbalancing these two opposite effects, numbers of jays will probably be unchanged.

Carolina Chickadee and Tufted Titmouse occur equally in forest and forest edge. No change is expected in their numbers. Forest disappearance will cause declined in White-breasted Nuthatches. Carolina Wren, a forest edge bird, already rather common, will increase. Blue-gray Gnatcatcher is a forest bird but seeks more open forest and forest edge. It will increase with forest canopy breakup.

The survey routes have seven species in the thrush and mimic thrush families, plus the closely related starling. Only one in this group, the Wood Thrush, now fairly abundant (table 1) will decrease with forest change. The others thrive in open country and forest edge and will increase: Eastern Bluebird, American Robin, Gray Catbird, Northern Mockingbird, Brown Thrasher and European Starling.

Seventeen species of nesting warblers were found on the two survey routes of which twelve are associated with upland oak-hickory forest or upland open habitats. Opening the forest will produce increases in five of these: Blue-winged Warbler, Yellow Warbler, Prairie Warbler, Common Yellowthroat and Yellow-breasted Chat. Seven will decrease: Cerulean Warbler, Black and White Warbler, Worm-eating Warbler, Ovenbird, Louisiana Waterthrush, Kentucky and Hooded Warblers. The Cerulean Warbler seeks forest canopies with small breaks (James and others 2001), so at first there will be an increase, later rapid decline as the forest becomes more open.

With regard to the two tanagers, the Summer Tanager has a southern affinity and the Scarlet Tanager is part of a northern avifauna. They seek different habitats. Summer Tanager will increase with forest thinning because it occupies broken forest and tall forest edge. Scarlet Tanager will decrease since it occurs in closed canopy forests.

There were nine species in the sparrow, bunting, finch group on the two Breeding Bird Survey routes. Two of these will show no change, the House Sparrow because it occupies barnyard and pasture sites, and the Dickcissel that depends on extensive hay fields. The rest are all open country thicket, forest edge, and old field birds. They will increase with opening of the upland forest: Eastern Towhee, Chipping Sparrow, Field Sparrow, Northern Cardinal, Blue Grosbeak, Indigo Bunting (already extremely common, table 2), and American Goldfinch.

Eastern Meadowlark will be unaffected by forest change since it occupies pastures and hayfields. All the rest of the

blackbird family will increase with forest degradation because they thrive in a landscape mosaic of forest and open country patches: Common Grackle, Brown-headed Cowbird, Orchard Oriole.

DISCUSSION

Two Breeding Bird Survey routes in northwestern Arkansas contain 44 years of information for predicting changes in bird populations if upland forests are thinned and opened by red-oak borer infestations. These two routes traverse high elevation forests where northern red oak is most abundant, and where forest birds predominate. Both routes also dip into a valley where open farmland exists inhabited by open country and forest edge birds. These latter birds will increase when the forest is opened; the forest birds will decrease. Among the species found on the two census routes there are 21 that will decrease in abundance, 38 that will increase, and 6 that will exhibit no change.

This investigation refers only to what will happen to breeding birds in the event of forest change in the study area. Decrease in forest cover will also affect winter resident bird populations and migrant species in passage. Predictions regarding these species will require further study. Some of the breeding birds mentioned herein are permanent residents and thus are present in winter too.

ACKNOWLEDGMENTS

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OAK DECLINE IN MISSOURI: HISTORY REVISITED

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INTRODUCTION

In the 1980s, following extreme winters in the late 1970s and severe droughts in 1976, 1980, and 1983, dead and dying scarlet and black oaks were found on 185,000 acres of the Mark Twain National Forest. That decline event was linked to environmental stresses (Law and Gott 1987). Severe oak decline is now affecting an estimated 500,000 acres on the Mark Twain. High-risk stands are predisposed to severe damage because mature scarlet (*Quercus coccinea* Muenchh.) and black oak (*Q. velutina* Lam.) dominate in fully stocked stands on droughty sites. The current decline was triggered by serious moisture deficits from 1999 until mid-May, 2001. Insects and diseases contributing to tree death and decline include *Armillaria* root rot, twolined chestnut borer (*Agrilus bilineatus* Weber), red oak borer (ROB) (*Enaphalodes rufulus* Haldeman), and insect defoliators.

The extensive areas now occupied by dense scarlet and black oak stands are artifacts of European settlement that replaced shortleaf pine (*Pinus echinata* Mill.) and oak-pine forests and woodlands of long-standing (Nelson 2002). Prior to European settlement, much of the Missouri Ozarks had more-open forests and woodlands dominated by shortleaf pine and maintained by large herbivores and by frequent, low-intensity fires set by Native Americans (Nigh 1992, Guyette and Cutter 1991, Yatskievych 1999, Stambaugh 2001). After extensive logging between 1870 and 1930, these lands were subjected to annual burning and overgrazing by free roaming livestock, resulting in erosion and loss of soil moisture holding capacity. Forest fire control began in the mid-1930s, which allowed sprouts and seedlings of the red oak group to survive and develop. Missouri botanist Julian Steyermark, in his 1937 study of newly acquired national forest lands, reported a hodgepodge of vegetation with some species out of place and others occurring in disproportional numbers.

METHODOLOGY

In winter 2001/2002 permanent oak mortality monitoring plots were established in 57 stands throughout portions of the Mark Twain National Forest located in the Ozarks.

- 43 high risk stands (upland scarlet/black oak > 70 years old)
- 10 DFC (desired future condition) stands (majority of stocking in shortleaf pine/white oak, with black/scarlet oak stocking < 40 percent)

- 4 Riparian stands to monitor oaks on drainageways/lower slopes

Tree species and condition were tallied using 10-BAF variable radius plots on 5 points/stand; three 1/100th acre regeneration plots were established at each sampling point (Mielke 2001).

RESULTS

Severe decline symptoms, mortality and ROB attacks were limited almost exclusively to the red oak group. Forest health was rated good only in the DFC stands; riparian and high risk stands were fair. Red oak borers (ROB) infested 85-90 percent of the red oak group to some degree in all stands except riparian stands, which had only 69 percent of red oaks attacked. All stand categories had comparable ratings for > 33 percent crown dieback (~ 40 percent), and ~ 8 percent red oak BA mortality in 2001. All districts had high percentages of red oak BA affected by ROB (70-98 percent). However, the average number of ROB attacks/tree was greatest on the Potosi/Fredericktown, Houston/Rolla and Cassville Districts. Ratings for red oak crown dieback > 33 percent varied from 28-48 percent between districts. White oak reproduction generally exceeded red oak group reproduction on all districts, in agreement with earlier surveys (Law and Johnson 1989) (Davidson 1990). Shortleaf pine reproduction was less abundant than that of oak species and pine regeneration was absent on some districts.

DISCUSSION

Based on monitoring of the 1980s decline on the Doniphan/Eleven Point District (Law and Johnson 1989), further decline and mortality of red oaks in declining stands is anticipated. Scarlet and black oak components in heavily stocked mature stands should be harvested and regenerated with mixtures including more drought-tolerant, longer-lived white oaks and shortleaf pine. Otherwise, red oak decline and mortality are likely to recur frequently in the Missouri Ozarks - history will continue to be revisited.

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MODELING GYPSY MOTH-RELATED TREE MORTALITY UNDER DIFFERENT OUTBREAK SCENARIOS IN INTERIOR HIGHLANDS FORESTS

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Abstract—A simulation was conducted to determine how growth of forests in the Interior Highlands would change under attack by the gypsy moth (*Lymantria dispar* L.). Simulations were conducted for three different outbreak intensities using the Gypsy Moth Stand-Damage Model. Forest Inventory and Analysis (FIA) inventory data were used as input for the simulation. An ecological approach was taken for the simulation runs by stratifying the FIA data by ecological subsection, to better understand how outbreak effects might differ by subsection. Results show significantly greater percentage losses in stem density in the southern part of the Interior Highlands under both the moderate and heavy outbreak scenarios. The percent decline in basal area is nearly doubled in all susceptibility classes between the moderate and heavy defoliation scenarios. This is the first detailed examination of the damage that will inevitably occur when, at some unforeseen point within the next 100 years, gypsy moth becomes established in the Interior Highlands.

RESEARCH SUMMARY

The purpose of this study is to quantify the gypsy moth-related mortality and subsequent mortality-induced growth losses that might be expected in these highly susceptible forests in the event of gypsy moth outbreaks in the forests of the Interior Highlands. The Gypsy Moth Stand Damage Model (Colbert and Racin 2001) was used to simulate these losses using the “canned” scenarios that have been built into the model. Three outbreak scenarios were considered—moderate, heavy, and none. The length of the simulation was set at 20 years since that period of time is long enough to simulate changes but not so long that simulations would be unreliable. Output from the model was averaged for each simulation, weighted by forested acres expansion factors, by each subsection and susceptibility class. These averages were then used to calculate percentage losses for each scenario by dividing the moderate or heavy outbreak result by the baseline result.

Inventory plot data were obtained from the Eastwide forest survey database and FIA plots were stratified within the Interior Highlands by ecological section and subsection. The sheer number of forest survey plots and the plot-by-plot processing required to translate plot data into the model dictated that a subset of forest survey plots be sampled for inclusion in the model. Within each ecological subsection, plots were placed in a gypsy moth susceptibility class based on percent of basal area in gypsy moth preferred species. The initial random sample of forest survey plots was conducted to include a minimum of three plots per subsection (without replacement) in each of the four susceptibility classes. If this was less than a 1 percent sample of the forested area of a subsection/susceptibility class combination, additional plots were sampled to bring the sample percentage up to 1 percent.

No significant differences were observed by section for basal area loss under either the moderate or heavy defoliation scenarios. Basal area declined over time; percent basal area decline varied from 34.9 to 40.1 percent under the moderate defoliation scenario, and from 74.6 to 81.3 percent under the heavy defoliation scenario. Conversely, changes in stem density were significant by section. When plots were stratified by susceptibility, the opposite effect was seen. Under both moderate and heavy outbreak scenarios, significant differences in percent basal area loss were observed by susceptibility class. Immune plots had a smaller percent loss than highly susceptible plots. Under the moderate outbreak scenario, percent basal area loss varied from 25.6 in immune plots to 48.2 percent in highly susceptible plots. Under the heavy outbreak scenario, the trend was the same but more pronounced; basal area decline varied from 64.0 percent in immune plots to 88.1 percent in highly susceptible plots. There were no significant differences in percent change in stem density by susceptibility class under either the moderate or heavy outbreak scenarios. The heavy outbreak scenario often caused a reduction in the susceptibility class due to the large amount of mortality in susceptible species. In these results, the immune species group has significantly lower percent declines than the other groups, which suggests they will become more dominant at the end of the scenario.

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Management

FITTING FIRE INTO OAK MANAGEMENT

Patrick Brose¹

SUMMARY

In the past decade, the use of prescribed fire in the mixed-oak forests of the eastern United States has markedly increased to help overcome the chronic lack of abundant, vigorous oak regeneration (Yaussy 2000). However, prescribed burns implemented under inappropriate circumstances can result in failure to establish oak regeneration and/or loss of existing oak reproduction. To correctly use fire to promote regeneration of mixed-oak forests, stand developmental dynamics (Oliver and Larson 1990) and the oak regeneration process (Sander and others 1984) must be considered simultaneously.

When a mature mixed-oak forest is in the understory re-initiation stage, timber harvest or other major disturbance will move it to the stand initiation stage. Before this can take place, oak regeneration must become established in the mature stand. Research has shown that prescribed fire can help by preparing the seedbed for acorn caching by wildlife, xerifying the soil surface to inhibit establishment of mesophytic species, and decreasing populations of acorn-infesting insects (Barnes and Van Lear 1998, Van Lear and Watt 1993). To do this, burning must take place shortly before an acorn crop occurs. This is a difficult treatment to time because acorn crop occurrence fluctuates annually and is an event impossible to accurately predict. Also, these benefits only last a year or two. Burning should not take place immediately after an acorn crop (Auchmoody and Smith 1993) or when oak regeneration is still young and small (Brose and Van Lear, this proceedings) because fire kills acorns and new seedlings. Burning in mature oak stands also can help reduce understory competition and shade. To do this, burning must occur repeatedly as single fires seldom produce sufficient intensity to remove midstory trees. Because of these caveats and limitations, using prescribed fire to establish oak regeneration in mature stands generally requires multiple burns beginning several years or more before an anticipated harvest. Mechanical site scarification or waiting for a bumper acorn crop are probably better management strategies for establishing new oak seedlings than prescribed burning.

A mixed-oak stand that is entering the stand initiation stage via the shelterwood system is an ideal site for the use of prescribed burning if it has abundant oak regeneration that is being out-competed by faster growing species (Brose and others 1999). In this setting, fire, especially during the growing season, top kills the regeneration, shifting oak reproduction to a position of dominance because of its superior fire survival and sprouting abilities. In this context, the residual crop trees must be protected from the fire by removal of logging slash near their bases before burning or prevention of slash accumulation during the logging opera-

tion (Brose and Van Lear 1999). A new oak stand formed by a complete overstory removal also may benefit from prescribed burning. Like a shelterwood, it, too, must have abundant oak regeneration that is being out-competed by faster-growing species. However, this scenario has not yet been adequately researched to provide sound guidance.

Once a new oak stand grows past crown closure into the stem exclusion stage, there is no reason to use fire in its management. To do so would damage the lower boles of the trees, resulting in long-term value loss (Carvell and Maxey 1969).

Fire in mixed-oak forests can inadvertently create a major regeneration obstacle. Burned areas attract deer as sprouting hardwoods are highly preferred browse and this could lead to a localized deer overabundance problem. If this happens, fencing will probably be necessary to protect the new regeneration until it grows out of the reach of deer.

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CONVERSION OF SUCCESSIONALLY STABLE EVEN-AGED OAK STANDS TO AN UNEVEN-AGED STRUCTURE

Edward F. Loewenstein and James M. Guldin¹

Abstract—Developing a silvicultural prescription to convert an even-aged or unmanaged oak stand to an uneven-aged structure depends in large part on the length of time the existing overstory will live. Four conversion prescriptions, representing three initial stand conditions, are presented. Each prescription partitions the cut of the original overstory differently in time and space depending on the interval between stand entries and the desired allocation of growing space among the newly developing age classes.

INTRODUCTION

Oak-dominated forests of the Central and Eastern United States have generally not been regarded as suited to uneven-aged silviculture (Roach and Gingrich 1968, Sander and Clark 1971). In fact, several attempts to apply the selection method of reproduction cutting in oak-dominated stands have resulted in compositional shifts toward more shade tolerant species (Trimble 1970). Given these results, one might legitimately ask why conversion of these stands to an uneven-aged structure would be attempted, if maintenance of a dominant oak component were an objective of management.

However, empirical and experimental data suggest that under certain specific conditions, oak stands can be managed using uneven-aged methods. Many landowners are interested in managing uneven-aged stands because of the attributes that such stands provide. Among these are the maintenance of continuous forest cover in the stand, sustained yield of high-value products over time, and conditions suitable for plant and animal species that can advantageously utilize the stratified canopies and minimal harvesting impacts that are found in such stands.

In the Interior Highlands, not all stands are suitable for application of uneven-aged silviculture. Of stands that are ecologically suitable for conversion from even-aged to uneven-aged condition, efficiency of conversion depends greatly on stand condition at the beginning of the conversion process. For example, some landowners in the region, most prominently the Pioneer Forest in Salem, MO, have had great experience in creating well-structured uneven-aged upland oak stands, but these stands had their origin largely as poorly stocked cutover stands that were rehabilitated through judicious tending of residual growing stock (Loewenstein 1996, Loewenstein and others 2000). This pattern, where uneven-aged stands were created through rehabilitation of understocked conditions resulting from overcutting, has been a common theme in southern pine experience as well (Guldin and Baker 1998).

Conversely, there has been little practical or research experience in creating an uneven-aged structure from well-stocked

even-aged oak stands. In this paper, a review of existing information on even-aged stand dynamics is presented from the perspective of applying that information to convert fully-stocked even-aged stands of varying ages—immature, mature, and overmature—into stands with uneven-aged structure. Emphasis is given to three elements thought to be critical to the success of such conversion—site conditions, species composition, and existing age structure. The goal of this review is to suggest working hypotheses on the patterns by which uneven-aged stands can be developed, the treatments that might be applied, and the length of time required to consider the conversion a success.

ATTRIBUTES OF SUCCESSIONALLY STABLE EVEN-AGED OAK STANDS

Barrett (1995) broadly categorizes oak-dominated stands in the oak-hickory type as either sub-climax or successional stable. Sub-climax stands have the highest site indices (75+ feet, base age 50 years) and are the most difficult to regenerate to oak. Succession on these sites tends toward more shade-tolerant and/or mesophytic species (Barrett 1995, Johnson 1993, Sander and Graney 1993). Successional stable oak stands often occur on poor to medium quality sites that tend to be droughty. Few non-oaks can persist on these sites as canopy dominants (Weitzman and Trimble 1957, Roach and Gingrich 1968, Sander and Clark 1971, Barrett 1995). The selection studies that showed a compositional shift were conducted in stands that tended toward the sub-climax end of the spectrum. Conversely, single-tree selection has been shown to be a viable silvicultural alternative for maintaining an oak-dominated forest in successional stable stands (Loewenstein and others 1995, Loewenstein 1996, Loewenstein and others 2000).

Thus, discussion focuses on the successional stable end of the gradient of oak-dominated stands. The methodologies presented may prove to be more or less successful (from the perspective of developing and maintaining three age classes of oak) depending on where a stand is classified along that gradient.

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CONVERTING EVEN-AGED STANDS TO UNEVEN-AGED STRUCTURE

The success of conversion prescriptions depends on stand age and species composition, which determine whether the dominant overstory is capable of surviving the conversion period. Species longevity, in conjunction with stand age, gives an estimate of the time available to complete the conversion before the remaining residual overstory must be removed or until the likelihood of age-dependent mortality increases dramatically. The ability to maintain this residual overstory is not, in and of itself, integral to the conversion process; what is important is managing the growing space allocated to this age class. Widespread natural mortality of trees in the main canopy is an unpredictable event that affects both the development of trees in subordinate canopy classes and the regeneration/recruitment process. By losing control of growing space allocation, the ability to manage stand structure is compromised.

The conversion of an even-aged (single tiered canopy) stand to a multi-tiered structure (uneven-aged), and following conversion the maintenance of this structure, is accomplished by vertically partitioning growing space among age classes or cohorts. For purposes of this discussion, growing space is defined as percent stocking based on Gingrich's (1967) tree area equations and stocking chart.

Conversion prescriptions will only work if stocking of all age classes is kept closer to 58-60 percent stocking (the Gingrich 'B' line of stocking) rather than to 100 percent stocking (the Gingrich 'A' line). The 'B' line represents the low end of full stocking in a stand, assuming a uniform distribution of trees across the site; each tree is at maximum crown spread and there are no gaps between adjacent crowns. A stand at 'B' level stocking is allocating growth to significantly fewer trees than is a stand approaching 100 percent stocking, and this will be important during the conversion process.

Three conversion prescriptions will be discussed, based on stand age—conversion of immature stands, mature stands, and overmature stands. Within the mature stand condition, two patterns of conversion—uniform conversion and patch conversion—will also be discussed.

Immature Stands

In this prescription, a fully stocked young stand must be heavily cut during the initial entry; as a result, residual stocking levels will be quite low in the early years of the conversion (table 1a). This heavy cut is needed because young stands grow rapidly, and will quickly reoccupy the available growing space. Stands subject to this prescription must be followed closely lest stocking accrue to the point where the Gingrich 'B' line is approached.

The prescription applies to stands that are immature and fully stocked. It can also be used in situations where the landowner wishes to develop an uneven-aged state, but the existing stand does not lend itself to conversion. In such a situation, the stand is regenerated, and the succeeding even-aged stand is allowed to develop for approximately 30 years before the conversion is attempted.

Table 1—Levels of stocking by cohort and year used to implement three prescriptions to convert successional stable even-aged oak stands to uneven-aged structure

Year	Cohort						
	1	2	3	4	5	6	7
----- percent stocking -----							
a. Immature stands							
C-30	100	0	0	0	0	0	0
C-15	100	0	0	0	0	0	0
C	30	30	0	0	0	0	0
C+15	30	30	0	0	0	0	0
C+30	30	20	10	0	0	0	0
C+45	30	20	10	0	0	0	0
C+60	0	30	20	10	0	0	0
C+75	0	30	20	10	0	0	0
C+90	0	0	30	20	10	0	0
C+105	0	0	30	20	10	0	0
C+120	0	0	0	30	20	10	0
C+135	0	0	0	30	20	10	0
C+150	0	0	0	0	30	20	10
b. Mature stands							
C-30	100	0	0	0	0	0	0
C-15	66	0	0	0	0	0	0
C	50	10	0	0	0	0	0
C+15	40	20	0	0	0	0	0
C+30	30	20	10	0	0	0	0
C+45	30	20	10	0	0	0	0
C+60	0	30	20	10	0	0	0
C+75	0	30	20	10	0	0	0
C+90	0	0	30	20	10	0	0
C+105	0	0	30	20	10	0	0
C+120	0	0	0	30	20	10	0
C+135	0	0	0	30	20	10	0
C+150	0	0	0	0	30	20	10
c. Overmature stands							
C-30	100	0	0	0	0	0	0
C-15	66	0	0	0	0	0	0
C	40	20	0	0	0	0	0
C+15	30	30	0	0	0	0	0
C+30	0	40	20	0	0	0	0
C+45	0	40	20	0	0	0	0
C+60	0	30	20	10	0	0	0
C+75	0	30	20	10	0	0	0
C+90	0	0	30	20	10	0	0
C+105	0	0	30	20	10	0	0
C+120	0	0	0	30	20	10	0
C+135	0	0	0	30	20	10	0
C+150	0	0	0	0	30	20	10

However, even if the prescription is properly implemented, the methodology is highly inefficient in that it requires investments that are not immediately recovered. Depending on the size of the dominant overstory and local markets for small diameter stems, there may be little income generated from the stand during the conversion process. Each entry may amount to a pre-commercial thinning. Thus, this prescription

should be implemented only with the understanding that the desire for an uneven-aged stand outweighs the costs of conversion.

Regeneration in this prescription is obtained almost exclusively from stump sprouting during the first cutting cycle entries. By age 30, most oak stands are not yet producing large quantities of acorns and the stand is sufficiently dense that accumulation of advance reproduction has not begun. By thinning the stand to approximately 30 percent stocking, only the largest, most vigorous trees with the best form are retained. In particular, one would select against trees that show a propensity for epicormic branching because these residual trees will be open grown, similar to the leave trees in an irregular shelterwood (see Miller 1996). The second age class is recruited from stump sprouts and the stand is allowed to develop for another 30 years at which time the dominant canopy tier has grown to approximately 55-58 percent (approaching 'B' line) stocking.

