

AN ECOLOGICALLY BASED APPROACH TO OAK SILVICULTURE: A SYNTHESIS OF 50 YEARS OF OAK ECOSYSTEM RESEARCH IN NORTH AMERICA

*Una aproximación ecológica a la silvicultura del roble:
síntesis de 50 años de investigación en ecosistemas de roble en Norteamérica*

Key words: ecology, oak, regeneration, *Quercus*, silviculture.

Palabras clave: ecología, encino, regeneración, *Quercus*, roble, silvicultura.

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ABSTRACT

Oak (*Quercus* L.) is an abundant and widely distributed genus in eastern North America. A history of periodic fire, grazing, canopy disturbance and timber harvesting has favored oak's dominance. But, changes in this regime toward much less fire or complete fire suppression, and selective cutting are causing the successional replacement of oak. High populations of forest herbivores such as white-tailed deer (*Odocoileus virginianus*), invasive species such as gypsy moth (*Lymantria dispar*), or dominance of native flora such as mountain laurel (*Kalmia latifolia*) can also inhibit oak regeneration and add to its loss within a region.

Successful oak regeneration is dependent on having an adequate number of large oak advance reproduction before stand regeneration. However, this prerequisite is often lacking in eastern oak forests. Many oak stands have either few or no oak advance reproduction, and when present, it is small and noncompetitive. These common situations can be addressed through silviculture.

The lack of oak seedlings in older, mature stands is addressed with a three-stage shelterwood method that promotes acorn production and site preparatory burning that increases acorn germination success. In younger, i.e., sapling and pole stands, crop tree thinning to release co-dominant oaks promotes crown development and future acorn production.

The lack of competitive-sized oak reproduction is addressed with a two – or three – stage shelterwood sequence because this method is very useful for providing adequate light to foster root development of the shade intolerant oak seedlings. Application of the shelterwood method often includes herbicides or prescribed fire to control competing vegetation either before or after the final overstory removal.

When adequate oak advance reproduction is present, then clearcutting is a viable option, but measures may be needed after harvesting to control competing vegetation. Prescribed fire applied several times after final removal of the shelterwood, or clearcutting is proving a useful tool to favor oak. These silvicultural practices generally have either no or positive

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impacts on non-target communities of herbaceous plants, mammals, birds, and herpetofauna.

RESUMEN

Los encinos constituyen un género (*Quercus* L.) abundante y ampliamente distribuido en los bosques del este de Norte América. La dominancia de los encinos se debe, en gran parte, a una historia de frecuentes disturbios que incluyen fuegos, herbivoría por mamíferos y explotación forestal. Alteraciones a estos regímenes de disturbios históricos hacia disturbios con menos frecuencia e intensidad, y la supresión de fuego, han ocasionado un remplazo gradual de los encinos. El aumento de poblaciones de herbívoros mamíferos (por ejemplo, *Odocoileus virginianus*), de insectos invasivos (por ejemplo, *Lymantria dispar*), o la dominancia de arbustos nativos (por ejemplo, *Kalmia latifolia*) impiden la regeneración de los encinos y contribuyen a su deterioro dentro de una región. La regeneración exitosa de los encinos depende de obtener un nivel adecuado de regeneración avanzada antes de que se inicien los cortes finales. La producción de bellotas puede incrementarse en rodales jóvenes con la aplicación de raleos para estimular el desarrollo de los doseles, o en rodales maduros utilizando una serie de cortes de protección para estimular la producción de semillas.

Los cortes de protección suelen estimular el desarrollo de especies heliófilas como los encinos, porque aumentan la luminosidad en el sotobosque. Estos cortes usualmente se aplican en conjunto con procedimientos para controlar la vegetación en el sotobosque que compite con los encinos, como el uso de herbicidas o quemas prescritas. Si existe una cantidad adecuada de regeneración avanzada, el uso de la tala raza es apropiado, pero usualmente requiere el control de la competencia (por ejemplo, de malezas) que puede desarrollarse después de la cosecha. La quema prescrita, aplicada una o varias veces después de los cortes de protección o de la tala raza, es una práctica viable que favorece a los encinos. Todas estas intervenciones generalmente ocasionan una respuesta relativamente neutra o positiva a las comunidades de otros grupos de organismos como plantas herbáceas, aves, mamíferos, y la herpetofauna.

INTRODUCTION

Oak (*Quercus* L.) is a dominant genus in eastern North America (east of the 100th meridian), where oak species are common associates in a majority of forest types (Johnson *et al.* 2009). Oak has had a significant presence in eastern forests for millenia, and today it is dominant on 51% of all forest lands in the eastern United States (Spetich *et al.* 2002). Here, oak species are found on a wide variety of sites: from rich, hydric floodplains to productive mesic coves to harsh xeric uplands and mountain ridgetops. The collective distribution of all oak species spans a wide macroclimatic gradient from the Humid Tropical Domain in southern Florida to the Humid Temperate Domain that extends into southern Canada (Bailey 1995). Within these Domains, oak occurs on a variety of soils and competes with a varying mix of hardwoods and conifers depending on location. In eastern North America, there are more than 50 oak species, among which there is considerable variation in their distributions and silvical characteristics (Burns & Honkala 1990).