A cutting cycle of thirty years is possible only because the residual stocking was reduced to 30 percent. If stocking had not been reduced so dramatically, or if growth rates were such that the dominant canopy class were to reach full stocking (B-line) before 30 years had passed, then the stand would have to be reentered in order to keep the subordinate age class alive. It is important to note that the point a stand must be reentered is before the dominant canopy reaches 58-60 percent stocking (the B-line), not at 100 percent stocking (A-line). As the dominant canopy layer approaches B level stocking, it is fully occupying the available growing space in the stand. This leaves all subordinate canopy layers with no free growing space. In reality, this point is reached somewhere above the B-line because the distribution of trees in a stand is not perfectly uniform; however, the concept still applies.

Following the first cutting cycle, overstory stocking is again reduced to approximately 30 percent stocking and the midstory is thinned to 20 percent stocking. The third age class is recruited primarily from stump sprouts, supplemented by advance reproduction. This second entry completes the conversion. Three age classes have been established and future stand entries are directed toward the maintenance of the existing stand structure (see Larsen and others 1999). The conversion is accomplished in thirty years, sixty if it were initiated by an even-aged regeneration of the stand (table 1).

Mature Stand, Uniform Reduction

In this second prescription, one is dealing with a fully stocked stand of mature trees, a portion of which must be capable of surviving an additional 60 to 70 years. This conversion prescription calls for a uniform treatment across the stand and because of this, the product yield during the conversion process may fluctuate greatly across cutting cycles. However, because the trees being managed are of larger size, each entry should produce commercial harvests of timber and should generate income for the landowner.

For the initial entry, stand stocking should be reduced by no more than one-third (to not less than 60 percent stocking) in an operation similar to the preparatory cut of a shelter-

wood (table 1b). This harvest is designed to increase the vigor of the residual overstory trees so they are less likely to degrade when the stand is opened further; an ancillary outcome is to develop the advance reproduction in the understory that will become the second age class. The amount of time between this harvest and the second is not critical because its primary goal was not to establish a new cohort. The second entry is made when the residual trees have increased crown spread and some advance reproduction has developed (approximately 5-15 years). However, if significant crown dieback occurs, possible in the shorter-lived or less vigorous residuals, then the timing of the second entry should be moved up to salvage the potential loss.

The second cutting-cycle harvest reduces overstory stocking to approximately 50 percent and is designed to recruit the first new age class of the conversion process. Any tree deemed likely to die or significantly degrade prior to the next harvest entry is removed. Beyond that, the best trees are left as uniformly as possible across the stand to meet the desired stocking level. Note that only 10 percent of available growing space is allocated to the new age class; 50 percent stocking is retained in the overstory, which leaves only 10 percent available for establishment of the new cohort. By retaining much of the growing space in the dominant canopy tier, the density of the newly established cohort is kept fairly low. This later reduces the amount of precommercial thinning needed when the next cohort is recruited at the subsequent cutting cycle harvest. However, the stocking of the dominant canopy tier(s) must be kept sufficiently low to maintain the vigor of the most subordinate age class throughout the cutting cycle. Thus, residual stocking levels and growth rates determine the length of the cutting cycle.

The vigor of the most subordinate age class is a function of the relative density of all superior age classes. When the dominant canopy tiers reach full stocking, density dependent mortality of the understory begins. The level of residual stocking can be modified in the event that a shorter or longer cutting cycle is desired; in this case, a 15-year cutting cycle is initially suggested.

At the end of the first cutting cycle, the dominant canopy tier is reduced to 40 percent stocking leaving approximately 20 percent free growing space for the developing understory layer. During this entry, the objective is not to develop a third age class. One only seeks to ensure that the second age class maintains sufficient growing space for continued development. Thus, even if the second age class occupies more than 20 percent stocking (growing space), it is left untreated. Following the second cutting cycle, the overstory is reduced in stocking to 30 percent, and the midstory to 20 percent, leaving approximately 10 percent free growing space for the establishment of a third age class. Following conversion, as canopy tiers become less distinct, the distribution of stocking between age classes is most easily allocated among size classes: sawtimber (overstory), poles (midstory), and seedlings/saplings (reproduction/understory).

There is no need to establish a new cohort with each entry. For an uneven-aged stand, only three age classes are required. Therefore, it is possible to regenerate a new

cohort every second, third, or fourth entry into the stand depending on the age of the oldest cohort and the length of the cutting cycle. If such is the case, total stand stocking should not be reduced to 50 percent until a regeneration event is desired. Reduce stocking in the two superior canopy tiers enough to ensure the most subordinate canopy class remains vigorous [e.g., thin all trees >5 inches in diameter at breast height ((d.b.h.)) to 50 percent stocking, thus leaving 10 percent growing space for the most subordinate class).

The suggested ratio of stocking among size/age classes (30:20:10) approximates a q -value of 1.3 (for 2-inch diameter classes). It maintains 70 percent of the stand basal area in the sawtimber size classes and ensures sufficient numbers of trees in the smaller size classes to sustain ingrowth while allowing for natural mortality, crop tree selection, and timber harvest. This stand structure has been found sustainable in the Ozark Highlands of Missouri (Loewenstein 1996, Larsen and others 1999, Loewenstein and others 2000). Using this ratio of growing space among age classes during stand conversion facilitates structural maintenance thereafter.

Mature Stand, Patch Reduction

In this third prescription for conversion, one is also dealing with a mature stand of trees, and one uses the same stocking levels as outlined for the uniform conversion (table 1b). However, the pattern of implementation is different.

Under this methodology, new cohorts are developed with each entry, but not across the entire stand. Unlike the uniform conversion prescription, the start of the conversion is staggered in patches across the stand. The initial reduction in stand stocking is the same between the two methods, a uniform reduction across the entire stand of one-third to not less than 60 percent stocking. Following the first entry, patches within the stand (for illustration, say 20 percent of stand area in patches of different size and pattern) are reduced in stocking to 50 percent to establish the second age class. Throughout the matrix of the stand between the patches, trees that are unlikely to survive the cutting cycle are marked for removal, otherwise stocking is maintained between 60 and 75 percent. After one cutting cycle, another 20 percent of patch area across the stand is reduced to 50 percent stocking; the section initially treated is reduced to 40 percent stocking, and the remaining 60 percent of the stand is examined for potential mortality and thinned to retain vigor. The cycle is continued until the entire stand has received the full series of conversion entries described in the uniform method, at which time the dominant overstory of the last portion of the stand is 175 years old (assuming the series was initiated in a 60-year-old stand). Each 20 percent portion of the stand may be treated as a contiguous block, or may be treated as several smaller patches that together equal 20 percent.

This patch approach to conversion results in a more even flow of timber throughout the conversion process and has the potential to ensure a regular income and a merchantable harvest with each entry. However, the ability to use this approach is dependent on the size of the ownership and local market conditions, which determine whether harvests of a given volume are operable. Mature patch conversion is

also constrained by the age and species composition of the stand. Under this scenario, the length of time required to complete the conversion may extend from 30 to 60 years beyond that of the uniform reduction strategy.

Overmature Stands or Short-Lived Species

Finally, one should consider those situations where the existing dominant canopy will not survive the conversion period. The immature method is applicable when the overstory trees in a stand either should not be retained or where they will only survive the establishment of a single new age class. The two mature stand methods assume that the overstory is capable of surviving the entire conversion process (three new age classes). If, however, the dominant overstory is expected to die after the establishment of the second age class, one should modify the allocation of growing space during initial stand entries so that control of density in the most subordinate age class becomes paramount. These stands need to be regenerated as soon as possible, and this prescription ensures that outcome (table 1c).

Wherever possible, the dominant overstory should be retained for as long as it can be maintained in a vigorous condition. However, in the case of an overmature stand, a substantially greater portion of the growing space must be allocated to the first cohort established during the conversion process because it will be used to constrain density in succeeding cohorts.

The preparatory thinning is similar to the uniform methods. Stocking is reduced uniformly by no more than one third to not less than 60 percent stocking. The first cutting cycle reduces overstory stocking to 40 percent, allocating 20 percent to the first new cohort. The second cutting cycle reduces overstory density to 30 percent stocking, leaving 30 percent for the subordinate age class. The third cutting cycle removes the original overstory rather than allowing it to die piecemeal over time. The first cohort is thinned to 40 percent stocking, allocating 20 percent to the second cohort. The first cohort is cut back to 40 percent during the fourth cutting cycle; no treatment is required in the subordinate cohort. Conversion is completed with the fifth cutting cycle; the first cohort is thinned to 30 percent stocking and the second cohort to 20 percent, leaving 10 percent stocking available for the establishment of a third.

Stand Structure—Is q Relevant During Conversion?

All of these prescriptions have one attribute in common—aggressive efforts to develop new age classes when called to do so. Eventually, a more formalized uneven-aged regulation method will be implemented to supplement and guide the retention of given levels of stocking in the different age classes. Thus, structural control will become essential for creating and maintaining an uneven-aged stand. During conversion, growing space has been allocated based solely on canopy position. Yet, it was never suggested that during the conversion period the stand should be marked to a guiding curve. Although a q based (or similar) approach is essential for maintaining an uneven-aged structure in an oak-dominated system (Larsen and others 1999), q has no place in stand conversion!

Conversion of a stand to an uneven-aged structure cannot be accomplished in the same manner as the maintenance of stand structure in an existing uneven-aged stand. During the conversion process, one should be treating each age class independently, thinning each from below—in effect, cut the worst and leave the best (Baker and others 1996) within an age class. Unfortunately, following conversion when one has three age-classes intermingled intimately on the same area, canopy tiers become less distinct; thus, it becomes more difficult to thin each cohort from below. It becomes increasingly difficult to recognize the difference between age classes (trees from all three age classes may be found in the same diameter class). The guiding curve is simply a methodology for ensuring the maintenance of a sustainable stand structure. It differs from the conversion prescriptions in that one would cut the worst from each size class (rather than age class) and growing space is allocated by diameter class (rather than by age class).

SUMMARY

The choice of a conversion strategy is most dependent on the expected longevity of the dominant overstory. If it will survive the establishment of one new age class, or if it is an immature stand, use the immature method. If it will survive the establishment of two new age classes, use the overmature method. If a substantial portion of the original overstory will survive the establishment of three new age classes, then either of the two mature stand methods is appropriate.

The goal at the end of conversion is to have partitioned growing space (stocking) among age classes/canopy tiers in a ratio of 30:20:10. This stand structure maintains a large proportion of the growing space in sawtimber and controls the density of small diameter trees (reducing the need for pre-commercial thinning). Even so, it allocates sufficient growing space to the most subordinate age class ensuring sustainable recruitment into the overstory.

The length of the cutting cycle is affected by residual stand density and growth rates. If a longer cutting cycle is desired, residual stand density must be reduced. Otherwise, one increases the risk of losing the youngest age class in the stand. Density dependent mortality begins in the most subordinate age class when the stocking level of all trees in a superior crown position reach full stocking.

There is no need to recruit a new cohort of trees into the stand with each cutting cycle. To recruit a new cohort, total stand stocking must be reduced to approximately 50 percent; this should be done only when needed to maintain three age classes in the stand. Alternatively, stocking of the midstory and overstory should be reduced to 50 percent, leaving 10 percent stocking available for the existing under-story, thus maintaining a fully stocked stand.

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REGENERATION POTENTIAL OF SELECTED FORESTED STANDS ON THE CUMBERLAND PLATEAU OF NORTH ALABAMA

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Abstract—Forested areas in the Cumberland Plateau region have experienced a myriad of disturbances over the last century. As a result, hardwood forests, such as those found in north Alabama, contain a mixture of species with wide ranges of shade tolerance and growth rates. Both site characteristics and past disturbance history have contributed to stands that are considered low to medium quality. Research into the outcome of regenerating these stands is limited. In this paper, we evaluated possible regeneration outcomes in several stands using a regeneration model that ranks expected postharvest performance based on reproduction origin, size, and competitiveness.

INTRODUCTION

The history of disturbance in the lower Cumberland Plateau region is similar to other forested sites that are dominated by mixed upland hardwoods. Harvesting practices have generally tended toward high grading, leading to stands of lower quality than expected on many sites. One possible reason for the lack of management in these upland forests may be a high level of uncertainty about viable silvicultural options and their results (Dubois and others 1997). Loftis (1992) previously outlined two problems associated with regenerating these stands. First, oaks (*Quercus* spp.) demonstrate better regeneration on lower quality, xeric sites, and second, oaks are poor competitors with other species, particularly yellow-poplar (*Liriodendron tulipifera* L.) and shade-tolerant canopy species.

Most desirable species in oak-dominated forests or in forests where oaks are prominent components are intolerant of shade. Therefore, all or most of a stand must be removed in order to develop a new age class.

Natural regeneration comes from three sources: (1) stump or root sprouts, (2) advance reproduction, and (3) new seedlings established after a disturbance (Beck 1980). The oak component in a new stand comes predominantly from advance reproduction and stump sprouts (Beck 1970, Loftis 1990, McQuilken 1975, Roach and Gingrich 1968, Sander 1972, Sander and Clark 1971). That is, these pre-existing vegetative structures persist through the disturbance of a regeneration cutting. Acorns that germinate after cutting provide new seedlings, but growth of these seedlings is slow, and they rarely reach a dominant or codominant position in the new stands (Loftis 1983, Sander 1972). Yellow-poplar, a major competitor with oaks on productive sites, demonstrates a different reproductive strategy. While new yellow-poplar in a stand may also come from stump sprouts from trees removed during the harvest and advance reproduction that existed prior to cutting, it also regenerates successfully from new seedlings established after harvest (Beck 1970, Clark and Boyce 1964). Seedlings are often very numerous and on better sites can dominate the

composition of the new stand (Beck and Hooper 1986, Merz and Boyce 1958, Sander and Clark 1971). In some other upland hardwood systems, desirable species such as ash (*Fraxinus* spp.) and black cherry (*Prunus serotina* Ehrh.) can also regenerate from new seedlings.

The oak strategy—pre-existing vegetative structures persisting through disturbance—is characteristic of the vast majority of upland hardwood species (Beck 1980, Johnson 1977, Loftis 1990). Prior to stand disturbance, because most species depend on advanced growth, an inventory of the number and size-class distribution of each species along with an estimate of new seedlings can predict the postharvest species composition. Researchers have developed methods for evaluating the natural regeneration potential of upland oak forests (Johnson 1977; Johnson and Sander 1988; Loftis 1988, 1990; Lowell and others 1987; Marquis and Ernst 1988; Sander and others 1976, 1984; Waldrop and others 1986). Following a model developed by Loftis (1989), this study uses size of advance growth, estimates of new seedling establishment, and competitiveness of various regeneration sources present to predict species composition after heavy regeneration cuts on two distinct land types. This paper examines model predictions of regeneration on stands located in north Alabama and compares these predictions between stands found on two distinct ecoregions.

SITES

Six upland hardwood stands located in Jackson County, AL, were surveyed in the summer of 2001. These stands can be broadly divided into two groups associated with the strongly dissected southern portion the mid-Cumberland Plateau region (Smalley 1982).

The first group of stands was located on the strongly dissected margins and sides of the plateau (the escarpment). The second group was located on the weakly dissected plateau surface (the plateau). The uniqueness of testing how stands located on these two landscape associations lies in their physiography and management potential. On

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the plateau, soils are moderately deep-to-deep, loamy, and clayey; slope does not exceed 10 percent. Soil drainage is considered well drained, and soil fertility is low. Site index is 60 (base age 50) for upland oaks and 85 (base age 50) for yellow-poplar, which typically occurs on concave surfaces on the plateau (Smalley Land type 1, broad, undulating sandstone uplands) (Smalley 1982). Oak reproduction is usually prolific on these sites, although tree size may be small. Clearcutting is commonly employed for regeneration, because competition is sparse and oak reproduction numbers are high.

On the escarpment, soils are deep to very deep and loamy. Soil drainage is considered well drained, soil fertility is moderate to moderately low, while slopes range from 5 to 70 percent. Stands on the escarpment surveyed for this study have slopes from 15 to 30 percent. Upland oak site index is 75 to 80, and yellow-poplar site index is 100 (Smalley Land type 16, plateau escarpment and upper sandstone slopes and benches, north aspect) (Smalley 1982). These stands are mixed mesophytic types; beneath mature stands oak reproduction numbers are low, the size is typically small, and competition, particularly by yellow-poplar, is great.

PROCEDURES

Researchers have studied species composition of regeneration and its predicted response following disturbance in the Southern Appalachian forest and in other predominantly deciduous forest regions. Prediction of oak response has led to the development of a regeneration model (Loftis 1989). Composition of a new stand following a regeneration cut is a function of the species composition and size structure of the advance reproduction and overstory of the existing stand; as well, new seedlings become established shortly after harvest. In particular, the model uses height as a basis for ranking expected postharvest performance of advance reproduction. Stump sprouts of the various species (from stems > 1.5 inches in diameter at breast height (d.b.h.) are assigned a rank for expected postharvest performance and a probability of sprouting. If data are available, a provision is also made for estimating probability of sprouting as a function of stem d.b.h. For the few species able to regenerate from new seedlings established after disturbance, a ranking of expected postharvest performance is assigned to new seedlings, and a probability of new seedling establishment is estimated.

The regeneration model accompanies an inventory of the existing stand that uses small (0.01 acre) regeneration plots to enumerate all existing regeneration sources. In particular, the model uses advance reproduction by height class and overstory trees (stems > 1.5 inches d.b.h.) that can potentially produce stump sprouts. The best performing regeneration sources present on each plot are chosen as "winners" based on their competitive rankings (table 1). Rules in the model chose fewer winners when space-consuming stump sprouts occur, and algorithms deal with ties if numerous individuals have the same rank.

Choosing winners on each plot in this fashion treats competition explicitly; i.e., the best competitors on these small plots are the winners. The use of small regeneration plots provides a representation of the variation in competitive

Table 1—Ranking of expected postharvest performance

Ranking	Expected postharvest performance
1	Yellow-poplar-SP, black cherry-SP, black locust-SP, basswood-SP
2	Red maple-SP, sugar maple-SP, silverbell-SP, Fraser magnolia-SP, cucumber-SP, ash-SP, birch-SP, white pine-L, yellow-poplar-L, black cherry-L, birch-L
3	Basswood-L, yellow-poplar-M, black cherry-M, birch-M, silverbell-L, Fraser magnolia-L
4	Oak-SP, oak-L, ash-L, red maple-L, cucumber-L, hickory-SP, dogwood-SP, sourwood-SP, blackgum-SP, beech-SP, buckeye-SP, yellow-poplar-S, birch-S, black cherry-S, sugar maple-L, hemlock-L, white pine-M
5	Yellow-poplar-SE, black cherry-SE, birch-SE, oak-M, basswood-M, ash-M, red maple-M, silverbell-M, Fraser magnolia-M, cucumber-M, white oak-SP, hickory-L, dogwood-L, sourwood-L, blackgum-L, beech-L, buckeye-L, fire cherry-SE, sugar maple-M
6	Hickory-M, white oak-M, sourwood-M, blackgum-M, beech-M, buckeye-M, hemlock-M, white pine-S
7	Oak-S, ash-S, basswood-S, silverbell-S, Fraser magnolia-S, red maple-S, dogwood-M
8	White oak-S, hickory-S, dogwood-S, sourwood-S, blackgum-S, beech-S, buckeye-S

SP = stump sprout; L = large advance reproduction (> 4 feet; > 3 feet for yellow-poplar); M = medium advance reproduction (> 2 feet; ≥ 1 feet < 3 ft for yellow-poplar); S = small advance reproduction (< 2 feet; < 1 ft for yellow-poplar); SE = new seedlings established after harvest.

situations in the stand. Combined data from the individual plots provide a summary of stand-level results. Overall, the results provide a projection of likely species composition of dominant and codominant stems at the time of crown closure. Since there are stochastic elements in the model, multiple simulations provide not only a mean regeneration outcome, but also a range of regeneration outcomes.

Six stands were inventoried in the summer of 2001. Twenty-one regeneration plots were randomly located within each stand. All trees on a 0.01-acre plot were tallied by species and 1-foot height classes following the categories 0 to 0.9 feet, 1.0 to 1.9 feet, 2.0 to 2.9 feet, 3.0 to 3.9 feet, > 4.0 feet but < 1.4 inches d.b.h., and > 1.5 inches d.b.h. Sixty-three 0.01-acre plots were inventoried on forested tracts on the escarpment (3 stands with 21 inventory plots each), and 63 were inventoried on the plateau. Overstory tree data (species, height, and d.b.h.) were obtained on 0.025-acre plots corresponding to the regeneration plots. Each stand was run through the regeneration model 20 times, and model output for the stand summary was assessed. The site index used for the plots on the plateau was < 75; site index for stands on the escarpment was set at > 75.

Table 2—Preharvest stand composition for escarpment and plateau stands in north Alabama

Species	Escarpment				Plateau			
	BA/A	Total	SPA	Total	BA/A	Total	SPA	Total
		%		%		%		%
Red oaks	11.5	11	6	5	56.6	44	44	8
White oaks	27.9	26	19	15	45.9	35	208	38
Ash2.3	2	3	2	0	0	0	0	0
Black cherry	1	1	1	1	0	0	0	0
Black locust	1.5	1	3	2	0	0	0	0
Blackgum	6.6	6	8	6	1.7	1	52	9
Basswood	0.9	1	2	2	0	0	0	0
Beech	2.6	2	4	3	0	0	0	0
Dogwood	0.4	0	1	1	0.1	0	4	1
Hickories	18.2	17	22	18	5	4	22	4
Red maple	4.4	4	11	9	7.6	6	82	15
Sassafras	0.8	0.5	2	2	1.3	1	18	3
Sourwood	1.7	2	4	3	9.5	7	114	21
Yellow- poplar	14	13	13	10	2.6	2	8	1
Sugar maple	14.1	13	23	19	0	0	0	0
All others	0.7	0.5	2	2	0.04	0	2	0
Total	108.6	100	124	100	130.3	100	554	100

BA/A = basal area per acre in square feet; SPA = number of stems per acre.

RESULTS

Tree stand composition differed at each site. Stands located on the plateau averaged 130.3 square feet of basal area per acre (BA/A) and had 554 stems per acre (SPA) (table 2). In these stands the dominant species were oaks (*Q. alba* L., *Q. prinus* L., *Q. velutina* Lamarck, *Q. coccinea* Muenchh.), representing 79 percent of the total BA/A. Other common mid- and overstory species on the plateau included sourwood (*Oxydendrum arboreum* DC.), red maple (*Acer rubrum* L.), and hickory [*Carya glabra* Sweet, *C. ovata* K., *C. glabra* var. *odorata* (Marsh.) Little, *C. ovalis* (Wangenh.) Sarg.], representing 7, 6, and 4 percent of the total BA/A. On the escarpment, basal area averaged 108.6 square feet per acre, with 124 SPA. Oaks (*Q. alba*, *Q. prinus*, *Q. velutina*, *Q. rubra* L.) accounted for 37 percent of the total BA/A of stands on the escarpment, followed by hickories (17 percent), sugar maple (*A. saccharum* Marsh.) (13 percent), and yellow-poplar (13 percent). Species richness was higher on the escarpment compared with the plateau.

There were more mid- and overstory canopy (canopy) SPA on the escarpment compared with the plateau. Escarpment trees had a quadratic mean diameter (q.m.d.) of 11.4 inches, with a range from 1.6 to 35.8 inches d.b.h. Quadratic mean diameter of plateau trees was 5.4 inches (1.6 to 24.0 inches d.b.h. range). Red oaks on the escarpment averaged 6 SPA, were 11 percent of the total BA/A, and had a q.m.d. of 18.7 inches. White oaks, at 19 SPA and 26 percent of the total BA/A, averaged 16.4 inches q.m.d. The q.m.d. for escarpment sourwood, red maple, black locust (*Robinia pseudo-acacia* L.), sassafras [*Sassafras albidum* (Nutt) Nees], sugar maple, and yellow-poplar was 10.1 inches. White oaks on

the plateau were 35 percent of the total BA/A, averaging 208 SPA, 6.3 inches q.m.d., with a range of 1.9 to 16.0 inches d.b.h. Plateau red oaks had 44 percent of the total BA/A and 44 SPA, averaging 15.4 inches q.m.d. (range 1.6 to 27.4 inches d.b.h.). The q.m.d. of plateau blackgum (*Nyssa sylvatica* Marsh.), sourwood, red maple, and sassafras was 3.5 inches.

The regeneration tally appears in table 3. There were 9,713 SPA tallied for plateau stands and 9,527 SPA for escarpment stands. Of these totals, 67 percent of plateau reproduction and 66 percent of escarpment reproduction were < 1 foot in height. The majority of these small size-class stems was in the "other" species category (*Diospyros virginiana* L., *Magnolia acuminata* L., *Ulmus* spp., *Cercis canadensis* L., *Ostrya* spp., *Ilex* spp., *Vaccinium* spp., and others). Small stems of oak were 28 percent of the total on the plateau and 13 percent on the escarpment. On the plateau, 468 SPA were > 1.5 inches d.b.h., or 5 percent of the reproduction total. Species distribution in this size class was 31 percent white oaks, 21 percent sourwood, 14 percent blackgum, and 13 percent red maple. On the escarpment, 229 SPA were 1.5 inches d.b.h. or larger (4 percent of the total number of stems) and were distributed as 32 percent sugar maple, 15 percent others, 11 percent hickory, and 9 percent blackgum.

The model predictions of SPA at crown closure appear in table 4. The model predicted an average of 462 SPA for stands on the escarpment, consisting of 27 percent black cherry, 21 percent black locust, 15 percent sugar maple, and 12 percent yellow-poplar. For plateau stands, the model

Table 3—Preharvest regeneration average stems per acre and percent of totals by size classes for escarpment and plateau stands in north Alabama

Species	< 1 foot				> 1 foot – < 1.5 feet d.b.h.				> 1.5 feet d.b.h.				All classes			
	Escarpment		Plateau		Escarpment		Plateau		Escarpment		Plateau		Escarpment		Plateau	
	ASPA	Total	ASPA	Total	ASPA	Total	ASPA	Total	ASPA	Total	ASPA	Total	ASPA	Total	ASPA	Total
	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%
Red oaks	186	3	1,014	16	16	1	162	6	3	1	38	8	205	2	1,214	13
White oaks	649	10	790	12	29	1	168	6	14	6	143	31	692	7	1,102	11
Ash	281	4	14	0	141	5	3	0	13	6	0	0	435	5	17	0
Black cherry	235	4	79	1	65	2	40	1	0	0	0	0	300	3	119	1
Black locust	5	0	5	0	14	0	17	1	2	1	2	0	21	0	24	0
Blackgum	171	3	90	1	89	3	113	4	21	9	65	14	281	3	268	3
Basswood	2	0	0	0	11	0	0	0	0	0	0	0	13	0	0	0
Beech	27	0	2	0	113	4	5	0	13	6	0	0	152	2	6	0
Dogwood	3	0	0	0	17	1	0	0	2	1	0	0	22	0	0	0
Hickories	332	5	225	3	48	2	57	2	25	11	40	8	405	4	322	3
Red maple	562	9	571	9	67	2	179	6	11	5	60	13	640	7	810	8
Sassafras	275	4	1,090	17	130	4	279	10	3	1	13	3	408	4	1,383	14
Sourwood	11	0	2	0	11	0	75	3	8	3	97	21	30	0	173	2
Yellow- poplar	29	0	0	0	13	0	2	0	6	3	3	1	48	0	5	0
Sugar maple	1,211	19	0	0	360	12	0	0	73	32	0	0	1,644	17	0	0
All others	<u>2,287</u>	37	<u>2,595</u>	40	<u>1,910</u>	63	<u>1,667</u>	60	<u>35</u>	15	<u>8</u>	2	<u>4,232</u>	44	<u>4,270</u>	44
Totals	6,265		6,478		3,033		2,767		229		468		9,527		9,713	

ASPA = average stems per acre; d.b.h. = diameter at breast height.

Table 4—Average stems per acre of predicted stand-level winners and post-harvest proportion in stand by species for escarpment and plateau stands in North Alabama^a

Species	Escarpment			Plateau		
	Predicted		Preharvest	Predicted		Preharvest
	SPA	Total	regeneration total	SPA	Total	regeneration total
	----- percent -----			----- percent -----		
Red oaks	3	1	2	16	5	13
White oaks	5	1	7	61	18	11
Ash	23	5	5	0	0	0
Black cherry	124	27	3	28	8	1
Black locust	97	21	0	15	4	0
Blackgum	12	3	3	44	13	3
Basswood	4	1	0	0	0	0
Beech	6	1	2	0	0	0
Dogwood	2	0.5	0	0	0	0
Hickories	10	2	4	20	6	3
Red maple	23	5	7	69	20	8
Sassafras	5	0.5	4	32	9	14
Sourwood	2	1	0	47	14	2
Yellow- poplar	56	12	0	2	1	0
Sugar maple	71	15	17	0	0	0
All others	<u>19</u>	4	44	<u>7</u>	2	44
Totals	462			341		

SPA = stems per acre.

^a Regeneration percentages for all size classes for preharvest stand data are also listed.

predicted 341 SPA, with 23 percent of this total oak, 20 percent red maple, 14 percent sourwood, and 13 percent blackgum. For those species categorized in "all others," note that these species are not necessarily eliminated from the new stand, but their dominance is altered in the predicted output.

The total predicted SPA of all oak species was greater on the plateau (77 SPA) compared with the escarpment (8 SPA). This difference is a reflection of the advanced growth-dependent reproductive strategy of oak and of stand composition prior to disturbance. On the plateau, 79 percent of the BA/A, and 46 percent of canopy SPA were oak. Oaks were also well represented in the reproduction tallies, averaging 24 percent of the total SPA, with 22 percent of the total oaks tallied > 1 foot tall. Large advance reproduction appeared as highly ranked winners in the model output (ranked fourth as stump sprouts). Oaks' competition were red maple stump sprouts (ranked second), sourwood stump sprouts and large seedlings (ranked fourth and second, respectively), and blackgum stump sprouts (ranked fourth). On the escarpment, oaks were 37 percent of the total stand BA/A, and 20 percent of the total canopy SPA. Only 9 percent of the advance reproduction total was oak, and only 7 percent of all oak advance reproduction was > 1 foot tall.

The four primary species competing with oak on the escarpment were black cherry, black locust, yellow-poplar, and sugar maple. Sugar maple was well represented on the escarpment (13 percent of the BA/A, and 23 percent of the canopy SPA). Reproduction of sugar maple averaged 1,644 SPA, with 74 percent of these stems < 1 foot tall. The shade tolerance of sugar maple and its ability to reproduce under an overstory of sugar maple and other less tolerant species, as well as the escarpment's higher site quality compared to the plateau, supports these predictions. The presence of yellow-poplar in the overstory should have increased the likelihood of new yellow-poplar seedlings postdisturbance, but did not (12 percent predicted postdisturbance compared with 13 percent of total SPA canopy predisturbance). Black cherry and black locust were predicted as higher proportions of the new escarpment stands than was yellow-poplar. Both yellow-poplar and sugar maple were minor components of plateau stands and retained this status in the new stands.

The proportion of the stands occupied by black cherry and black locust was predicted to increase substantially following overstory removal. On the escarpment, black cherry stems increased from 1 canopy SPA to 124. The presence of black cherry in the overstory (3 percent of the BA/A) and the presence of medium-sized reproduction (22 percent of the total reproduction, 65 of 300 black cherry SPA) contributed to its response, ranked first as stump sprouts and third as medium-sized reproduction. Although black cherry was not present in the overstory on the plateau, 17 SPA were tallied as advanced reproduction, and 43 percent of the total was medium-sized. The model predicted 28 SPA of black cherry, or 8 percent of the total stand composition. The lack of other high-ranking competition allowed for black cherry to assume this proportion in the new stand.

On the escarpment, black locust was predicted to have 97 SPA, or 21 percent of the total number of stems. Prior to

disturbance, black locust had three SPA canopy and 1 percent of the BA/A. The number of black locust stems tallied was 21 SPA, with 67 percent of these stems in the medium-sized reproduction class. These black locust were winners (ranked first) postdisturbance, primarily as sprouts. Although black locust was not present in the overstory on the plateau, 71 percent of the 24 SPA tallied in the plateau reproduction were medium sized. Postdisturbance, these contributed to 15 SPA of black locust, or 4 percent of the total SPA.

CONCLUSIONS

Topographic position often dictates management in the Cumberland Plateau region. In general, clearcutting regenerates stands on the plateau, as lower site quality, less competition from other species, and relatively high numbers of advance reproduction of oaks contribute to a desirable species composition in the next stand. After disturbance, 23 percent of the new stand was predicted to be oak, followed by red maple and sourwood.

If the preservation of the oak component for escarpment stands is desired, management techniques can encourage more and larger advanced oak reproduction and can reduce competition. Following Loftis (1983), altering the light level by reducing overstory or midstory basal area is being tested on escarpment stands to examine the impact on oak regeneration. The large increase in black cherry and black locust and the relatively unchanged proportion of yellow-poplar that the model predicted were surprising. Black cherry is a small component of escarpment stands and most likely will not be competitive after crown closure. The rapid growth, shade intolerance, and short-lived nature of black locust negates its importance as a long-term competitor (McGee and Hooper 1975). However, yellow-poplar may play a more dominant role than predicted by the model, as documented by others on similar sites (Beck 1970, Kuers and Kuthe 1998, Loftis 1988, McGee 1967). Results from these predictions will be compared with measured response in the field, and the model will be adjusted accordingly.

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SURVIVAL OF HARDWOOD SEEDLINGS AND SAPLINGS FOLLOWING OVERSTORY THINNING AND PRESCRIBED FIRES IN MIXED-OAK FORESTS OF SOUTHERN OHIO

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Abstract—Prescribed fires in combination with thinning are being investigated as silvicultural tools in the regeneration of mixed-oak forests in central Appalachia. Burns were conducted in spring 2001 within three forests in southern Ohio. Each site was divided into four treatments of roughly 20 ha each: control (C), burn only (B), thin only (T), or thin plus burn (TB). The basal area of T and TB stands was thinned from about 28 to 20 m² ha⁻¹ in the 4 months prior to the burns. Ten seedlings (≤ 140 cm tall) and 10 saplings [stems >140 cm tall and <10 cm in diameter at breast height (d.b.h.)] within each of nine 1,000-m² plots in a treatment area at each site were evaluated before (2000) and after (2001) treatment. Oak and hickory species were targeted for seedling evaluations. Dominant sapling species evaluated were red and sugar maple, blackgum, hickory, and beech (oak was sparse or absence). At 4 months postburn, 0, 13, 62, and 80 percent of the pretreatment seedlings were dead with living sprouts on the C, T, TB, and B plots, respectively. Nearly half of the 10 original saplings per plot were dead with sprouts in the TB and B plots (4.9 and 4.2). Sapling mortality (dead with no live sprouts) was highest in TB plots (1.6 of original 10 per plot) compared with T (0.6), B (0.2), and C (0.07) plots. Seedling mortality was highest in TB plots (3.4 seedlings of original 10 per plot), followed by T (2.2), B (1.6), and C (0.7) plots. We anticipate that resprouting seedlings in the TB plots will respond vigorously to increased light conditions if maintained by subsequent fires.

INTRODUCTION

In many Midwestern and Eastern States, oak-hickory forests, e.g., black (*Quercus velutina*), chestnut (*Q. prinus*), scarlet (*Q. coccinea*), northern red (*Q. rubra*), white oak (*Q. alba*), and shagbark (*Carya ovata*) and mockernut hickory (*C. tomentosa*) are converting to forests dominated by maples (e.g., red (*Acer rubrum*) and sugar (*A. saccharum*)), beech (*Fagus grandifolia*), and tulip-poplar (*Liriodendron tulipifera*). In Ohio, USDA Forest Service inventory data indicate that the annual removal of white and red oaks (8 billion board feet of sawtimber) equals or exceeds annual growth, while the growth of maples and tulip-poplar, far exceeds removal (~56 to 74 percent) (Griffith and others 1993). Currently, oak regeneration on xeric sites is successful, but failures are common on high-quality mesic sites (Abrams and Downs 1990). Fire suppression, deer browsing, pathogens, insect herbivory, acorn predation, and inadequate competition for limited resources such as light, soil nutrients, and moisture contribute to the poor regeneration of oak (Johnson and others 2002, Loftis and McGee 1993).

Fire has been a component of oak-hickory forests in central Appalachian mixed-oak forests since pre-European settlement (Brose and others 2001). Since the 1930's, fire has been actively suppressed concurrent with a shift in the composition of the understory and subcanopy to more shade-tolerant and fire-intolerant species, e.g., maples.

In 1994, a large study was initiated in southern Ohio to assess the use of low-intensity prescribed fires as a management tool to regenerate oaks, and to examine the effects of fire at an ecosystem level (Sutherland and Hutchinson

2003). Preliminary findings indicate that despite annual and infrequent burns, the canopy did not open sufficiently to promote adequate oak regeneration (Personal communication. Daniel Yaussy. 2002. Research Forester, USDA Forest Service, Northeastern Research Station, 359 Main Road, Delaware, OH 43015). Consequently, a new study was initiated in 2000 to assess the effects of overstory thinning and fire on regenerating mixed-oak forests in southern Ohio. It is one of 13 sites participating in the national Fire and Fire Surrogates (FFS) Project, which has incorporated a common "core" design to quantify the ecological and economic impacts of prescribed fire and thinning. A multi-disciplinary cooperative research team is studying how fire and/or thinning treatments promote the sustainability of mixed-oak ecosystems in central hardwood forests. In this paper, we present the first-season posttreatment effects of prescribed fires and thinning on the survival and health of hardwood seedlings and saplings.

STUDY AREA

The Ohio Hills site of the FFS Project is replicated on three study areas in southeastern Ohio: Zaleski State Forest (ZAL), Tar Hollow State Forest (TAR), and Raccoon Ecological Management Area (REMA). These sites have a highly dissected topography with elevations ranging from 200 to 300 m, and slopes of 10 to 40 percent. Located within the unglaciated Allegheny Plateau, the study area comprises a variety of sandstones, shales, and clays. Each study area is about 80 ha and is divided into four 20-ha treatment units: thin only (T), burn only (B), thin+burn (TB) and control (C). Within each treatment area, ten 50- by 20-m plots were established across a range of moisture conditions (three

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xeric, four intermediate, three mesic) determined by the Integrated Moisture Index (IMI) (Iverson and others 1997). Within each 50- by 20-m plot, ten 10- by 10-m subplots were identified.

Due to logistical and personnel limitations, only 9 of the 10 plots in each treatment area were used. A plot was eliminated if its IMI value was redundant or nearly redundant with another plot in the same treatment area; 108 plots were used for the pathology and health evaluations of seedlings and saplings.

THINNING AND PRESCRIBED FIRES

The initial basal area (BA) averaged 28.8 m² ha⁻¹ across all areas. T and TB treatment areas were commercially thinned from below to a BA of 20 m² ha⁻¹ during the fall and winter of 2000. Low-intensity surface burns were conducted on 28 March and 4-5 April 2001 at the TAR, ZAL, and REMA study sites. Air temperature was measured at 25 cm from the forest floor with stainless steel temperature probes and logged every 2 seconds with buried data loggers. Fires at TAR were the least intense with maximum air temperatures ranging from 21 to 226 °C in TB units and 21 to 293 °C in B units. At ZAL, maximum air temperatures during fires ranged from 42.2 to 414.6 °C in the TB unit and 63.8 to 397 °C in the B unit. At REMA, maximum air temperatures ranged from 50 to 354 °C in the B unit and 36.2 to 496 °C in the TB unit. Details of the prescribed fires are reported elsewhere (Iverson and others 2004).

PROCEDURES

Health Evaluations

In May and June 2000, 10 seedlings and 10 saplings were identified in each plot. Seedlings were defined as woody stems <140 cm tall and were further divided into three height-based size classes: small (<10 cm), medium (10 to 50 cm), and large (50.1 to 140 cm). Saplings were defined as >140 cm tall and <10 cm in diameter at breast height (d.b.h.) and were divided into three d.b.h. classes: small (<3 cm), medium (3 to 6 cm), and large (6.1 to 10 cm). Attempts were made to ensure that individuals were distributed across the range of size classes for both seedlings and saplings, and that they were distributed evenly across the 50- by 20-m plot. For evaluations of seedling health, tree species were selected in the following order of preference: *Quercus spp.*, *Carya spp.*, and others. Oaks and hickories were preferred for saplings, but generally were infrequent. As a result, health evaluations for saplings focused on stems likely to be killed by fire, e.g., such as red and sugar maple, blackgum (*Nyssa sylvatica*), and beech.

For seedlings, initial measurements included height to terminal bud, basal diameter, and stem origin. If seedlings were of sprout origin, the diameter of the root collar was measured also. Since stems would be reevaluated numerous times over several years, seedlings were flagged and locations were recorded on a plot map. Saplings were similarly identified and mapped but only d.b.h. was measured. In all, 1080 seedlings and 1080 saplings were identified (360 each within a study area).

Pretreatment health evaluations were conducted in June and July 2000. For seedlings, number of leaves, leaf color and size, crown shape, percent herbivory/disease/injury, and percent fine twig dieback were determined using a rating system adapted after Carvell (1967) and Gottschalk (Personal communication. Kurt W. Gottschalk. 2000. Research Forester, USDA Forest Service, Northeastern Research Station, 180 Canfield St., Morgantown, WV 26505) (see table 1). If problems related to pathogens or insects were obvious during evaluations, seedlings with similar symptoms from off-plot locations were sampled destructively to determine probable causal agents. Small saplings were evaluated with the health protocols for seedlings. For medium and large saplings, evaluations of over-story health included crown vigor, percent dieback of fine twig, percent herbivory/disease/injury, and presence or absence of any stem injury (wounds and defects) (table 1). Sapling protocols (stem injury, crown vigor, and dieback) were adapted from methods developed for the North American Maple Project (Cooke and others 1997). All stems were reevaluated in June and again in late August/September 2001 to determine postthinning and postfire impacts.

RESULTS AND DISCUSSION

Pretreatment Evaluations

Shagbark, mockernut, bitternut [*Carya cordiformis*], and pignut [*C. glabra*] hickory, represented ~35 percent of the seedlings evaluated at each of three study sites (fig. 1a). Oak (black, chestnut, red, scarlet, and white) represented ~64 percent of the seedlings evaluated at each site. Tulip-poplar, white ash [*Fraxinus americana*], and American chestnut [*Castanea dentata*] represented 0 to 4 percent. Eighty-four percent of the seedling stems originated from seedlings with the remainder 16 percent originating from sprouts.

Saplings evaluated were represented primarily by shade-tolerant and fire-intolerant species. Red and sugar maples represented 26 to 60 percent of the stems evaluated at each study site (fig. 1b). Sugar maple was the dominant species evaluated at TAR (40 percent), blackgum at ZAL (28 percent), and hickory spp. at REMA (31 percent). Nearly 75 percent of the evaluated seedlings were 10 to 50 cm tall while saplings were distributed more equally across all size classes.

Posttreatment Evaluations

Survival and mortality of seedlings—Four months after the prescribed fires (late August-early September 2001), survival of the original 10 seedlings per plot averaged 0.37 (±0.14) and 0.41 (±0.13) in the TB and B units, respectively, compared to average survival of 9.33 (±0.15) and 6.52 (±0.35) of the original 10 seedlings in the C and in the T plots, respectively (fig. 2a). Sprouting was greatest in the B plots (~80 percent), followed by the TB (~62 percent) plots (fig. 2b). This level of postfire sprouting was anticipated since oaks and hickories are fire-tolerant and readily sprout from the root collar (Brose and Van Lear 1998). Seedling mortality (dead with no live sprouts) was greatest in the TB plots (~34 percent), followed by T (~22 percent), B (~16 percent) and C (7 percent) plots (fig. 2c).