From historic times until today, the oak resource has been and is of great economic importance to people in eastern North America and the world (Williams 1989, Logan 2005). Oak is used in a variety of products including furniture, flooring, paneling, barrels, dimension lumber, railroad ties, pulpwood, and fuelwood. Further, the acorns produced by oaks are important food to wildlife in eastern North America. Additionally, oak canopies and leaf litter provide habitat for a rich abundance of insects and other invertebrates that support diverse populations of songbirds, waterfowl, reptiles, amphibians, and small mammals (Rodewald & Abrams 2002, Rubbo & Kiesecker 2004). Finally, oak ecosystems in eastern North America contain exceptionally high levels of plant diversity and endemism for temperate biomes (Ricketts *et al.* 1999, Kier *et al.* 2005).

Despite oaks long-history of dominance and importance in eastern North America, over the past 50 years, there have been widespread reports of failure to regenerate oak and sustain its stocking in future forests (Johnson *et al.* 2009). This paper provides

an overview of the ecology and silviculture of oak dominated forests in eastern North America based on the large body of research published over the past century. We lay the foundation of our understanding of oak silviculture with an ecological and historical perspective of the disturbance regimes and cultural land use that led to oak's dominance in modern times. Next, we discuss the regeneration ecology of oak and silvicultural practices that can be used today to regenerate and sustain the desired oak stocking in the future forest. We conclude by addressing how these silvicultural practices affect important plant and animal communities in these eastern North American forests.

THE CHANGING ROLE OF FIRE IN EASTERN NORTH AMERICAN OAK FORESTS

Against a backdrop of natural forest disturbances caused by wind, ice, drought, flooding, insects, and disease, wildfire was the single most influential factor that shaped the nature and distribution of vegetation across much of eastern North America. Wildfire in this region was and continues to be primarily an anthropogenic phenomenon and naturally occurring wildfires are rare (typically < 2%) (Dey & Guyette 2000, Guyette *et al.* 2002). As long as humans have inhabited eastern North America they have used fire as a management tool (Pyne 1982, Williams 1989, Krech 1999). Historic fire frequency in eastern North America varied spatially and temporally as shifting human populations and cultures interacted with the land under variable climates (Guyette *et al.* 2005) (Figure 1). Differences in topography, water features such as lakes and streams, climate, and vegetation all interact to modify the anthropogenic fire regime at any given time and place. Average mean fire intervals (MFI) ranged from 1-17 years across the south-eastern United States, 15 to 25 years in the Midwest, Mid Atlantic and southern New England, and > 30 years for northern areas for the period before 1850.

Native Americans used fire for a variety of reasons including to promote grasslands, to favor browse and forage production, to manage fruit and nut crops, in hunting wildlife, to clear forests for crop production, and in conflicts with surrounding tribes. They burned in spring and fall seasons

when fuels were cured and weather was conducive to fire's spread. In the south, they were also able to burn in the winter months because snow is seldom covering the ground. Fires were also set in drought years. Fires were ignited with no intention of controlling their spread and no effort was made to put them out when the intended purposes were met. Sometimes fires would be set just before the nomadic people left an area.

Native use of fire favored the expansion and dominance of fire-adapted oaks and pines (*Pinus* L.), promoted the expansion of the tallgrass prairie into the eastern North American deciduous forest region, and sustained open oak woodlands and savannas (Figure 2). The frequency of fire largely determined what vegetation would dominate. For example, annual fires promoted grasslands and savannas, and fires every 3-5 years would favor hardwoods over pines.

Colonization of eastern North America by Europeans triggered a change in the frequency of fire (Brose *et al.* 2001). Initially, European settlement brought an increase in fire frequency (i.e., MFI < 5 years), a greater consistency in fire occurrence than in the former period, and an increase in ignitions in more remote areas (Dey & Guyette 2000, Dey 2002, Guyette *et al.* 2002). Settlers began forest clearing and burning to convert land to agriculture production, and set fires in forests and woodlands to improve forage for livestock.

Continued European settlement and the advent of the Industrial Revolution led to an escalating demand for wood products. Forest lands throughout eastern North America were subjected to large scale commercial logging and the entire region was cleared within a span of about 100 years (Williams 1989). Cutover lands were often burned, and fires were severe as they spread through the logging slash. By the early 20th century, widespread forest clearing and catastrophic fires were so problematic that they led to the modern conservation movement and formation of public land management agencies throughout the United States. The primary initial task of most forestry programs was the prevention and suppression of wildfires. In the past 80 years,

fire prevention and suppression efforts have been so successful that fire has been largely marginalized as a forest disturbance. Compared to the frequency of fire observed in the Native American period (Figure 1), fire has essentially been eliminated as a forest disturbance and fire rotation periods for most of the eastern United States range from 700 to 2000 years in modern times (Dey 2002). Although many fires are still ignited by humans each year, they are quickly extinguished and average fire sizes are < 5 ha in most years (e.g., Westin 1992).