Table 1—Health evaluation criteria and classes used to assess the effects of prescribed fire, thinning, and fire plus thinning on hardwood seedlings and saplings

Parameter	Seedlings and small saplings		Medium and large saplings		All saplings and seedlings	
	Class	Parameter	Class	Parameter	Parameter	Class
Size	1 = Small, < 10 cm tall 2 = Medium, 10 – 50 cm tall 3 = Large, 50.1 – 140 cm tall	Size	1 = Small, < 3 cm d.b.h., > 140 cm tall 2 = Medium, 3 – 6 cm d.b.h. 3 = Large, 6.1 – 10 cm d.b.h.	Stem injury	W = Wounds C = Cracks O = Open 1 = Closed	
Origin	S = Seedling P = Sprout	Vigor ^a	1 = Healthy, < 10% dieback, discolor 2 = 10 – 25% dieback, discolor 3 = 26 – 50% dieback, discolor 4 = 51 – 75% dieback, discolor 5 = 76 – 100% dieback, discolor 6 = Dead	Dieback ^a	0 = No trace or dieback 1 = < 10% dieback 2 = 11 – 25% dieback 3 = 26 – 50% dieback 4 = 51 – 75% dieback 5 = 76 – 100% dieback 6 = Dead	
Crown shape	1 = Normal, leader present 2 = Flat-topped, no leader 3 = Flat-topped, with major fork below crown 4 = Dead					
Leaf size	1 = Large, > 15 cm long 2 = Medium, 10 – 15 cm long 3 = Small, < 10 cm long			Herbivory and disease	0 = None, trace 1 = < 10% 2 = 11 – 25% 3 = 26 – 50% 4 = 51 – 75% 5 = 76 – 100% 6 = Dead	
Leaf color	1 = Normal, dark green 2 = Light green between veins, and dark green along veins 3 = Chlorotic, yellowish green between veins and light green along veins 4 = Brown edges and tips					
Leaf number	1 = < 10 2 = 10 – 25 3 = 26 – 50 4 = 51 – 100 5 = 100+					

^a For dieback and sapling vigor estimates, only fine twigs included in estimates if other twigs with foliage present in the same area of bole or crown. Isolated dead twigs with no foliage nearby considered dead due to shading excluded from estimates.

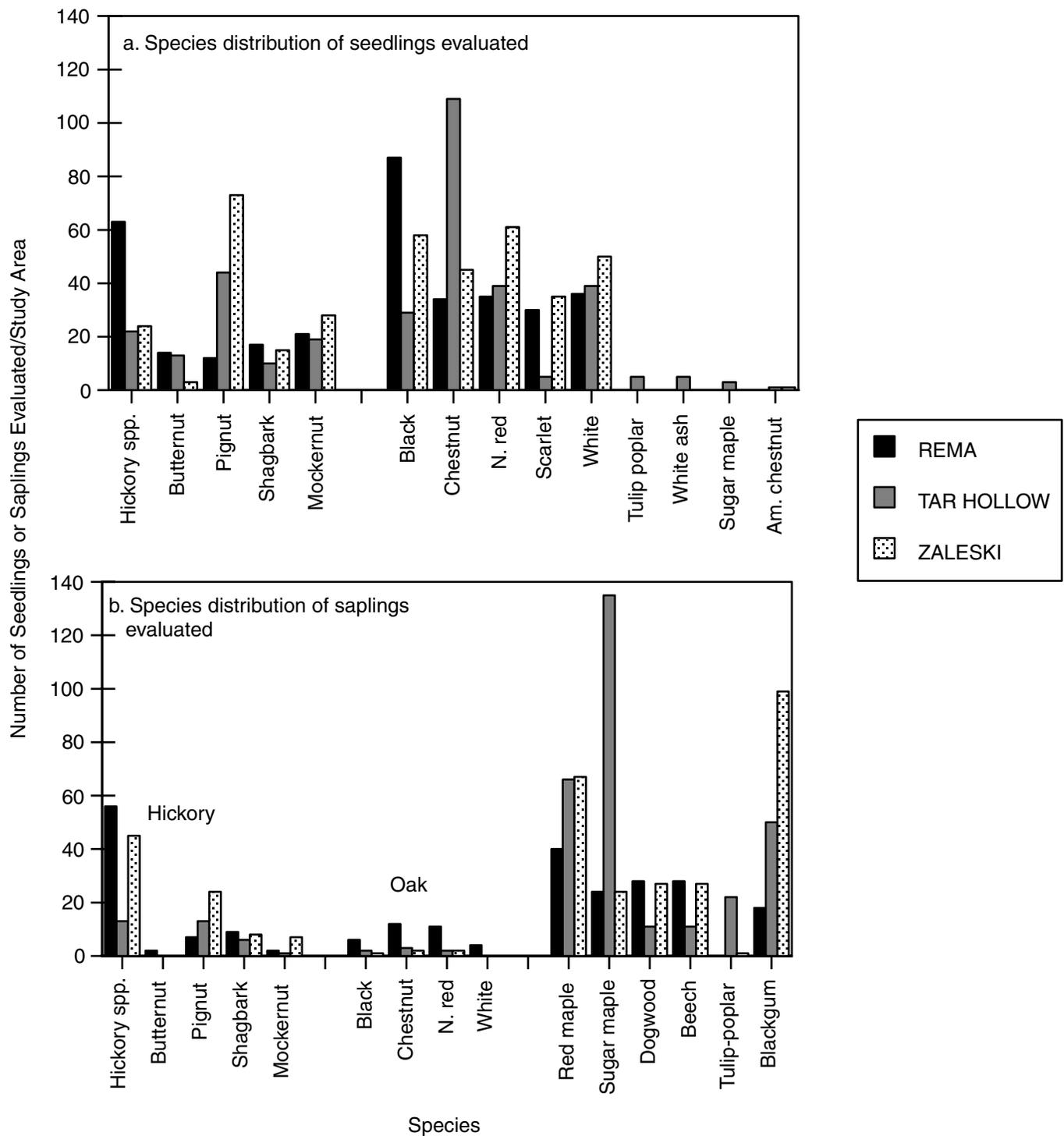


Figure 1—(a) Number of seedlings evaluated per species at REMA, Tar Hollow, and Zaleski study sites; (b) Number of saplings evaluated per species at each site.

Survival and mortality of saplings—As expected survival of original sapling stems was far greater than that observed for seedlings. C plots had the highest survival at 98.9 percent (± 0.6), while TB plots had the lowest at 48.5 percent (± 3.8) (fig. 3a). Survival was 90.4 percent (± 1.7) in T plots and 56.7 percent (± 4.8) in B-only plots. At Tar Hollow, B plots had the highest number of surviving original saplings

of all B and TB units. This was not surprising since the lowest maximum air temperatures during the prescribed fires were observed at Tar Hollow. Likewise, the lowest number of dead saplings with sprouts (2.9 saplings per plot) was also observed at the TAR B-only unit (fig. 3c). Almost half of the 10 original sapling stems per plot were dead with sprouts in the TB (4.9 ± 0.4) and B (4.2 ± 0.5) plots (fig. 3b). Four

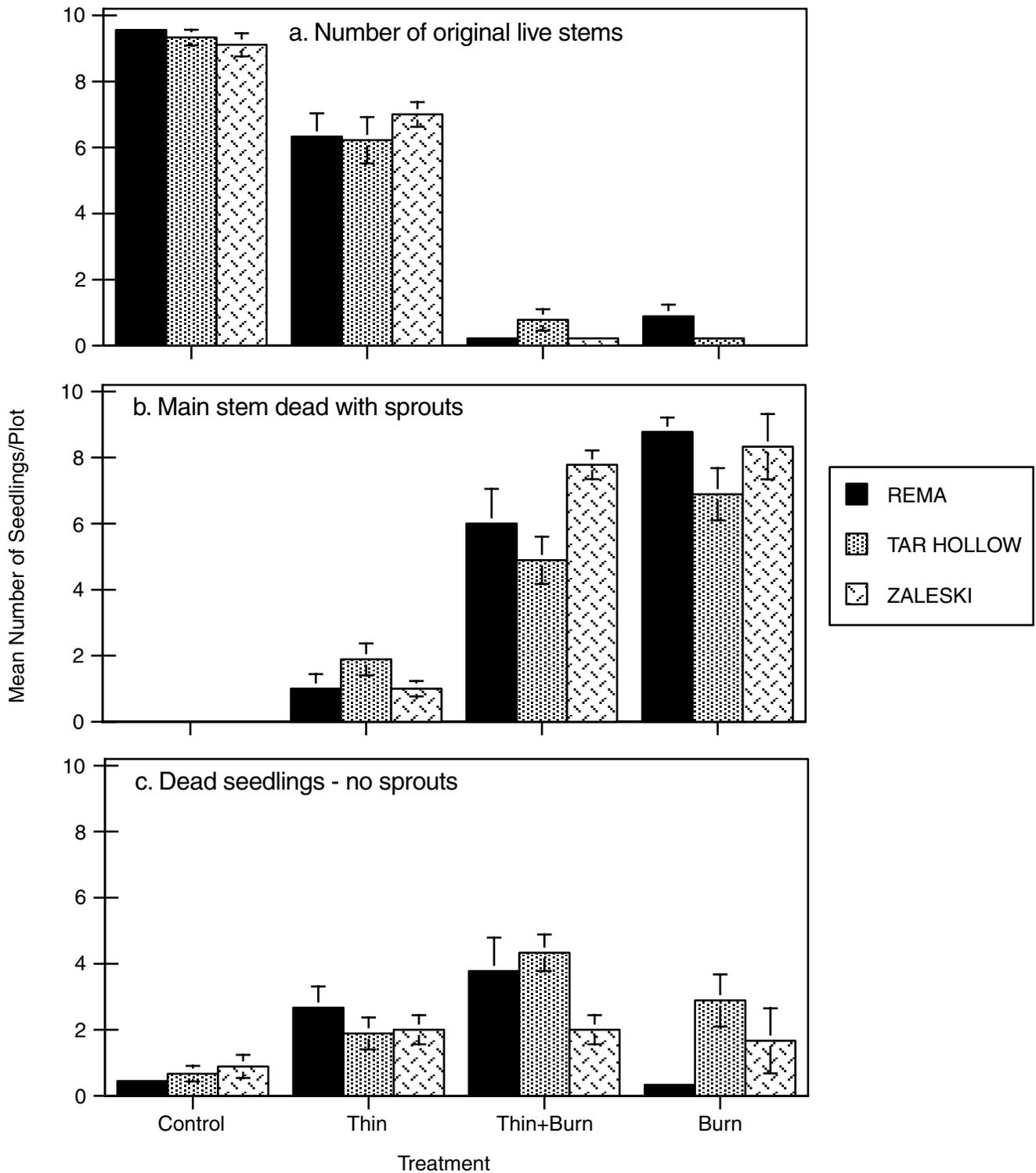


Figure 2—Survival of oak and hickory seedlings 4 months after low-intensity prescribed fires and/or overstory thinning at three sites in southern Ohio: (a) mean number of original live stems per plot; (b) mean number of dead stems with live sprouts per plot; (c) mean number of dead seedlings with no live sprouts.

months post-fire, sapling mortality (dead saplings with no live sprouts) was highest in the TB plots (~16 percent of the original saplings), compared with T alone (6.3 percent), B alone (2 percent), and C (0.7 percent). Logging injury (stem snapping, breakage, and wounding) was patchy and most

prevalent closest to cutting and skidding operations. In some plots, the slash may have enhanced fuel loading or provided fire breaks, depending on slope aspect, twig/branch size and slash moisture content.

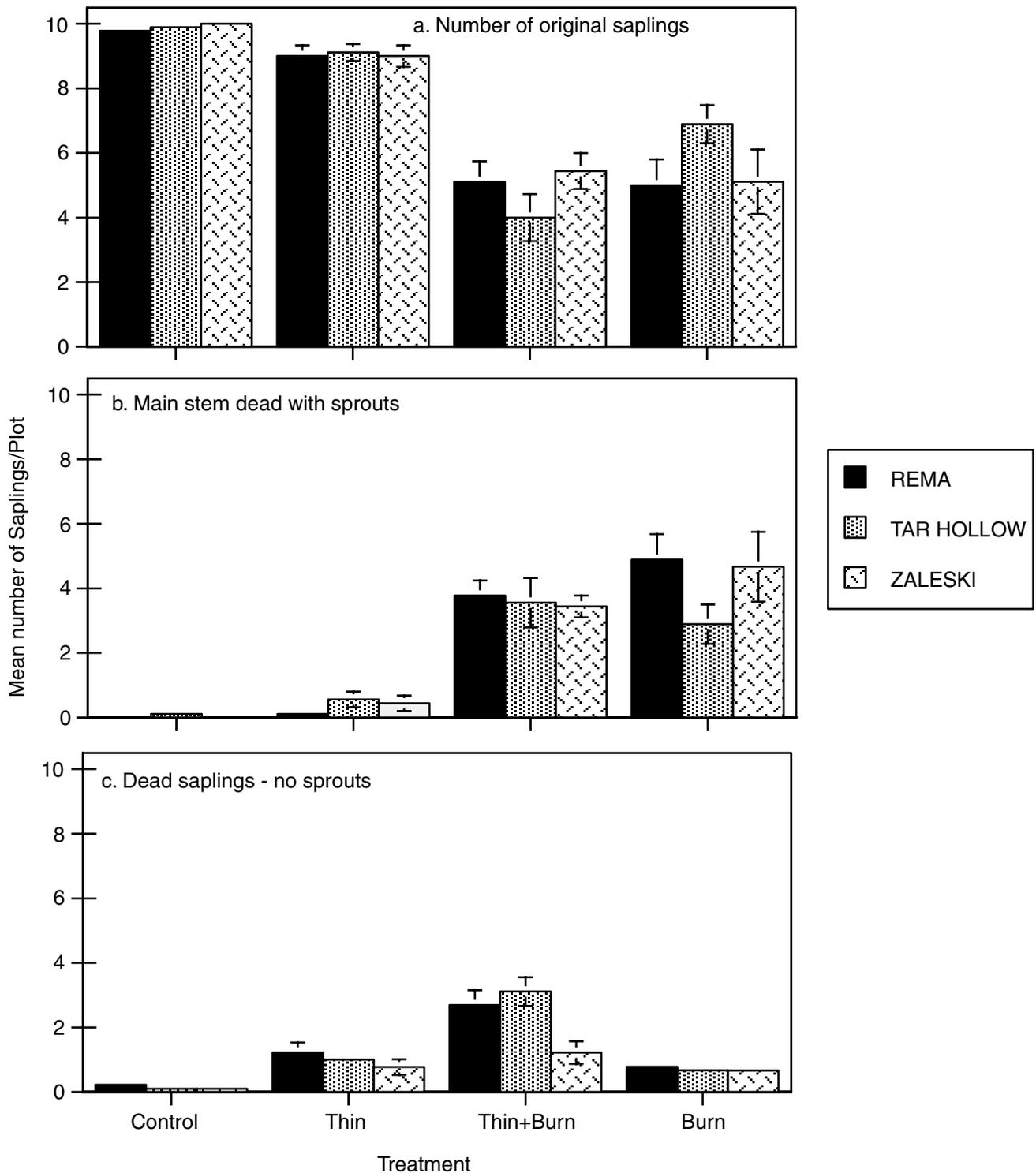


Figure 3—Survival of hardwood saplings (<3 to 10 cm in d.b.h.) 4 months after low-intensity prescribed fires and/or overstory thinning at three sites in southern Ohio: (a) mean number of original live stems per plot; (b) mean number of dead stems with live sprouts per plot; (c) mean number of dead seedlings with no live sprouts per plot.

Sapling vigor—Vigor was assessed only for medium and large saplings. The proportion of control saplings in the healthy and light decline (10 to 25 percent dieback) vigor classes did not change between 2000 and 2001 (fig 4a). The proportion of T saplings in the severe decline vigor class

(76 to 100 percent) increased from 0 to 20 percent from pre- to post-treatment measurements (fig. 4b). In the B and TB plots, there were dramatic increases in the proportion of saplings with severe decline (76 to 100 percent dieback) fig. 4c and d), particularly at REMA and ZAL where fires were intense.

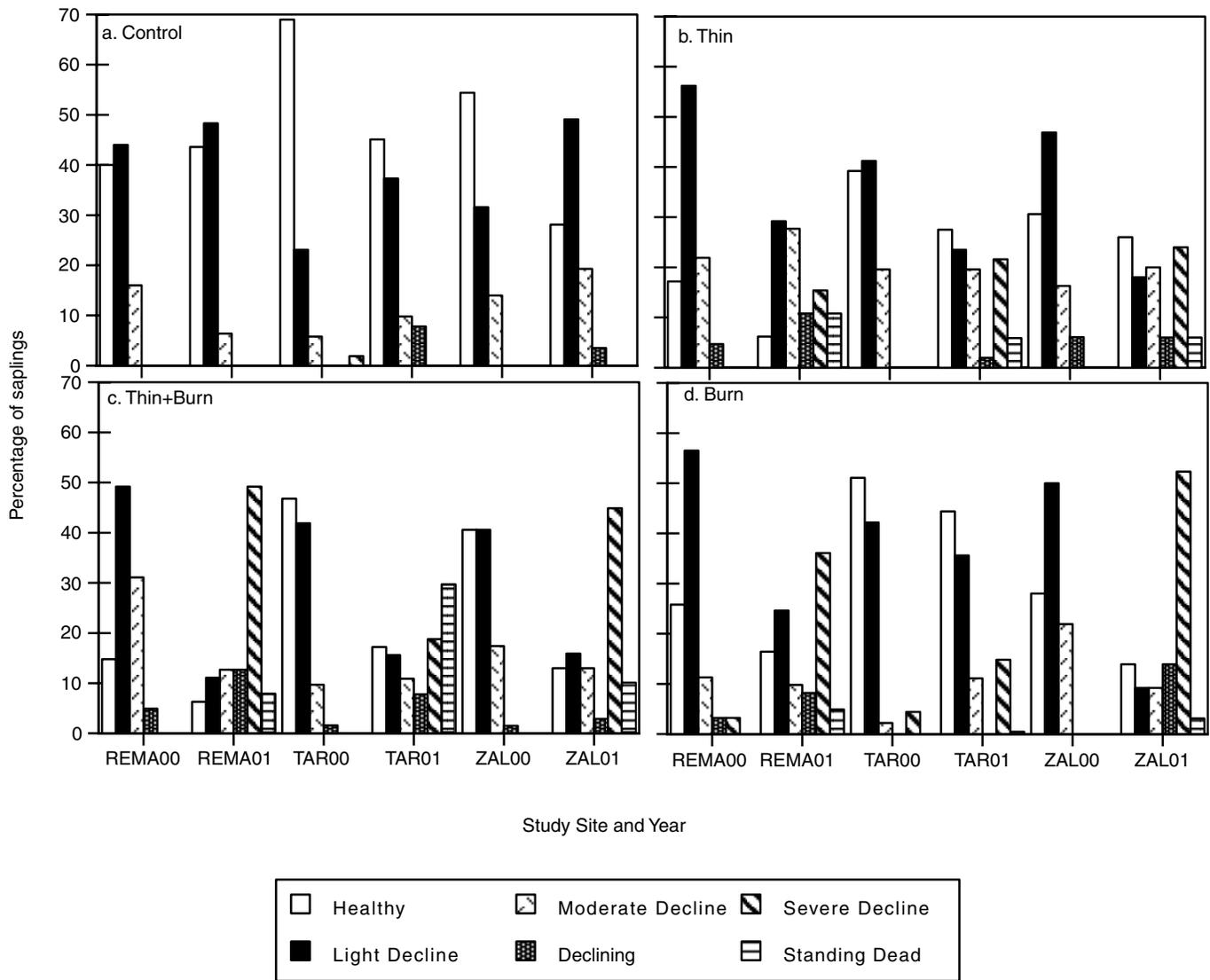


Figure 4—Percentage of hardwood saplings in vigor classes (healthy = <10 percent dieback and discolor, light decline = 10 to 25 percent, moderate decline = 26 to 50 percent, declining = 51 to 75 percent, severe declining = 76 to 100 percent, and standing dead) pretreatment (2000) and posttreatment (2001) for control, thin, thin+burn, and burn units.

Dieback—Seedling dieback in control and burn plots averaged <10 percent (fig. 5a). Dieback was higher (11 to 25 percent) in the T and TB units. Since most of the B and TB seedlings had resprouted, these evaluations indicated new current-year stems. Not surprisingly, dieback of small saplings in B and TB plots was similar to that of seedlings (fig. 5b). For larger saplings, dieback was highest in the T and TB plots, averaging 51 to 75 percent (fig. 5c). It is likely that the position of these taller stems within the midcanopy made them more prone to logging damage, as evidenced by stem bending, breakage, and wounding, and thus more vulnerable to fire-related injuries.

Incidence of foliar herbivory and disease—At 4 months following the prescribed fires, there were no changes in damage by foliar insects or diseases associated with thinning or burning among seedlings or small saplings (fig. 6).

Mean herbivory-disease index values were similar across treatments. Damage associated with foliar insects and pathogens generally was insufficient in the summer of 2001 to adversely affect seedling or sapling growth.

SUMMARY

These first-season postfire results suggest that initial seedling and sapling mortality is highest when prescribed fire is combined with overstory removal. The incidence of foliar herbivory and disease was not affected by fire or thinning treatments. Sprouting of seedlings and saplings (all size classes) was common in both the B and TB units at all 3 study sites. We anticipate that resprouting seedlings in the TB plots will respond vigorously to increased light conditions if maintained by subsequent fires. Competition from fire-intolerant species such as red maple should be minimized with a second prescribed fire (planned for spring

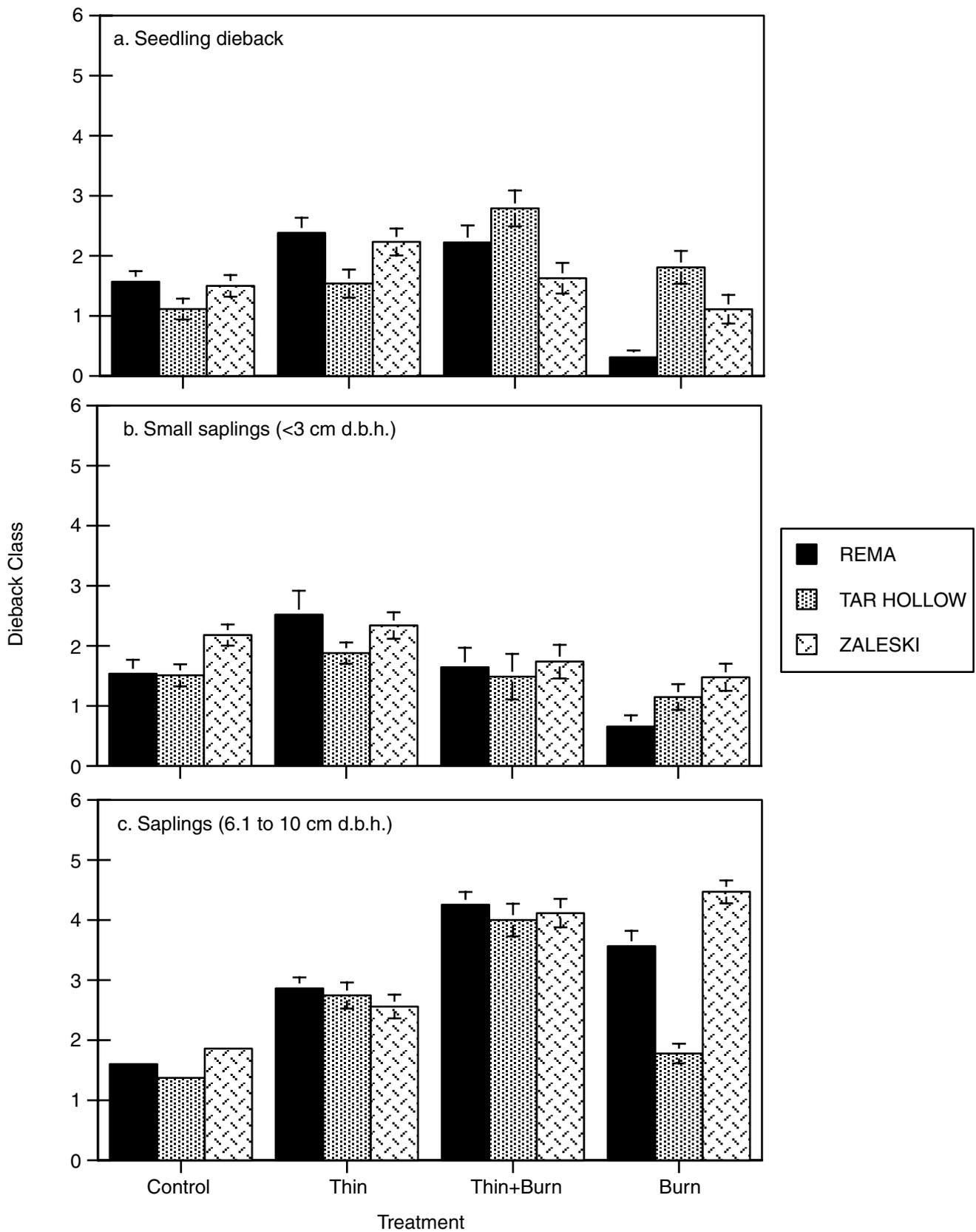


Figure 5—Late summer assessments of dieback of hardwood seedlings and saplings following prescribed fires and/or overstory thinning: (a) mean seedling dieback per plot; (b) mean small sapling dieback per plot; and (c) mean sapling dieback per plot. Rating of 1 = <10 percent dieback, while a rating of 5 = 76 to 100 percent dieback.

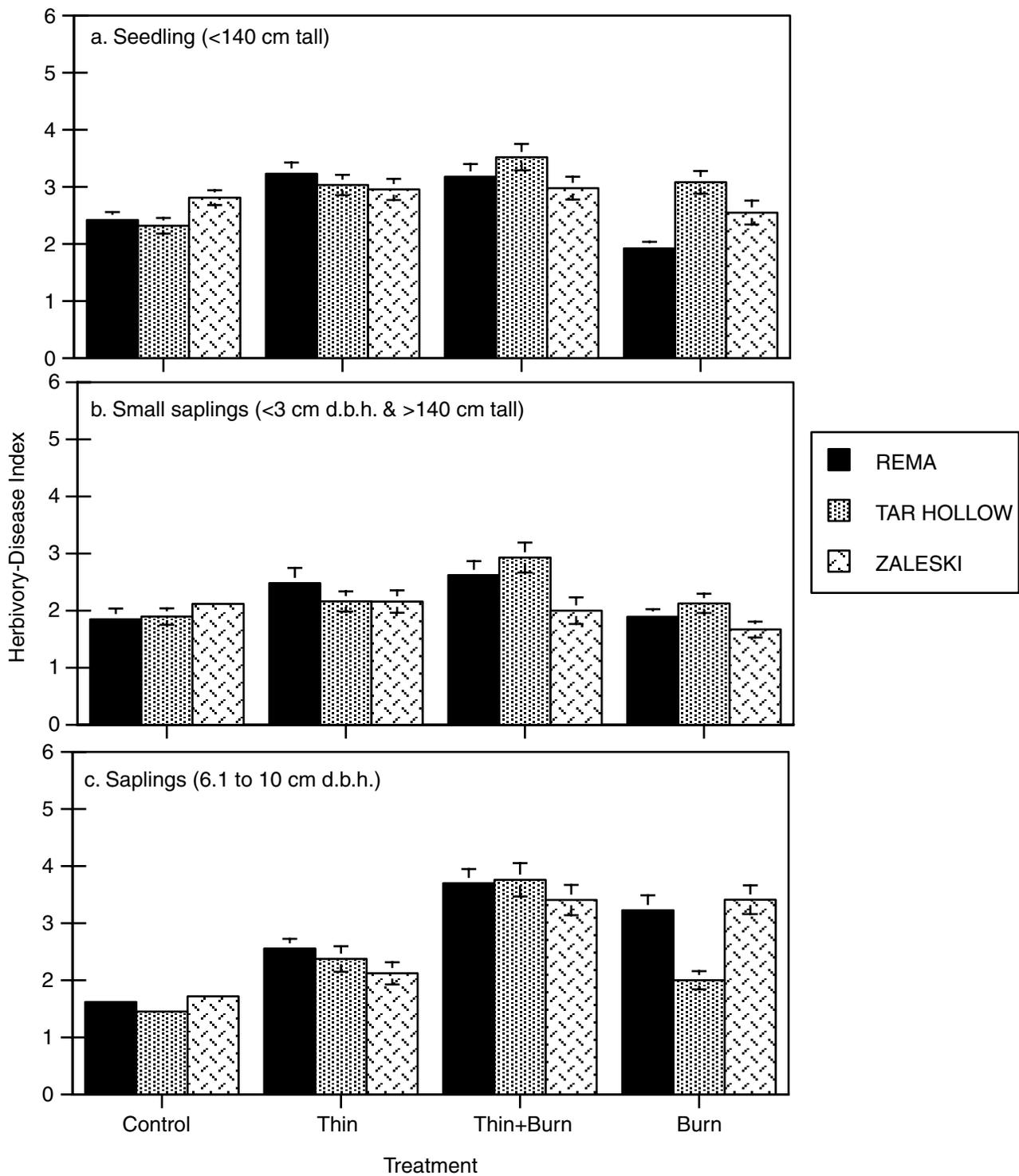


Figure 6—Incidence of foliar herbivory and disease (Herbivory-Disease Index (HDI) on hardwood seedlings and saplings following prescribed fires and/or overstory thinning: (a) mean seedling HDI per plot; (b) mean small sapling HDI per plot; and (c) mean sapling HDI per plot. Rating of 1 = <10 percent, while a rating of 5 = 76 to 100 percent.

2005). Fire improved height growth in oak and hickory and enhanced stem form in oaks (Brose and Van Lear 1998). Annual growth measurements and health evaluations of these stems will allow us to determine whether prescribed

fire alone or combined with thinning results in larger and more competitive oak and hickory stems compared to unmanipulated controls in southern Ohio's mixed-hardwood forests.

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UNDERSTORY RESPONSE TO DISTURBANCE: AN INVESTIGATION OF PRESCRIBED BURNING AND UNDERSTORY REMOVAL TREATMENTS

Benjamin J. Dolan and George R. Parker¹

Abstract—Lack of disturbance in the Central Hardwood Region has caused a decrease in abundance of shade-intolerant species, such as oaks (*Quercus spp.*) and hickories (*Carya spp.*), while shade-tolerant species have proliferated in the understory. The goal of this research is to determine how two disturbances, prescribed fire and mechanical understory removal, affect woody species regeneration, as well as herbaceous species diversity. Preliminary analysis indicates that all treatments had little effect on herbaceous species diversity; however, prescribed burning changed the composition of woody species seedlings. While fire top-killed most seedlings, regardless of shade tolerance, shade-intolerant species responded by resprouting. As a result of the reduction in the number of shade-tolerant species, burning treatments produced greater equitability among tolerant and intolerant species seedlings. Removal treatments increased the level of photosynthetically active radiation (PAR) reaching the forest floor, while a combination of burning and removal provided both greater equitability among species and higher levels of PAR.

INTRODUCTION

Disturbances of both natural and anthropogenic origin have shaped forests in the Central Hardwood Forest Region for centuries. Human-induced disturbances, such as fire and clearing, have affected the region for approximately 10,000 years as large populations of native peoples and Europeans have passed through or settled. By choosing to burn, clear, or suppress disturbances, their actions have affected succession and forest composition.

Upland forests of this region are typified by oak-hickory (*Quercus L.-Carya Nutt. spp.*) overstories, with more shade-tolerant species, like maples (*Acer L. spp.*), dominating the understory. Advanced oak regeneration struggles to compete with the abundant shade-tolerant species in the understory and rarely survives long enough to grow to the overstory. Succession of plant species is similar throughout the Central Hardwoods: forests are first dominated by shade-intolerant, fast-growing species, characterized in the region by oaks and hickories, and are followed by those more tolerant of the dense shade beneath the forest canopy. The forests eventually reach a state where the overstory is composed of maples, beech (*Fagus grandifolia Ehrh.*), and other shade-tolerant species. In central and northern Indiana, where small isolated fragments of forest are dwarfed by the agricultural landscape and disturbances have been lacking, shade-tolerant species have gained in dominance over the past century. Spetich and Parker (1998) showed that the mid-story composition of an old-growth forest in east-central Indiana had changed from 14 percent oak and 12 percent sugar maple (*Acer saccharum Marsh.*) in 1926 to 1 percent oak and 43 percent sugar maple by 1992. It has been predicted that gradual replacement of the oak-hickory overstory in this forest will lead to a canopy dominated by sugar maple by the end of the twenty-first century (Spetich 1995).

Disturbances can be used to slow the succession toward shade-tolerant species dominance and encourage regener-

ation of early successional species. One of the greatest impacts that disturbances have on a forest is the reduction of trees in the mid- and understory layers which consequently increases the light that reaches the forest floor. Merritt and Pope (1991) have shown that the result of prescribed burning is to increase the intensity of light penetrating the forest canopy. They also found an increased density of early successional species following burning.

Burning alone, however, may not be sufficient for oak regeneration, especially if the understory is already dominated by late successional species. Research suggests that burning will have little effect on species composition and may even increase the number of shade-tolerant species that are already prolific beneath the canopy (Arthur and others 1998, Dolan 1994, Huddle and Pallardy 1996, McGee and others 1995, Merritt and Pope 1991). Furthermore, harvesting treatments can encourage the growth of shade-tolerant species by allowing light to reach seedlings which are already present in the understory prior to cutting (Abrams and Scott 1989, Jenkins and Parker 1998, Weigel and Parker 1997). Therefore, altering only the light regime may not be sufficient for increasing oak dominance in the understory.

Brose and others (1999) have shown that the combination of burning and shelterwood cuts can have a positive effect on the composition of shade-intolerant species. While harvesting provided light for growth of shade-intolerant species like oak, fire acted to reduce competition from more abundant species like red maple and tulip-poplar. Because of physiological differences in the species, oak, which develops a strong root system as a seedling, is able to sprout quickly following a fire and take advantage of the increased light created by the harvesting and subsequent maintenance by the fire (Barnes and Van Lear 1998, Huddle and Pallardy 1999, Kelty 1999, Kolb and others 1990).

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The objective of this research is to investigate whether prescribed fire and sub-canopy removal within mid-successional forests can be used to shift the species composition of understory communities. This study examines how disturbances can be used to increase the abundance of shade-intolerant species through the control of shade-tolerant species dominance and the simultaneous modification of light conditions at the forest floor.

METHODS

Research Sites

Research was conducted on three Purdue University properties in west-central Indiana. Two properties, Martell Forest (mesic slope) and Cox-Haggerty Woodland (dry slope), are located at the break of the Tipton Till Plain and consist of several areas with 18 to 50 percent slopes. South facing slopes with oak-hickory overstories were chosen as study sites on these two properties. Soils are classified in the Strawn-Rodman complex and are well drained with moderate to low available water capacity (Ziegler and Wolf 1998). The third property, McCormick's Woods (mesic upland), is located on the till plain and has level topography. The soil is classified as Starks-Fincastle complex and is somewhat poorly drained with high available water capacity (Ziegler and Wolf 1998). The forest overstory at McCormick's Woods is also dominated by oak-hickory.

The disturbance and management history of these sites is not well documented, but recent disturbances within these woodlands have been minimal. The site at Martell Forest burned accidentally in 1981, and though the intensity was low, it completely burned the hillside of study. The understory is composed mainly of American elm and flowering dogwood, though neither is dominant. The Cox-Haggerty Woodland site was grazed until 1990 and, as a result, has an understory dominated by plant species associated with grazing, especially Amur honeysuckle (*Lonicera maackii* (Rupr.) Herder). McCormick's Woods was harvested several times in the 1960s and 1970s using group and single-tree selection cuts. The understory is dominated by sugar maple and white ash (*Fraxinus americana* L.), which often grow thick enough to prevent easy movement through the forest.

Plot Design

Study sites were divided into several 20 x 20 meter plots for study and treatment. Treatment plots were established on a grid system, oriented by cardinal directions, with a 10 meter wide buffer left between plots to reduce treatment overlap. Sampling was restricted to a 10 x 10 meter plot centered within the treatment plot, leaving a 5 meter buffer surrounding the sampling plot to reduce edge effect from adjacent, untreated areas. Twelve plots each were established at the mesic and dry slope sites, and 20 plots were established at the mesic upland site.

Sampling Design

Cover of herbaceous species and density of woody species within the understory were sampled prior to treatment during May and June 1999 and after treatment in May and June 2000 and 2001. Cover of herbaceous species was determined on a four-point scale based on percent cover: 1 = less than 1 percent cover, 2 = 1-5 percent cover, 3 = 5-15

percent cover, and 4 = greater than 15 percent cover. Woody and shrub sprouts resulting from stem top-kill were counted as seedlings; each sprouting plant was counted as one seedling. Finally each tree greater than 2 cm in diameter at breast height (d.b.h.) within the sampling plot was identified and measured at breast height.

Transmitted photosynthetically active radiation (PAR) was measured prior to treatment in July 1999, and following treatment in July 2000, for each sample plot. Measurements were not recorded in 2001. A Sunflece Ceptometer (Decagon devices, Inc., Washington, USA) was used to measure PAR at five points within each plot: one at each corner and one in the center. Measurements in full sunlight were also taken each day plot measurements were taken. All PAR measurements were made on cloudless days between 12:00 p.m. and 2:00 p.m. eastern standard time.

Treatments

One of four treatments was randomly assigned to each plot. Each treatment was replicated five times at the mesic upland site and three times at both the dry and mesic slope sites. The treatments assigned were mechanical removal of the subcanopy, prescribed burn, a combination of burning and removal, and control.

Mechanical removal of the subcanopy occurred in August 1999 on plots designated for removal and combination treatments. Woody stems greater than 1 cm in d.b.h. but less than 15 cm in d.b.h. were cut using a chain saw and completely removed from the treatment plot. Trees greater than 10 cm in d.b.h. that would have been difficult to maneuver and could not be felled easily were double girdled and allowed to remain standing in the plot.

Prescribed burns were conducted in October and November 1999 on plots designated for burn and combination treatments. One meter wide fire break lines were constructed around each treatment plot prior to burning using fire rakes and a leaf blower. Depending on the weather and dryness of the fuel, either a strip head or ring fire technique was used to burn each plot. After ignition, the fires were allowed to burn through the plots and extinguish themselves. Any large debris left burning was extinguished using water sprayed from backpack pump sprayers.

Data Analysis

Woody seedling data were analyzed to find differences in diversity, evenness, and density between treatments at each site. The Shannon-Wiener index was used to computer diversity and evenness. To simplify results and interpretation, tree species were separated into two categories, shade-tolerant and shade-intolerant seedlings. Shade tolerance was classified by each species' ability to grow from a seedling to a sapling beneath a dense overstory. Some species typically defined as shade-intolerant, such as black cherry or white ash, were classified as shade-tolerant for this study, because their abundant seedlings often grow to sapling size and present immense competition to oaks, hickories, and other shade-intolerant species typically unable to grow beyond seedling size before mortality. The effect of treatment and time on diversity, evenness and density was analyzed with a repeated measures analysis

in SAS using Wilk's Lambda to determine significance. Square-root transformations were performed on density data in order to decrease the amount of variability between plots.

Herbaceous species abundance data were analyzed with partial detrended correspondence analysis (pDCA) in CANOCO to determine the effect of treatment on herbaceous community composition. PDCA, a variation of DCA allowing for covariables, provided a graphical analysis of community composition, as well as a plot depicting the relationship between sites based on species compositions. Using plot and time as covariables, the effects of these factors were taken into account while the effect of treatment remained as a potential source of variation. Sites plotted on the graph were most similar to those plotted near it, while those farther away were dissimilar. From this method, treatment effect was evaluated by looking for clusters of sites which had the same treatment applied.

Photosynthetically active radiation data from each plot, along with measurements taken in full sunlight, were used to calculate the percent of full sunlight beneath the canopy for each plot. Comparisons and analysis of the percent full sunlight between plots and treatments were done using an ANOVA in SAS.

RESULTS

Analysis of the three forest sites with burning, mechanical removal, and combination treatments resulted in no significant difference in diversity as measured by the Shannon-Wiener index. Compared to the change over time at plots which received no treatment, the overall diversity of seedlings did not increase or decrease with treatment (fig. 1). Further, the difference between treatments at each site was not significant. In comparison to the control plots, the graphs show a decrease in diversity for burn treatments at the mesic slope site by the third year (fig. 1b). This can be attributed to an overall loss in the total number of seedlings because of burning. The loss of species was not seen however after the first year at this site or after the first or second years at the dry slope (fig. 1a) or mesic upland sites (fig. 1c).

Evenness of species distribution within each plot increased after the first year with burn treatments at each site. Both burn treatments at the dry slope site showed a dramatic increase in evenness over the change at the control site (fig. 2a). The effect was continued through the second year of treatment at which time the increase became statistically significant ($p = 0.05$). The increase in evenness at the mesic upland site was significant for the combination treatment ($p = 0.02$), but not for the burn treatment (fig. 2b). At this site, the increase in evenness after burning was apparent after only the first year of treatment. The following year saw a sharp decrease in evenness on all treatment plots. The change in evenness at the mesic slope site tended to follow that of the mesic upland; however, the results were not statistically significant (fig. 2c). All treatments showed a slight increase in evenness over the control plots, but evenness decreased after the second burn treatments. The removal treatment at all sites tended to increase evenness slightly over the control, though these changes were not significantly large.

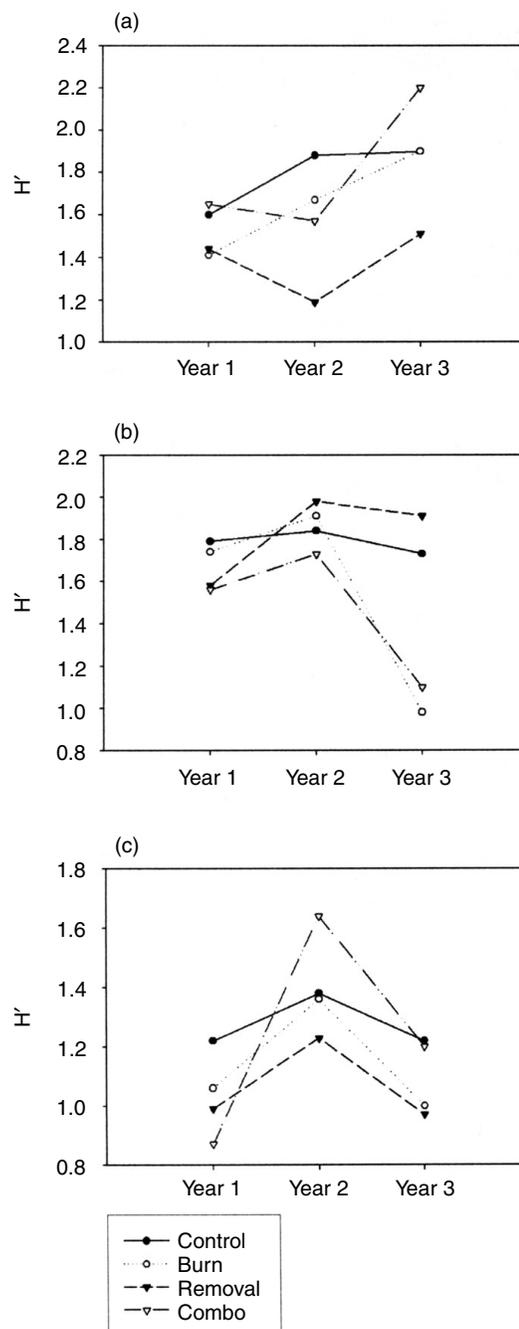


Figure 1—Plot of Shannon-Wiener index of diversity for each treatment over time at the dry slope site (a), the mesic slope site (b), and the mesic upland site (c).

Analysis of shade-tolerant seedling density reveals that only plots which received the combination treatment changed significantly ($p = .10$) in response to treatment. The greatest decrease was found at the dry slope site (fig. 3a) where the number of shade-tolerant seedlings was originally very high. Both burn treatments largely reduced the number of shade-tolerant seedlings at this site. The mesic slope (fig. 3b) and mesic upland sites (fig. 3c) showed similar responses to the burn treatments with a decrease in the number of shade-tolerant species, though to a lesser degree than at the dry slope site. At the mesic upland site, there was a large spike

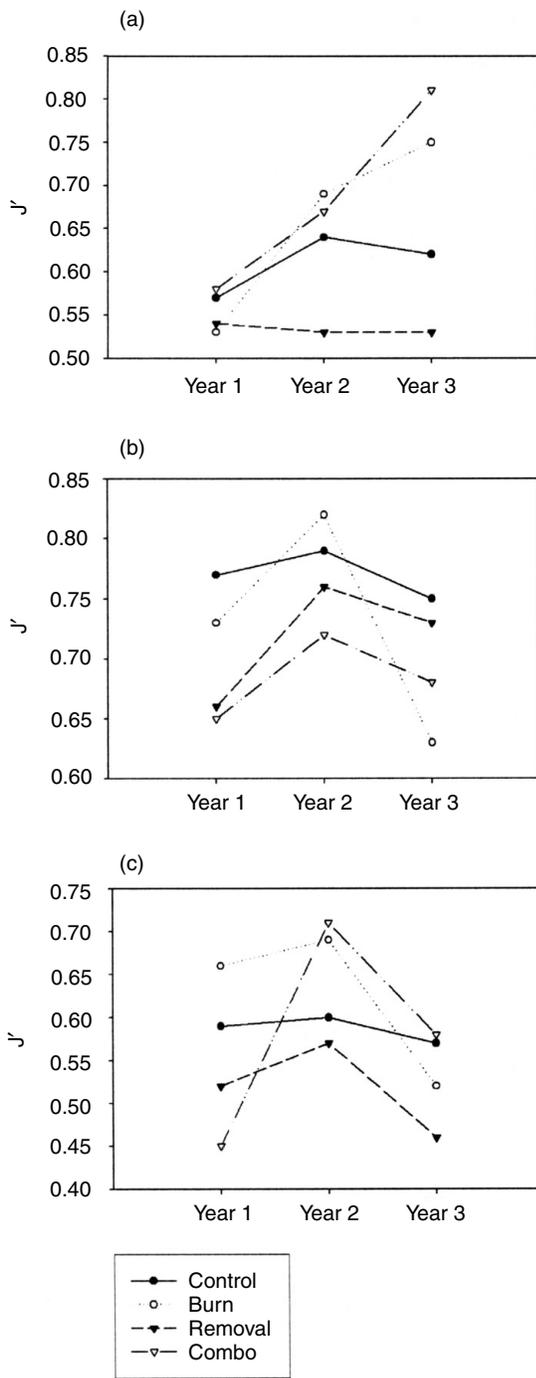


Figure 2—Plot of evenness index for each treatment over time at the dry slope site (a), the mesic slope site (b), and the mesic upland site (c).

in the number of seedlings after the second year of treatment. This increased response in seedlings follows a large mortality of saplings 2 to 5 cm in d.b.h. after the second burn (table 1). These new sprouts were counted as seedlings and increased the total number of seedlings within each plot. The response of the shade-tolerant seedlings to the removal treatment did not differ significantly from that of the control plots at any site.

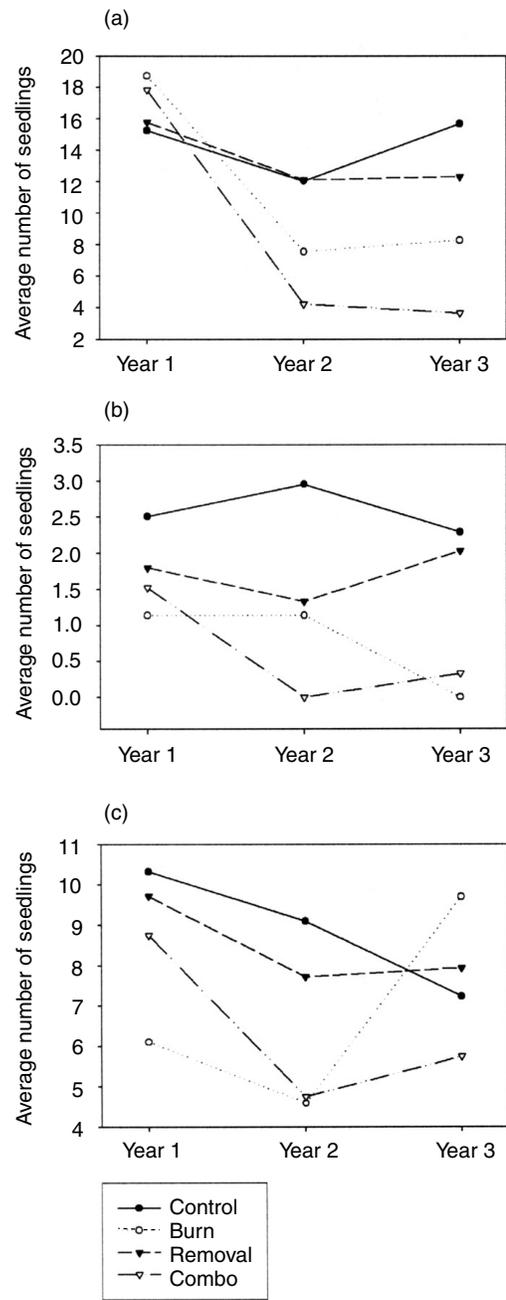


Figure 3—Plot of the average number of shade-tolerant seedlings per plot for each treatment over time at the dry slope site (a), the mesic slope site (b), and the mesic upland site (c).

Shade-intolerant species, including oaks and hickories, showed much the same response to treatment as the shade-tolerant species (fig. 4). The removal treatment seemed to have the greatest influence on shade-intolerant species, with a slight increase at the dry slope site after the first year (fig. 4a), a slight increase at the mesic slope site after the second year (fig. 4b) and a rapid increase at the mesic upland site after the first year (fig. 4c). Response at all sites to the burn treatment was a decrease in the number of shade-intolerant seedlings.

Table 1—Average number of saplings per plot > 5 cm d.b.h. and < 1 m tall for each site and year

Site	Treatment	Year		
		1	2	3
Average number per plot				
Dry slope	Control	5.00	5.00	5.33
	Burn	3.67	0.00	0.33
	Removal	0.67	0.00	0.33
	Combination	10.67	0.00	0.00
Mesic slope	Control	15.33	15.33	10.00
	Burn	5.33	1.33	0.33
	Removal	4.67	1.00	0.00
	Combination	12.00	0.00	0.00
Mesic upland	Control	32.40	27.00	28.60
	Burn	34.40	0.60	4.00
	Removal	59.80	14.20	1.40
	Combination	50.80	0.00	0.00

D.b.h. = diameter at breast height.

Table 2—Percent of full sunlight as measured by PAR at the forest floor taken in mid-July before and after each treatment

Site	Treatment	Year	
		1	2
-- percent PAR --			
Dry slope	Control	1.37	9.50
	Burn	8.92	5.40
	Removal	15.22	41.93*
	Combination	3.45	29.72*
Mesic slope	Control	3.83	2.93
	Burn	3.62	8.03*
	Removal	3.23	6.68*
	Combination	2.57	12.30*
Mesic upland	Control	4.41	2.80
	Burn	1.38	9.41*
	Removal	2.37	5.63*
	Combination	1.42	13.68*

PAR = photosynthetically active radiation.

An asterisk indicates a statistically significant change from year 1 to year 2.

Detrended correspondence analysis at each of the three sites reveals that there are no consistent changes in herbaceous communities as a result of the treatments (figs. 5a, 5b, and 5c). Site scores of the treated plots are scattered among the control plot scores and are not clustered together. A treatment effect on the herbaceous communities would result in site scores being similar; however this is not the case. Patterns based on disturbance treatment are not clearly identifiable.

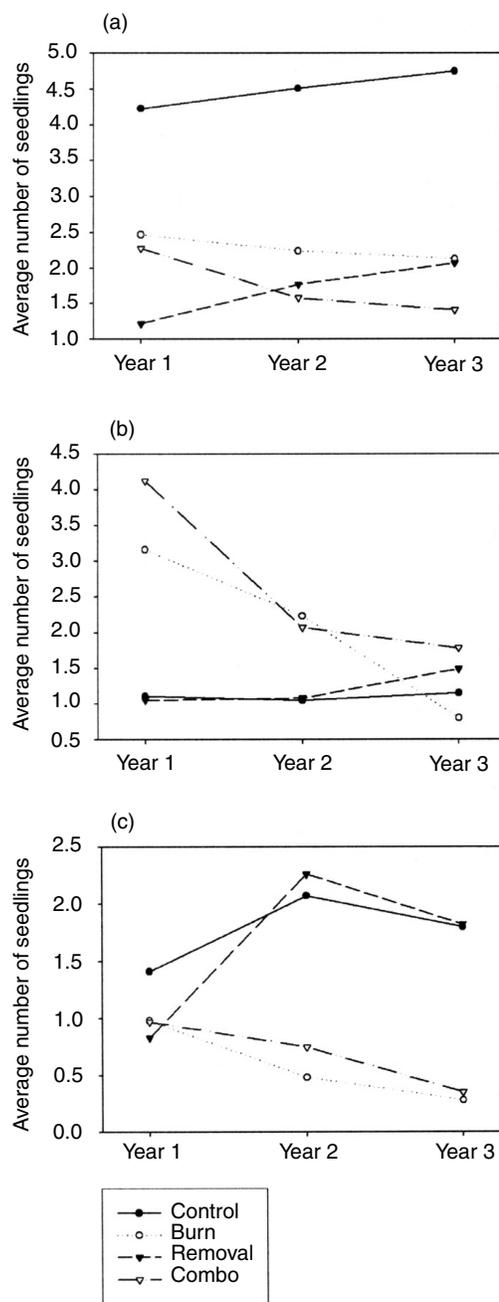


Figure 4—Plot of the average number of shade-intolerant seedlings per plot for each treatment over time at the dry slope site (a), the mesic slope site (b), and the mesic upland site (c).

The percent of full sunlight as measured by the amount of photosynthetically active radiation (PAR) increased with each treatment at all sites, except the burn treatment at the dry slope site (table 2). At this site, the abundance of Amur honeysuckle and its ability to profusely resprout, caused a decrease in PAR because of burning. Plots that were treated with understory removal increased between 3 to 25 percent full sunlight at the forest floor, while those treated with the combination treatment had an increase of 10 to 25 percent. Burn treatment plots had an increase of only 4 to 8 percent.

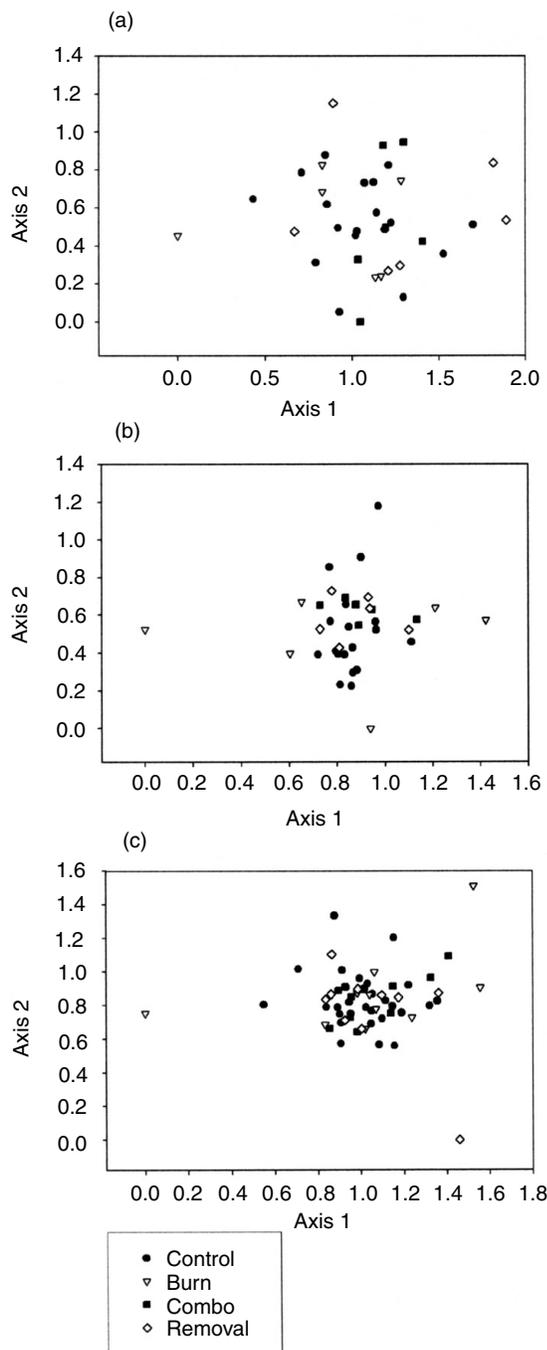


Figure 5—pDCA of herbaceous species showing site values before and after treatment at the dry slope site (a), the mesic slope site (b), and the mesic upland site (c). Axis 1 and 2 are shown in each graph with 13 and 8 percent of variation explained for graph (a), 13 and 9 percent for graph (b), and 12 and 8 percent for graph (c).

DISCUSSION

Consistent results across all three sites reveal important patterns related to the disturbance treatments. The results indicate that burning alone may not be sufficient to increase the pool of shade-intolerant species in the forest understory, especially if the forest has already transitioned into a dense understory of shade-tolerant species. It is important

to provide not only an environment suitable for oak establishment, but also for sustained growth. In providing increased light through removal treatments, it may be possible for shade-intolerant seedlings to survive until an opportunity for growth to the overstory occurs, such as a tree fall or some other disturbance which affects the forest canopy.

Although the Shannon-Wiener index indicates that there is little change in diversity because of treatment, a closer look at evenness shows that burning can reduce competition between species by reducing the total number of seedlings. Further study is necessary to determine how the new and surviving seedlings will respond to the changes in environmental conditions created by the burning and removal treatments.

The response to the removal treatments is not yet clear because of the short duration of this study. Research has shown that light levels at or near 50 percent full sunlight provide the best conditions for oak establishment, while greater amounts of light are necessary for increased growth rates (Crow 1988, Gardiner and Hodges 1998, Guo and others 2001). The amount of light provided by the sub-canopy removal treatments in this study may not be sufficient for sustained growth; however, it may provide adequate light conditions for a greater amount of shade-intolerant species to establish. It will be several years before the effect of the current removal treatments on establishment and sustained growth of species like oak can be determined on these research sites.

The lack of effect of burning and removal treatments on the herbaceous species communities merits more research; however, results of this study are encouraging for the use of small disturbances to alter the composition of seedling communities without affecting the herbaceous communities. Response of the herbaceous communities was random, proving that the treatments did not greatly affect the overall composition. The effect of treatment on individual species is not clear through this research, because the sampling design was not structured for such a study. Further analysis of continued disturbance on individual species is necessary, but single disturbances do not affect individuals in such a way as to change the overall community structure.

Results of this study support existing research concerning the regeneration of oak and associated species. Low-intensity disturbances, like the combination of burning and sub-canopy removal, can be used to improve conditions for oak seedling establishment while reducing competition from shade-tolerant species. While successive burns do not dramatically alter the composition beyond that of a single burn, repeated burns every few years will be necessary to lessen competition from shade-tolerant seedlings. Through the use of burning and sub-canopy removal, oak seedlings can be maintained in the understory until they are provided with adequate light conditions for growth to the overstory that would occur with higher severity disturbances such as harvesting or wildfire.

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Appendix—List of species included in shade-tolerant and shade-intolerant species analyses

Common name	Scientific name
Shade-tolerant species	
American basswood	<i>Tilia americana</i> L.
American beech	<i>Fagus grandifolia</i> Ehrh.
American elm	<i>Ulmus americana</i> L.
Black cherry	<i>Prunus serotina</i> Ehrh.
Flowering dogwood	<i>Cornus florida</i> L.
Hackberry	<i>Celtis occidentalis</i> L.
Sugar maple	<i>Acer saccharum</i> Marsh.
White ash	<i>Fraxinus americana</i> L.
Shade-intolerant species	
Black oak	<i>Quercus velutina</i> Lam.
Black walnut	<i>Juglans nigra</i> L.
Bur oak	<i>Q. macrocarpa</i> Michx.
Chinquapin oak	<i>Q. muehlenbergii</i> Engelm.
Hickory species	<i>Carya spp.</i> Nutt.
Northern red oak	<i>Q. rubra</i> L.
Sassafras	<i>Sassafras albidum</i> (Nutt.) Nees
Tulip-poplar	<i>Liriodendron tulipifera</i> L.
White oak	<i>Q. alba</i> L.

THE INFLUENCE OF SOIL SCARIFICATION ON OAK REPRODUCTION: REVIEW AND MANAGEMENT CONSIDERATIONS

John M. Lhotka, James J. Zaczek, and Russell T. Graham¹

Abstract—Changes in historic disturbance regimes and the resulting changes in forest composition and structure have contributed to oak (*Quercus* spp.) regeneration difficulties across much of its geographic range. One important component of oak regeneration is the establishment and development of advance oak reproduction. Another is reducing competing vegetation to enhance the development of oak reproduction. Past and ongoing research in the use of soil scarification to enhance establishment and competitive position of oak reproduction from seed is summarized in this paper. Within each study presented, initial establishment of oak reproduction was significantly greater in scarified areas compared to the controls. From these studies, a series of management recommendations have been developed and will be presented to provide researchers and land managers with information on applicability of soil scarification treatments to enhance initial establishment oak reproduction.

INTRODUCTION

Alteration of disturbance regimes in the central and eastern United States has developed understory conditions that have led to the dominance of shade-tolerant species in the understory of many oak (*Quercus* spp.) stands (Lorimer 1984, Abrams 1992, Abrams and Nowacki 1992). With the change in the understory environment following this shift in forest structure, the establishment and development of oak reproduction has diminished (Abrams 1992, Lorimer and others 1994, Brose and others 1999). Other factors such as vertebrate predation, sporadic acorn production, weevil (*Curculio* spp) infestations, and microsite variability may also play a role in limiting the establishment of oak reproduction (Gribko and others 2002). The lack of periodic disturbance compounded with inherent biotic and abiotic factors influencing oak establishment has made the regeneration of many oak stands difficult.

Acorn survival and germination is a necessary precursor for the establishment of oak reproduction. However, few acorns ever germinate into seedlings due to factors such as losses from predation and exposure of acorns to unfavorable environmental conditions (Crow 1988, Ostfeld and others 1996). It has been suggested that soil scarification, in the presence of abundant acorns, may be useful to disrupt competing vegetation and enhancing the initial development of oak reproduction (Lhotka and Zaczek 2003a, 2003b; Zaczek 2002). Specifically, scarification promotes favorable germination conditions for acorns, provides protection from predation, and plays a role in controlling competing vegetation (Crow 1988). The results of four soil scarification studies and a discussion of the implications of these studies in using scarification to enhance the density and development of oak reproduction is outlined in this paper.

PAST AND ONGOING STUDIES

Two recent studies conducted in southern Illinois suggest that, in the presence of abundant acorns, soil scarification

can help increase the initial density of oak seedlings (Lhotka and Zaczek 2003a, 2003b). One study was conducted in an upland forest dominated by white oak (*Quercus alba* L.) and black oak (*Quercus velutina* Lam.). The stand contained a dense midstory of well-established sugar maple (*Acer saccharum* Marsh.) saplings and suppressed trees and little advance oak reproduction. In October 1999, a 78-hp crawler tractor with a 2.44-m-wide six-tooth brush rake was used to scarify the soil. One year after treatment, scarified areas had greater oak seedling densities (5,164 ha⁻¹, 20 percent of total seedlings) when compared to undisturbed areas (1,273 ha⁻¹, 9 percent of total seedlings). Scarification also reduced midstory density by removing 31 percent of the sugar maple stems within the scarified areas (Lhotka and Zaczek 2003a).

A second study conducted in southern Illinois during the same period was established in a bottomland forest composed primarily of cherrybark oak (*Quercus pagoda* Raf.) and post oak (*Quercus stellata* Wangenh.) (Lhotka and Zaczek 2003b). The understory had sparse tree regeneration and was dominated by poison ivy (*Toxicodendron radicans* L.). A 42-hp wheeled tractor pulling a 2.44-m wide field disk was used to conduct the soil scarification. One year after scarification, scarified plots had greater oak seedling densities (7,243 ha⁻¹, 42 percent of total seedlings) than did control plots (453 ha⁻¹, 9 percent of total). At the same time, poison ivy cover in the scarified plots (7 percent) was reduced compared to controls (35 percent). First year results, from the upland and bottomland studies conducted in Illinois, suggest that soil scarification has the potential to increase initial establishment of oak and may have the ability to control competing vegetation.

An early soil scarification study conducted within a northern red oak (*Quercus rubra* L.) stand using disk scarification also showed increased establishment of oak following soil scarification (Scholz 1959). However, seven years after treatment the initial advantages of disk scarification were

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no longer present. From the study, it was apparent that the stand conditions were not conducive to oak seedling development, for the average seedling height was only 19 cm after seven years. This trend suggests that without the appropriate growing conditions for oak in place at the time of treatment such as adequate light levels, protection from deer browse, or control of competing vegetation the early advantages gained by scarification may diminish over time.

A fourth study reviewed in this paper was conducted within a poorly regenerating upland mixed-oak fenced shelterwood in central Pennsylvania. The stand's understory was dominated by red maple seedlings and had relatively few small oaks. A soil scarification treatment was applied in 1993 within the shelterwood using a small crawler tractor and 1.8-m-wide brush rake. Soil scarification conducted within shelterwood and in the presence of abundant viable acorns increases the initial density and competitive position of oak and that the advantage is apparent through year five (Zaczek and others 1997, Zaczek 2002, Zaczek and Lhotka, in press). One year after scarification, 32,618 oak seedlings ha⁻¹ (78 percent of total seedlings) were found in the scarified plots, while only 9,435 oak seedlings ha⁻¹ were located in the control. The overwood and fence were removed at year three. Five years after treatment, a greater density of oaks (39,432 ha⁻¹) still remained in scarified plots when compared to controls (12,971 ha⁻¹). Additionally, within the disturbed areas, greater oak densities were present in the larger size classes compared to other species including red maple. The competing red maple reproduction was significantly reduced in density and height in response to scarification. Unlike the Scholz (1959) study, the Pennsylvania upland study was conducted in a stand with an understory environment more conducive to the development of oak seedlings. This contrast in understory environments between the two studies may explain the differences in understory dynamics seen over time.

MANAGEMENT IMPLICATIONS

While soil scarification can increase the initial establishment of desired oak species, operational and biological influences may control the success of an operation. First, abundant viable acorns must be present at the time of treatment, for without the necessary seed, a soil scarification operation will only serve to disrupt the existing vegetation and fail to develop new oak germinants. Timing of scarification operation is also crucial. It is recommended that areas be scarified in the autumn of an abundant mast year following acorn drop, but before leaf fall. This is important because it is suggested that the litter accumulation after leaf fall may provide additional protection against acorn predation (Bundy and others 1991).

Extremely wet or dry conditions at the time of treatment may also influence the success of the operation. Extremely dry conditions may cause acorns to desiccate and fail to germinate (Olson and Boyce 1971) and the depth of penetration by a disk in dry soils is limited. On the other hand, scarification may compact or displace soils and may bury acorns too deeply, resulting in decreased seedling emergence.

A wide array of power sources and implements have been used for scarification in forest operations. Selection of an

appropriate system must balance traction, soil scarification, and maneuverability. An important factor influencing a scarification operation is the presence of a dense midstory and understory. Density is important because it may hamper machinery maneuverability. The small-wheeled tractor with disk, small crawler tractor with brushrake or Salmon blade, and a modified drag-chain scarifier pulled by a small crawler tractor are three methods that may be used for scarification in partial harvests (Karsky 1993, Zaczek and others 1997, Lhotka and Zaczek 2003b). These systems have the size and maneuverability to operate in a partially harvested stand without damaging residual trees, but still have sufficient power to complete the operation (Karsky 1993). The disking and drag-chain method may be preferred in open stands, but the mobility of the equipment may be severely limited in dense stands or those containing large amounts of slash. Therefore, it may be necessary to thin and/or remove slash prior to implementing the disk or drag-chain method. In contrast, the bulldozer/brushrake method has the ability to operate in dense and recently harvested stands, while still providing scarification benefits (Zaczek and others 1997, Zaczek 2002). Damage to residual crop trees is possible so careful operation of equipment is necessary. For these reasons, it is important to consider stand conditions prior to planning a scarification operation.

Precision application of disturbance is another benefit that scarification can provide. In contrast, other oak regeneration enhancement treatments such as prescribed fire may be difficult or impractical to apply in small or irregular-shaped patches and exclusion from sensitive areas may be problematic. With the ability to pinpoint treated areas, a manager could scarify poorly regenerating areas, while avoiding streamside buffer zones, temporal ponds, or other unique habitats.

Soil scarification may increase initial establishment, but this silvicultural treatment alone may not create appropriate conditions for the development of large, vigorous seedlings. Without the necessary environmental conditions in place, continued growth and survival of scarification produced seedlings may be limited. Many factors can influence further development of understory reproduction. A well-developed midstory and associated low light levels will greatly hinder the development of oak seedlings (Lorimer and others 1994). The intolerant to midtolerant oak species are especially harmed and cannot survive over a long period in these low light levels (Crow 1988, Nowacki and Abrams 1992). Competing vegetation, deer browse, insects, disease, and other environmental variables may also add to seedling mortality (Crow 1988, Lorimer 1993, Oak 1993). It has been suggested that a manipulation of the midstory or overstory may help alleviate some of the problems created by low light levels (Loftis 1983, Janzen and Hodges 1985, Loftis 1990, Lockhart and others 2000). Without release, seedling survival will be limited. This resulting mortality may leave the stand in a condition similar to that present prior to the scarification treatment.

Given the presence of abundant viable acorns, scarification has been shown to increase oak seedling density. It is also suggested that scarification may control competing mid-story and understory vegetation (Lhotka and Zaczek 2003a,

Zaczek and Lhotka, in press). However, scarification may also promote sprout development and therefore the response of competing vegetation should be evaluated prior to scarification. Finally, we stress that silvicultural procedures such as an overstory thinning should be applied prior to or in concurrence with scarification to help enhance the survival, growth, and development of newly established oak seedlings.

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THE EFFECTS OF LIME, FERTILIZER, AND HERBICIDE ON FOREST SOIL SOLUTION CHEMISTRY AND NORTHERN RED OAK RADIAL GROWTH FOLLOWING SHELTERWOOD HARVEST

Angela M. Happel and William E. Sharpe¹

Soil acidity, nutrient deficient soils, lack of light penetration, herbivory, and understory competition are the major obstacles encountered in regenerating and sustaining northern red oak. Changes in soils that may occur during soil acidification include: reduced soil pH, increased availability of aluminum (Al) and manganese (Mn), loss of base cations due to leaching; and competition between base cations and Al for exchange sites in the fine roots (Robarge and Johnson 1992).

Cronan and Grigal (1995) proposed that a calcium/aluminum (Ca/Al) ratio of 1.0 or less in soil solution posed at least a 50 percent risk of adverse impacts on tree growth and a ratio of 0.2 (or less) a 100 percent risk. Soil acidity increases Al concentrations in the soil and has been implicated in oak regeneration failure in Pennsylvania (Lyon and Sharpe 1995). Northern red oak (*Quercus rubra* L.) is sensitive to Al toxicity (Cronan and Grigal 1995, Demchik and Sharpe 1999). Standard red oak regeneration practice in Pennsylvania requires a shelterwood cut to provide seeds for the new forest and allow enough light penetration to promote seedling growth. In addition, herbicides, such as sulfometuron methyl (Oust[®]), are used to reduce competition. Applications of lime and fertilizer have the potential to ameliorate soil acidity; therefore, their use could be very beneficial in the establishment of new seedlings. The objectives of this study were to determine the effects of shelterwood harvest with herbicide application on soil and soil solution chemistry; to test the efficacy of liming and fertilization as an acidity remediation treatment; and to determine the effects of these treatments on red oak tree growth.

Three sites with extremely acidic soils, forest floors dominated by hay-scented fern (*Dennstaedtia punctilobula*), and predominately northern red oak (*Quercus rubra* L.) overstories were selected for study in southwestern Pennsylvania. Soil solution samples were taken bi-weekly using tension lysimeters for three growing seasons, from plots receiving herbicide (Oust[®], sulfometuron-methyl, 2.0 ounces per acre) (H); lime and fertilizer (LF) (Dolomitic lime - 1.5 tons per acre and 10-20-20 Nitrogen-Phosphorus-Potassium (NPK) fertilizer - 0.5 tons per acre); and a combination of the herbicide, and lime, and fertilizer (HLF) treatments. Two plots served as controls (C). All plots were previously shelterwood harvested (within the year) to leave a residual basal area of 4.9 m² – 11.1 m². Northern red oak tree diameters at breast height (d.b.h.) were measured and basal area increment (BAI) was calculated.

Median soil solution data indicated calcium (Ca), magnesium (Mg), potassium (K), and pH increased with the addition of lime and fertilizer. Soil solution from plots receiving lime and fertilizer had increased Ca/Al and base cation/aluminum (BC/Al) ratios above critical levels. The addition of herbicide alone caused increased soil solution Al and H⁺ concentrations and reduced Ca/Al ratios to critically low levels. Within the HLF treatment plot, the addition of lime and fertilizer counteracted the acidifying effects of herbicide treatment, while still providing hay-scented fern control.

Northern red oak measurements indicated that under normal moisture conditions trees in the HLF plot had significantly increased radial growth over all other treatments. Both the LF and H treatments had significantly increased radial growth over the control treatment. The improved soil solution chemistry conditions on all plots receiving lime and fertilizer seemed to increase red oak radial growth.

Soil solution results indicated that even with the relatively modest lime and fertilizer application rates used, important soil chemistry improvements were produced. Sulfometuron-methyl herbicide application by itself lowered Ca/Al and BC/Al ratios well below critical levels implicated in Al toxicity to red oak, decreased soil solution pH, and increased plant available Al. Liming and fertilization with hay-scented fern control ameliorated soil acidification effects associated with sulfometuron-methyl application and resulted in Ca/Al and BC/Al ratios above critical levels and significantly improved plant available Ca and Mg concentrations. Based on the unfavorable soil chemical changes observed and their amelioration by lime and fertilizer application, sulfometuron-methyl herbicides should not be used to promote northern red oak regeneration on extremely acidic soils without accompanying lime and fertilizer treatment.

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OAK BOLE-WOOD CHEMISTRY RESPONSE TO FERTILIZATION AT TWO OZARK SITES

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INTRODUCTION

Bole-wood chemistry can be a useful indicator of the nutrient status of trees. Liming generally increases Ca and/or Mg and decreases Mn concentrations in bole-wood. Acidifying treatments, such as ammonium sulfate or nitrogen fertilizers without lime, generally cause Mn increases and concomitant decreases in Ca and Mg. Bole-wood concentration ratios of Ca/Mn have been found to be good indicators of soil alkalization or acidification trends (DeWalle and others 1999). Whether the timing of past chemical changes in soil is accurately preserved in tree rings remains uncertain. In this study we had an opportunity to study bole-wood chemistry in *Quercus* spp. two decades after an acidifying N-only (AR site) and NPK+liming (MO site) treatment.

METHODS

Multiple wood cores were removed at breast height from ten trees on control and treated plots at each site in 1995. At the Arkansas site, 336 kg N/ha had been added as ammonium nitrate fertilizer to *Q. rubra* trees in 1977-78. At the Missouri site, NPK+lime (1345 kg N/ha as urea) had been added to *Q. velutina* trees in 1973. Destructive chemical analysis (ICP) was performed on composite wood samples for tree core segments formed before and after treatment. Significant growth responses to fertilization were previously reported at each site (AR-Graney and Murphy 1993, MO-Harris and others 1980).

RESULTS

Arkansas

At the AR site, fertilization only caused a significant reduction in Ca concentrations in bole-wood formed in the 5-yr segment after treatment. No other significant changes in Ca and Mn concentrations and Ca/Mn ratios were detected. Regardless, Ca/Mn ratios in red oak appeared to be reduced by treatment in bole-wood formed 5-yr after and up to 20 years prior to treatment (fig. 1).

Missouri

At the MO site, significant decreases in Mn concentrations and increases in Ca/Mn ratios (fig. 2) occurred in nearly all segments of bole-wood of black oak due to treatment. Ca/Mn ratios were increased in bole-wood formed up to 20 years prior to and up to 20 years after fertilization. Ca concentrations were not significantly affected, but appeared to be increased by treatment.

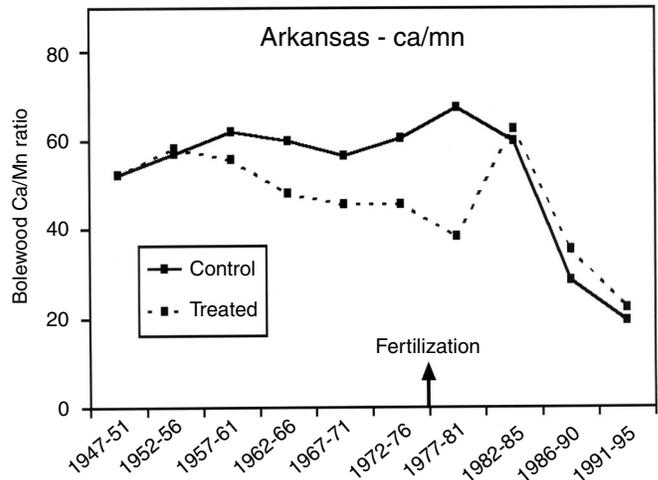


Figure 1—Molar Ca/Mn concentration ratios in bole-wood of red oak in 1995 at an AR site that had been fertilized with ammonium nitrate in 1977-78.

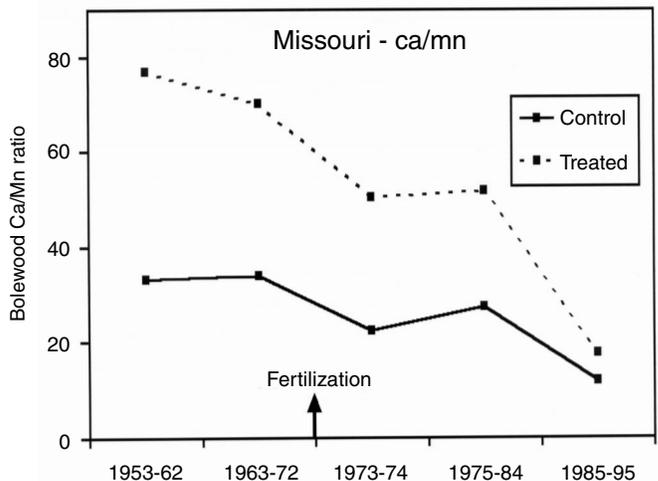


Figure 2—Molar Ca/Mn concentration ratios in bole-wood of black oak in 1995 at a MO site that had been fertilized with NPK+lime in 1973.

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CONCLUSIONS

Nitrogen fertilization without liming in AR caused slight, short-lived soil acidification that could be detected in bole-wood of red oak trees 20 years after treatment. In contrast, urea N-fertilization with lime in MO had a long-lasting effect on bole-wood chemistry of black oak. Bole-wood chemistry changes were evident in a wide band of wood formed prior to treatment, limiting the usefulness of dendrochemistry to precisely chronicle soil changes.

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SPATIAL AND TEMPORAL DISTRIBUTION OF WEEVILED ACORNS WITHIN A NORTHERN RED OAK SEEDLING ORCHARD

D.R. Miller and S.E. Schlarbaum¹

SUMMARY

Acorn insects can have a severe impact on mass production and regeneration. Gibson (1972) reported losses of 10 to 100 percent of acorn crops in stands of white oak, whereas Gibson (1982) reported losses of up to 96 percent in stands of northern red oak. Acorn insects can be divided into two groups: primary and secondary insects. The primary insects include the *Curculio* weevils, filbertworms, and gall wasps, and damage acorns directly to introduce larvae. The secondary insects include acorn moths, midges, and *Conotrachelus* weevils, and take advantage of existing holes or damage. The most damaging of all these insects are the *Curculio* weevils, with 23 species recorded on oak in North America, often accounting for most, if not all, damage caused by acorn insects. Myers (1978) found that weevils accounted for half of the 62 percent loss of acorns in stands of white, black, northern red, and scarlet oaks in Missouri between 1973 and 1976; wildlife only took 11 percent. Three or four species of *Curculio* weevils can be present at the same time in a forested stand or seed orchard. Currently, there are no registered control products or tactics for acorn insects, although various pesticides are registered and used for related *Curculio* weevils in pecan and chestnut orchards. Adult weevils generally emerge from the forest floor in August and September, climb trees, mate, and lay eggs inside acorns. Larvae feed freely within acorns, often with numerous larvae inside the same acorn, until the acorns fall and larvae leave the acorns to burrow into the ground to depths approaching 12 inches. Larvae remain underground for about 2 years, pupate, and re-emerge as adults.

Our objective was to examine the level of acorn losses in a northern red oak seedling orchard in northeastern Tennessee, looking for relationships of damage with the size of acorn crops and time of acorn fall. In summer of 2000, 42 northern red oaks bearing acornets were selected at the Watauga Seedling Orchard in northeastern Tennessee. During the fall of 2000, all acorns falling from each tree were collected at 2-week intervals and floated to determine damage levels. Damaged acorns float while healthy acorns sink. Prior to floating, a subsample of 100 acorns was taken and dissected for comparison with the floating method. The level of damage to acorns at the Watauga Seedling Orchard in 2000 was 42 percent (SE = 2 percent), with 67 percent of the damage caused by weevils. Floating overestimated damage by 36 percent. Acorns that fell in early fall were more likely to be damaged by weevils (39 percent) than acorns that fell in late fall (10 percent). The levels of damage by weevils were higher in trees with small acorn crops than in those with large acorn crops ($r^2 = 0.418$; $P < 0.01$).

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Closing Remarks

WHERE DO WE GO FROM HERE?

Martin L. Blaney, Scott Simon, James M. Guldin,
Tom Riley, Donny Harris, and Rebecca McPeake¹

Abstract—The structure and diversity of the upland oak ecosystem has changed significantly, primarily caused by fire suppression and historic forestry practices, leaving the ecosystem vulnerable to outbreaks of pathogens and insects. These conditions, coupled with periods of drought, have caused significant oak mortality throughout the Interior Highland region shifting the communities to different forest types. There is great concern among conservationists that a shift in forest type will cause declines in wildlife populations and rare species dependent upon these ecosystems. Upon witnessing this continued degradation of upland oak forests and woodlands, a momentum of purpose and resolve became established among a diverse group of conservation partners that lead to the idea of gathering various resource disciplines to this “state of our understanding” conference. Once assembled and with the quality of papers presented, it was easy to see that it would be beneficial to capture more of the expertise attending the event. Many of the research findings presented by the scientists can now be used by those in positions of management authority to make better decisions about the resources entrusted to their professional care. In keeping with the overall strategy of the symposium, the conference committee attempted to take advantage of the expertise gathered at the conference by polling the audience for ideas of “where we go from here.” In concluding the symposium, the last session’s focus was to provide closing comments by a panel of experts in each of four broad categories that encompass the various issues surrounding oak sustainability; restoration, research, policy and management. Audience responses to posed questions were then collected and tabulated. It was agreed by many present that information exists to restore the ecosystem, but political and economic barriers must be overcome for landscape level restoration to occur.

INTRODUCTION – MARTIN L. BLANEY

In the process of putting this symposium together with a diverse group of conservation partners, a momentum of purpose and resolve developed that seems to be unprecedented in our region. Upon witnessing our upland oak forests and woodlands slowly degrade in health and vigor through the last decades of our collective careers and then to watch their accelerated decline in the last three years has brought us to the same question. Can we continue in our own spheres of responsibilities and allow such a shift in forest communities to occur without our concerted efforts to find and affect solutions? With defiant conviction, the response was a collective “not on our watch.” A strategy formed around the oak sustainability issue that had its beginnings in the Forestry Subcommittee of the Arkansas Wildlife Federation with the formation of a coalition of partners. At the same time, acting as a catalyst, an issue of the Arkansas Wildlife magazine focusing on oak decline was printed and widely circulated. The many and widely favorable responses received from the widespread distribution of this publication, further heightened the resolve of the coalition to the possibility of changing public opinion regarding the need for human intervention into the oak communities. With the onset of the red oak borer outbreak, questions from the public regarding hardwood forest management began to accelerate and the obvious gaps and conflicts in our professional understandings was apparent. These events lead to the eventual need of assembling the various resource professions to gain a cohesive awareness and

understanding of oak ecology to both provide answers to the public and affect management solutions through better techniques. It was clear that we, as resource professionals, were quite divided in our understandings of how these systems worked and what were and were not appropriate recommendations when lending technical assistance to the inquiring public. Once assembled at the conference and with the quality of presentations and subject matter, it was easy to see that we also needed to capture more of the expertise attending this event.

We chose to conclude the symposium with a panel discussion focusing our attention upon what needs to happen for oak sustainability to occur. For the purposes of addressing this we divided the issues surrounding oak ecosystem restoration into four broad categories affecting oak restoration and provide a presentation on each by a qualified panelist. These categories are (1) an understanding of the history, ecology and restoration requirements, (2) what research needs and challenges await us, (3) the important public attitudes that will influence us and the policies that present hurdles, and (4) the importance of trying and finding appropriate management tools and affecting solutions on landscape scales. The session then concluded by polling the audience with two questions regarding barriers they perceive stand in the way of restoring our upland oak communities. The responses are summarized at the end of the paper. Following are the panel presentations as witnessed by the conference participants.

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RESTORATION – SCOTT SIMON

Historically, the interior highlands landscape consisted of a mosaic of prairies, savannas, woodlands, and forests. Based on Government Land Office survey (GLO) records interpreted by Tom Foti, only 33 percent of the Ozarks was described as closed forest (much of this in the steep slopes of Arkansas' Boston Mountains and Current River Hills in southeast Missouri), with the remaining 67 percent of the landscape described as open forest, savanna, and prairie. Densities calculated from the GLO records indicate average densities per subsection ranging from 38 trees per acre in the Central Plateau subsection to 76 trees per acre in the Upper Boston Mountains subsection per acre. Average density in the Upper and Lower Boston Mountain subsections combined is 54 trees per acre. Underneath these forest, woodland, and savanna communities was a diverse herbaceous understory that supported wildlife of elk, bear, bison, turkey, deer and over 150 species of plants and animals found no where else in the world.

The Ozarks was a landscape extensively maintained by fires and adapted to disturbance. Ignition sources from Native Americans and lightning strikes created fire frequencies that Richard Gyette and others estimated ranged from 1 to 6 years in prairie communities, 2 to 7 years in open woodlands and 5 to 50 years in the closed forest communities on steep slopes. These regular understory fires maintained a relatively open tree structure and a diverse herbaceous layer. What we've learned is that to this ecosystem, fire is as essential as rainfall.

Eventually with some of the changes in European settlement and extensive cutting that followed, the fires stopped and the forests, woodlands, savannas, prairie, and forests grew up (densified) before our generations' eyes. The new Ozark landscape was now much denser. Nearly all of the forested areas could be classified as closed forest. Historically there were 52 trees per acre in the Boston Mountains there are now 148 trees per acre based on Jim Guldin's data from the Ozark Ouachita Highlands Assessment. A threefold increase over what the historic landscape contained. An even greater increase has occurred in the sapling and shrub layer with 300 to 1,000 stems per acre currently—a staggering increase.

As David Van Lear, Michael Steele, James Fralish, and others described, this densification has had some effects. Very little light reaches the forest floor in the summer in the Ozarks. Because of the shade, oak regeneration is negligible, herbaceous layer diversity abundance is low (typically 20 to 40 plant species per acre compared to 150 to 200 species per acre in open, restored stands) and a new forest of shade intolerant woody species with maples, ashes and ostrya is the dominant understory. We really don't know what the future overstory would be. Moving us from an overstory of oaks to some other forest type, Tom Foti asked me to mention, isn't going to be a moist or a mesophytic forest that typically occurred on the moist lower north-facing slopes. It's going to be a subset of that historical forest type, it's going to be junk.

Because there are so many trees per acre that are competing for the same amount of nutrients and water, the ecosystem

is under stress. Just like when humans are stressed, we're vulnerable to any individual pathogen and we get sick. Our oak ecosystem is susceptible to an epidemic of native insects like the red oak borer that as Rose-Marie Muzika described, had never been reported at epidemic levels in the history she was able to derive from tree ring data. Although there are many contributing factors to oak decline, it seems the root cause is too many trees per acre. There is nothing in the post-glacial record that suggests that the Ozark ecosystems have been previously impacted by changes of this magnitude or rapidity. These changes and their impacts to soils, water and other habitat conditions, may be occurring at a rate that is too fast for many of the species to adapt. Animal species are dependent on the plants. If plant communities change, we can assume that there are going to be changes in the animal population and wildlife populations. Of particular concern to us at The Nature Conservancy are those species adapted to the Ozark and Ouachita ecosystems found nowhere else in the World.

Over the millennia, this system has been maintained and stewarded by humans for about 12,000 years. In recent years with all good intentions, we have probably failed it and ultimately ourselves, our children, and grandchildren. We have the information to restore the structure, diversity, and sustainability of the oak ecosystem through the use of prescribed fire and silvicultural treatments utilized on numerous successful, small restoration projects conducted by many agencies and organizations. We need to utilize what we learned from these pilot projects and expand to selected larger areas on the landscape. It is up to our generation to restore the sustainability of the system. We don't want to restore the system to keep it in a box, with some preconceived idea of what it should look like. We need to restore its historical structure and diversity so that as the climate changes and the world changes, this system can change and adapt in a resilient way with the full complement of species for future generations to benefit from and enjoy. Future generations will have as many options in addressing their future as we have.

RESEARCH – JAMES M. GULDIN

Before reviewing the scientific high points that emerged from presentations during this symposium, a few comments are in order regarding the role of the scientist in matters of forest policy.

First, scientists are not decision makers. The work of the scientist is to develop the conceptual and quantitative understanding of natural resource issues—essentially, to add tools to the toolbox of the decision-maker. The many research findings presented by the scientists who spoke at this symposium can now be used by those in positions of management authority to make better decisions about the resources entrusted to their professional care.

Second, definitive research on natural resource issues does not and will never exist. This enhances, rather than diminishes, the responsibilities of the scientist and the decision maker. For example, some would argue that decisions should be deferred if the science about the issue is incomplete. But the ultimate costs of deferring decisions may frequently be greater than the costs of executing them,

especially in the long term. A case in point has been repeatedly discussed during this symposium—the decline in the health of Interior Highlands forest stands attributable to stand age in a forest landscape that has been under-managed for decades, especially on Federal lands.

Scientists will continue to study questions of forest health, sustainability, productivity, and diversity in the Interior Highlands from our comfortable ivory towers. Some of the products produced by this process may be informative, some will be useful, and a few will enable major scientific and conceptual understandings of the ecology and management of oak ecosystems. This process is maddeningly inefficient and seems conspiratorially independent of details such as decision deadlines and timely public discourse. As a result, the decisions that are made by those responsible for making them will continue to fall short of definitive scientific support. But a decision made without definitive science is not necessarily bad. There are a host of legal, political, economic, biological, and social considerations that bear upon a decision, many of which might be contrary to accepted scientific findings—and which nevertheless might result in an excellent decision in the public policy context or for a private landowner.

With respect to the scientific findings presented at this symposium, suffice it to say that the decision maker's toolbox has become heavier. A number of points deserve recapitulation for both the scientists and the decision-makers in attendance. These points were jotted down as speakers made their presentations, and in some instances the speaker's name appears in parenthesis after the salient point. The reader might refer to the appropriate paper in this proceedings for further detail.

The importance of fire in oak ecosystems is becoming increasingly appreciated, and speakers at this symposium suggested that its use could be expanded considerably. It was suggested that fire could be of great benefit in maintaining species and habitats (Ladd). Research opportunities to refine the influence of fire include the effects of fire on soil dynamics, the importance of growing season burns, and the manner by which fire influences landscape pattern (Foti, Heitzman, Benac). In addition, the role of fire in wood quality and utilization requires additional research (Patterson). Finally, the influence of fire, or lack thereof, was discussed in reference to stand recovery after exploitation; this was especially prominent in southeastern Missouri, where the acreage of land on which shortleaf pine was dominant has declined from 6 million acres at the turn of the century to less than 600,000 today (Benac). Certainly one part of the question regarding the fire-mediated restoration of the upland oak ecosystem is the degree to which shortleaf pine should be favored, either in mixture with hardwoods or as a dominant forest type on appropriate sites.

Conversely, several speakers observed that the limitations to broader application of fire in the oak ecosystem are real. Those constraints to burning more frequently over larger areas include the increasing human population in the region, both in absolute terms and in distribution through the wildland-urban interface, and the associated increased fragmentation of forests (Guyette, Fralish). These considerations

suggest that less fire, not more, is likely in the future. This also speaks to the continued importance of research on fire surrogate treatments that emulate the ecological effects of fire in oak ecosystems.

A third topic of considerable interest to the research community at this symposium is wildlife, specifically deer. Several speakers pointed to the fact that numbers were fewer 200 years ago than today (Van Lear, Dickson), and there are implications regarding the adequacy of oak regeneration related to this point (Miller, Brose, Healy). It's too bad deer don't leave tree scars as fires do, so we can quantify their effects. But just because we can't quantify the effect doesn't mean the increase hasn't been ecologically significant. Among the reasons for the higher deer numbers may be loss of predators (Healy). An interesting question raised by these ideas is whether the detrimental influence of high deer populations exceeds that resulting from the lack of fire as a primary factor limiting oak sustainability. That would be easy to test—exclude deer from one area, increase cyclical burning in another, do both in a third, and see what happens.

There have been many advances in oak silviculture over the past several decades, and more are needed. Speakers identified a number of areas where advances might be in order, including study of stand dynamics in oaks under decline (Kabrick), oak seedling silvics, and regeneration potential under various fire prescriptions (Brose). The potential for the application of uneven-aged silviculture in oak stand, especially on the better sites, remains to be established (Loftis); group selection probably works better than single-tree selection, but more data are needed. However, the potential inherent in the single-tree selection method was convincingly shown by the 50-year, 150,000-acre case study at Pioneer Forest (Trammel).

A number of speakers mentioned the fact that the knowledge base for better management of oaks exists, but that knowledge may not be getting into the hands of users. Better approaches to technology transfer are being sought. Scientists will need to translate results from research studies into practical application for a wider variety of research data. Several good examples of this were presented, such as the ingenious planting guidelines for oaks based on survival probabilities (Spetich) and the development of oak regeneration models (Loftis, Schweitzer).

Finally, several speakers pointed to key challenges for oak management, especially regarding undesirable consequences in the absence of change. Speakers questioned whether management for oak sawtimber is consistent with oak ecosystem sustainability. Two emerging themes that captured this pessimism were that the next century will be a tough time to be an oak tree (Shifley), and that extraordinary efforts to modify the structure of Interior Highlands oak forests to resist gypsy moth appear to be justified (Gottschalk).

In summary, the research perspective points to many interesting directions and avenues of continued research. But one cannot help but be concerned that continuing the present course of affectionate, laissez-faire, hands-off

development of the upland oak forests of the Interior Highlands may essentially be little more than loving them to death.

POLICY – TOM RILEY

My challenge was to talk about the policy issues that we have to deal with related to management of the oak forest. First of all, I want to ask a question of the audience – maybe you can just give me a show of hands – how many of you have as your primary responsibility water quality protection? How many of you have air quality protection as one of your primary responsibilities? I think that is a challenge for all of us because I think everybody should raise your hands in both questions (three people in an audience of 200 raised their hands). We have a natural resource management responsibility and forestry is a part of that. We all have a responsibility to resource, to the implications of what we do relative to that resource and there are a lot of people out there who are looking at what we do, not from the standpoint of “what are you doing to my forest?” but “what are the actions that you are taking on that forest doing to my water quality, what’s it doing to the quality of my air?” If you’re living in Memphis, you are in an air of quality attainment zone, so anything that you do within that airshed is going to be influenced by what the city of Memphis says it wants to do. Those are the regulations, those are the rules that are going to apply. If you are in Little Rock or if you are in the vicinity of Little Rock, that same circumstance is going to apply. The numbers are getting so large now in terms of air quality that Fort Smith and Fayetteville may also be included. Think about it, in Arkansas, a million people, over 40 percent of the population of this state, resides in about five counties in northwest Arkansas. When you think about the future of that in terms of the population dynamics between the people and the resource, what we do out there on that resource is very much influenced by what it is those people think, what they understand. The question would be “how can you have an educated policy if you don’t have an educated public?” If you don’t have a public that understands exactly what you are doing, if you don’t have a public that trusts you, trusts you and believes that what you are doing is actually right for the resource that’s going to be a benefit to them. We’ve got a lot of opportunity, we have a lot of tools that are available to us. We’ve got one of the best conservation provisions in the Farm Bill that we’ve had in my memory, and I’ve done a lot of historical work associated with the history of farm conservation legislation. We can treat this in a lot of different ways: we can regulate, we’ve got all kinds of tools, we can do an incentive-based program, we can change our tax structure, we can also be influenced by the courts. If you’ve paid any attention to the way we have come to do some of the things we’ve done in the state of Arkansas, you’ve got a pretty sound logic if you think about a lot of the things that we do being influenced or directed by the courts. I’ll guarantee if we don’t do this right, if we don’t do it with an educated public, that’s where we will be. We’ll be directed by one federal judge from some court somewhere. So we have to pay close attention to that as one of the policy options that’s out there. We can use markets, economies, we can pay attention to landowners, and we have heard something about private landowners, a lot about moving private landowners to do things. What motivates the private landowners? What is the policy issue

that they’re going to be most concerned about? Most of them, it’s a bottom line thing, it’s a dollars and cents thing, or it’s a social thing. It’s something having to do with what I want to do on my property or what I believe my property rights to be. We talk a lot about the concepts of watershed management, of ecosystem management, and we use a lot of our scientific terms in that process and it scares individual private forest landowners and they become so distrusting that they won’t listen to the logic. So we have to understand and deal with the language issue, the way we approach, and the way we communicate with individual landowners. We have this mix of resources that are available to us if you think about the Farm Bill and all the opportunities that are there: EQIP, the Environmental Quality Incentives Program, CRP, Wetlands Reserve, all of these include in them forest management opportunity, new forest potential within those different programs. We’ve got the FLEP (Forest Land Enhancement Program) that’s specifically for private landowners. But where is the NRCS relationship that guarantees that fire is one of the management alternatives that’s provided to the individual private forest landowner? If it’s not in their tech guide, if it’s not in their set of tools that they have available to them, working with that private landowner on an individual daily basis, it’s not coming to ground, it’s not going to be used. If those individual resource people who are out there working day to day with landowners don’t know how to use fire, don’t trust that concept in management, it’s never going to be used in a private setting the way it ought to be used. Those are circumstances that we have an opportunity to overcome, but we can’t overcome them in this audience – we have to broaden it. We have to broaden the audience, we have to broaden the understanding, that’s how policy change gets made. It won’t get made in this room. It gets made in taking this knowledge, this understanding, to another step and another step. There is a poet I think a lot of (Shel Silverstein) who says a lot of things – he wrote a poem that’s very short and it kind of fits here:

You, all of us, have a magic carpet that will whiz you
through the air

To Spain, to Maine, to Africa, you just tell it where

So will you let it take you where you have never been
before?

Or will you just buy drapes to match and use it on your
floor?

MANAGEMENT – DONNY HARRIS

I’m not sure I even understand that... but I’m sure it’s all good. A few months ago, Martin Blaney approached me and asked me if I would be willing to serve on this panel and I said, “Man I’d be honored.” I said, “Who’s on the panel and what’s my role gonna be?” and Martin said, “Well we’ve got Scott Simon, we got Jim Guldin and we got Tom Riley. Those people are extremely intelligent and very articulate. However, since you possess neither of those qualities, I’d like for you to serve on the panel to represent some balance.” I said, “if you’re tellin’ me you need somebody to dumb it down, I’m your man.” After all, as Bob McAnally so eloquently put it, “I was sixteen years old before I found out my name wasn’t “get wood.” And uh, for my Game and Fish brethren in the audience if I get to talkin’ too fast, raise your hand and I’ll slow it down just a little bit.

As we started this symposium, Paul Johnson enlightened us about oak forests and, how they're actually created by disturbance influences, and that we can actually perceive management activities as planned disturbances. Tom Foti went on to give us a historical perspective of how these oak forests, evolved and what the influence of fire was and what the influence of fire suppression was. Additionally Jim Dickson, Joe Clark and others spoke to, wildlife populations and how they've evolved in these habitat types and their dependence on the benefits derived from those habitat types. I said that to say this, I believe that we have the science. It's pretty obvious if you've set in the sessions and read the abstracts you have to come to that point that you believe we have adequate science, while it's not what we would desire, I believe it to be adequate. But science alone is not enough. Paul Sears in his book entitled *Deserts on the March*, which he actually wrote in 1947 said this and I quote, "Science has the power to illuminate, but not solve the deeper problems of mankind. For always after knowledge comes choice and action, both of which are intensely personal and individual." In keeping with that, in my closing remarks I'd like to extend this challenge. I believe we are at a fork in the road and must make a choice. We can leave here from this symposium and hope that through some factor of osmosis, a miraculous healing will take place in our ailing ecosystems. If that is our choice, future generations will sit in judgment and we'll be indicted and actually found guilty of negligence and outright malfeasance. Unfortunately those future generations will have to suffer the consequences of the choices that we make. On the other hand, if we link arms fortified with good science and bring the collective expertise, energy and resolve to bear on the issue at hand the outcome will not be the same. Those same future generations will sit in judgment, but I believe the conclusion will be much different. They may say in October 2002, in Fayetteville an assemblage of resource professionals decided that the upland oak ecosystems, we have come to love and appreciate, are worth everything we can do to save and perpetuate them, therefore we conclude that these professionals were responsible stewards of the resources that were placed in their care. And in summary I believe the acorn is truly in our court.

SUMMARY OF AUDIENCE COMMENTS – REBECCA MCPEAKE

After panelists responded to questions from the audience, the audience was asked their perceptions about sustaining the upland oak ecosystem. Notecards were distributed and audience members responded to two questions: (1) what are the barriers to sustaining upland oak ecosystems, and (2) what strategies or actions or solutions are needed to restore upland oak ecosystems?

Barriers

Barriers identified by many respondents were (1) a lack of recognition and support by the general public about managing oak ecosystems, particularly the importance of fire and tree harvest, (2) a lack of funding and resources to adequately implement prescribed fire treatments, given the large number of acres, limited timeframe within which controlled burns are optimally implemented, and smoke management regulations, and (3) an economic climate

which favors landowners making short-term profits over long-term gains.

Respondents indicated a number of conflicting agendas between forestry professionals and public opinion, particularly those of landowners, radical environmentalists, politicians, urbanites, and the media. Examples of their comments are as follows:

The Forest Service is perceived as timber beasts, not an interdisciplinary group of conservation professionals. The... national forests should dedicate a large amount of resources to changing public opinion or they will fight us every step of the way.

The power of the decision makers is largely in the hands of non-informed or non-scientists – landowners - judges.

We are allowing environmental advocacy groups to educate our educators. I am continually stricken with Muirist philosophy from third graders.

Public opinion – not landowners' opinion necessarily – that prevents the use of good management and fire.

Diversity of owners and in turn diversity of needs/ objectives.

Radical environmentalism... we need to collectively utilize the media to get a clear message to the public about the need to actively manage forest resources.

Media, the corporate media (all owned by very few corporations) is reactionary and very focused on blame – natural resource professionals tend to get a bad rap.

Other respondents noted that not only conflicts exist between different stakeholder groups, but that forestry professionals themselves debate the various practices for oak sustainability:

Poor research or lack of research or conflicting research has led to opposition among scientists.

Like panelist said, NRCS has programs which do not include fire programs for private landowners. Agencies such as NRCS were not included/represented in this symposium.

Knowledge: I think our information on past history is still a little thin in certain areas. Too much dependence on old records.

Gap in total understanding of the upland oak landscape with regards to all its components and users, e.g., plants, animals, etc.

Many conference participants indicated a lack of public support for various fire management strategies. Some respondents linked this lack of support with policies, rules, and regulations counter to management strategies that enhance oak sustainability.

[A barrier is a] Smokey Bear fear of fire by Baby Boomers.

Public aversion to fire, smoke management programs, public aversion to fire surrogates (e.g., chemicals). [Another

barrier is] environmentalists' aversion to active management of forests. Doing nothing is not the solution.

Public perception about negative effects of fire.

Another category of responses dealt with a lack of funding and resources to adequately implement prescribed fire treatments, given the large number of acres, limited time-frame within which controlled burns are optimally implemented, and smoke management regulations. Examples of these comments were:

Not enough resources, \$, or manpower to address acres at risk even without considering policy or social barriers.

Not all resource management agencies have adequate manpower, equipment and dollar resources to be as effective as they could be.

Lastly, many noted that landowners are responding to an economic climate which favors making short-term profits over long-term gains, which are not conducive to sustainable oak ecosystems.

The majority of the land is in private ownership. Currently, all private landowners consider is selling timber. As a private consultant, timber sales are basically the only services I can sell because it puts dollars in the owner's pockets.

Human nature focusing on personal gain over decisions which could improve the big picture.

Management of forests that focus strictly on lumber/timber production and the political and social procedures that push only for production.

Strategies/Actions/Solutions

The second question asked audience members what strategies/actions/solutions they recommended for restoring upland oak ecosystems. Responses can be broadly categorized as (1) public education directed towards youth and private landowners, (2) political influence to facilitate the use of fire management, redesign the decision process for public forest management, leverage monetary support for landowner incentive programs, (3) a need for leadership and partnerships to direct and/or influence policy, education, and research, (4) improved technology transfer, and (5) increased awareness of the impact of deer and invasive plant species on the oak ecosystem.

Responses pertaining to public education identified increased educational efforts focusing on school-aged children. Justifications included presenting a counter-balance to some of the messages that are in opposition to management practices promoting oak sustainability. Examples of these comments were:

Fund early educational programs to re-educate our young people. At best, they presently hear one radical point of view in the media, at school, and from parents who truly think they understand.

Get a mascot for the oak ecosystem like Smokey Bear is for fire. Maybe an oak tree that talks!

Programs for school kids that will let kids see that cutting trees is not bad and may even be needed.

Several audience members recommended that the next step after this symposium was to focus on NIPF (non-industrial private forest) landowner education as a large-scale effort. One proposed that the message should be to "convince landowners that we can deal with these problems through proper management." Other specific recommendations were:

Disseminate information by special article: stateside papers, agency/NGO (Inc), publications.

Involve private landowners in information gathering and implementation plans. Have similar symposia to this one (small scale, not so intense) for interested landowners (at reduced cost, of course) to educate them in their importance of achieving overall goal(s).

We want to educate the public. Would it have been a step in the right direction to have given a free pass to this symposium to the network press, local legislators, local mayors, local chamber of commerce, executives, etc., representative of governor's office? Every AR Legislator and the Governor and others listed above need to have a copy of the final report.

Respondents indicated that they expected the outcomes from educational efforts would result in support for oak ecosystem management. Specifically, two audience members stated:

We know what to do in many cases but what we often do not have is public support (which mandates to political support). We need to reach the public and inform them on principles of forest ecology and what our options are.

Build on renewed "pride" of our homeland. Engage the community of the public/private/landowners to take actions. The Ozarks aren't a tree museum - it's a dynamic community that requires action on a landscape scale.

Some linked educational efforts to improved political influence. Targeted policies were those that facilitate the use of fire management, redesign the decision-making process for public forest management, and leverage monetary support for landowner incentive programs. One respondent stated,

This isn't a problem of science, it is a political problem. It can only be won in the political arena.

Respondents indicated that for policy changes to occur, partnerships are needed that directly address specific regulatory, legal, technical, and financial hurdles. Several recognized the need for legislation that facilitated implementation of prescribed fire, for example legislation that would reduce liability and risk. Examples of comments were:

ID agencies and groups that can provide technical and financial assistance to private landowners to use recommended practices. Get \$ for landowner education programs. Quantify economic value of environmental assets (plant and animal, soil, water, air, etc). Must have a credible link (organization) between the scientific community, conservation community, state and federal agencies and

private landowners. Must develop mechanism that facilitates payment for environmental assets to private landowners.

There is a national initiative to restore ecosystems to a healthy level. There will be competition to direct the funding associated with the initiative to the protection of communities at risk while this is important, it will take funding away from those programs designed to restore the landscape on a broad scale. We must correctly identify to our political leaders the importance of landscape management.

Many comments indicated a need for leadership to form partnerships and make progress in addressing oak ecosystem management. A couple of these statements were:

Some of the brain trust needs to come up with a well-conceived long-term (no flash in the pan) political and educational initiatives to take this body of issues to the public, to congress to NGO's to other agencies more marginal, etc. As Donnie Harris says, "future generations depend on us and will judge us."

It seems to me that there needs to be a board (committee?) of informed, landscape-scale decision makers that is comprised of representatives from each of the public land agencies. This needs to be a group of small number that can actually begin to (1) prioritize manageable areas (2) develop integrated restoration/maintenance methods. This group will interface with private landholders in those target areas; also interface with politicians and media to affect decision - making and public education/outreach (television!).

Use current tools available and move forward in area where we can make immediate changes. For those areas where barriers are too great, work to make changes in policies, [and] partnerships, partnerships, partnerships. I think we can under current policies get a good start on restoring oak ecosystems. Policy changes would certainly help us be more efficient in making changes. If past related matter is a barrier, if there is a policy change would we have the resources available to take advantage of those changes?

Develop the Oak alliance association to develop strategic plan to sustain Oak Ecosystems. This alliance would provide leadership - be the catalyst - form partnerships, statewide, regionally, nationally - move us forward NOW without delay. It would be representative of the natural resources agencies, landowners, conservation groups, industry etc. that own, manage and are stewards.

Many recognized the importance of "technology transfer" as a solution to restoring upland oak ecosystems. Some audience members focused specifically on prescribed fire for restoring and improving forest health in upland oak ecosystems. Other audience members emphasized the need to conduct research and educate private landowners about "ALL available tools, thin, fire, herbicide, etc." Specific recommendations were establishing demonstration and interpretive areas that applied a variety of management treatments.

Begin establishing testing sites to showcase various burn, burn trials to show landowners what it looks like, how to do it, and focus on fire surrogates which will be more popular.

Design a landowner kiosk that pinpoints the problems existing in the non-oak understory and tells how to identify when an establishment problem may be serious.

Designate a land (e.g., a watershed 10,000+ acres) and designate a management team to implement the best ideas (the current best science-based adaptive management) to create a healthy landscape (diverse, sustainable) and a productive one (in terms of timber, wildlife, and other commodities) Demonstrate what can be (free from administrative barriers). Natural Forest Planning is a good way to get public ideas but management on Natural Forests is too constrained by the appeals process. Do such a demonstration on state lands or on a private - public partnership. Get the best minds in the state together and implement, demonstrate, and educate.

Establish what regeneration techniques work within particular areas and prepare to implement them. This will require some specific, short-term research coordination... Enlist the public in our efforts. Show them the value of these methods on private and industry property.

One audience member challenged participants individually to put into practice the information presented at the symposium. The audience member stated,

Become an advocate for sustainability. Take some of that retirement money and buy forestland yourself. Invest in what you are trying to do.

A few indicated the need for continued research about fire surrogates, restoration of tree composition, and restoration of forest structure in the sustainability of an oak ecosystem. Even though specific information about management practices may be incomplete, audience members recommended that demonstrations and public education efforts should continue. As one respondent explained,

Research [will] focus on the problem which will be a function of \$ available, hence must get political support, forest industries, NGO's etc public awareness.

Another commented,

Assuming that control of species composition in oak stands is an action that is needed to achieve desired conditions, we should begin to allocate/identify lands where fire can be used and where a fire surrogate like cutting or herbicides would be more appropriate. This is the first step in a strategy, and it can be started now by all agencies, organizations, and landowners while other details are being worked out by researchers and land managers. The public should be made aware that the resource professionals here are in agreement with this strategy.

Lastly, a couple respondents noted other influences should not be ignored when addressing strategies for restoring

upland oak ecosystems, particularly the control of expanding deer herds and invasive plant species.

In summary, it was agreed by many present that information exists to restore the ecosystem, but political and economic barriers must be overcome for landscape-level restoration to occur. Audience members were fairly consistent in their recognition of needs for education, policy, and research in addressing barriers and developing strategies for restoring

upland oak ecosystems. This included developing a large-scale public education effort coupled with targeted landowner education efforts through demonstrations and workshops. Audience members recommended forming multi-stakeholder partnerships to affect policy that is more amenable to forest management practices and landowner incentive programs, and the need for leadership to develop strategies for addressing education, policy, and research.

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Spetich, M.A., ed. 2004. Upland oak ecology symposium: history, current conditions, and sustainability. Gen. Tech. Rep. SRS-73. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 311 p.

Fifty-one papers address the ecology, history, current conditions, and sustainability of upland oak forests—with emphasis on the Interior Highlands. Subject categories were selected to provide focused coverage of the state-of-the-art research and understanding of upland oak ecology of the region.