THE ECOLOGY OF OAK AND FIRE

Given adequate acorn crops and seedling establishment, periodic fire promotes the accumulation of oak advance reproduction by increasing light in the understory through reduced overstory stocking and elimination of fire sensitive woody competitors in the mid and understory. Adequate light in the forest understory is essential for good growth of oak advance reproduction because oaks are predominantly shade intolerant (Burns & Honkala 1990). Through repeated cycles of fire-caused shoot

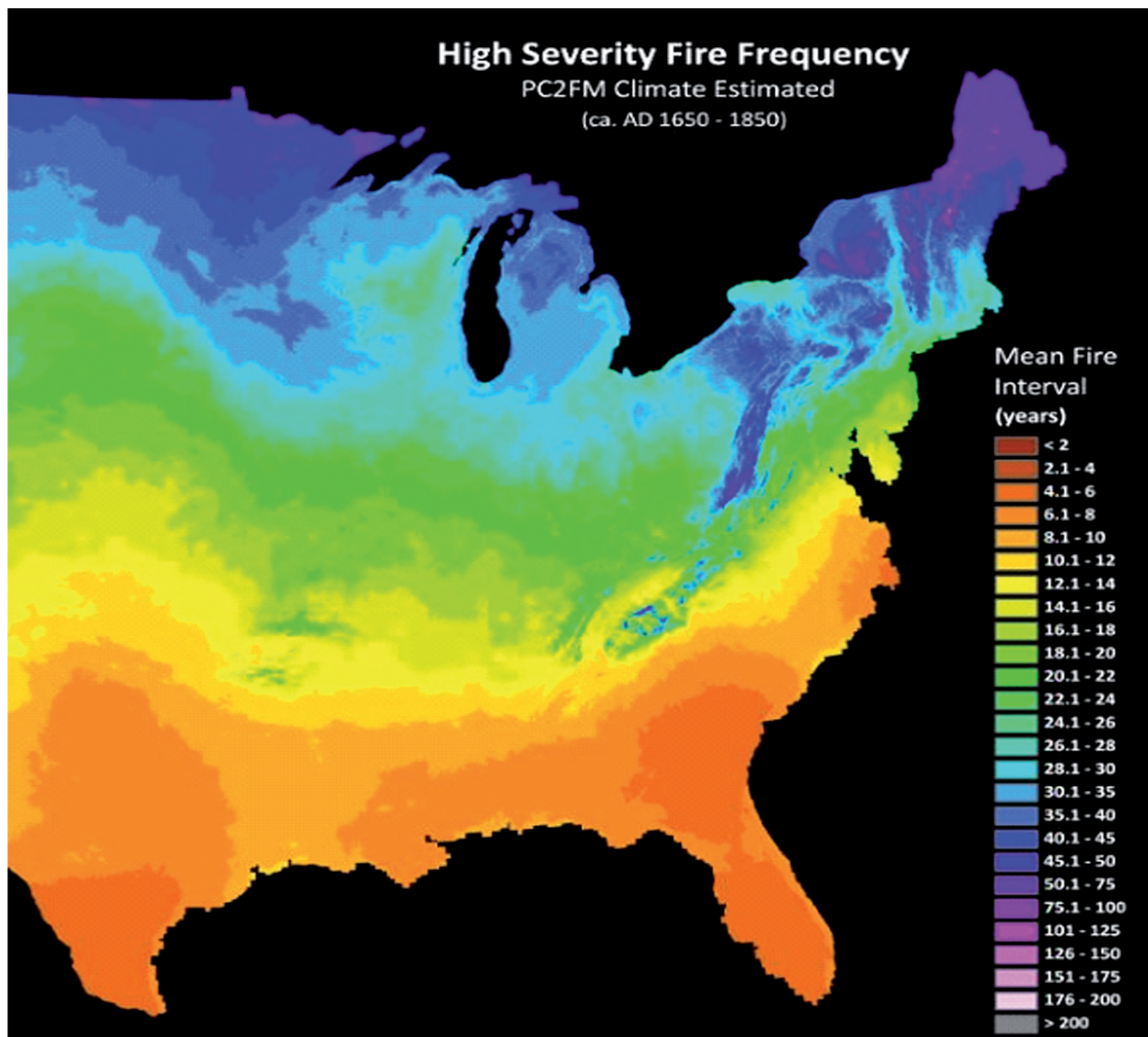


Figure 1. Estimated mean fire intervals in the eastern United States as predicted by Guyette *et al.* (2005). The mapped mean fire intervals are modeled based on fire scar tree-ring histories from forested landscapes throughout the eastern United States, and represent estimates of fire frequency for the historic period 1650 to 1850, which is the end of the Native American occupation in this area. The map illustrated here is a revision of that originally published in Guyette *et al.* (2005), and is presented here with permission of Dr. Guyette .

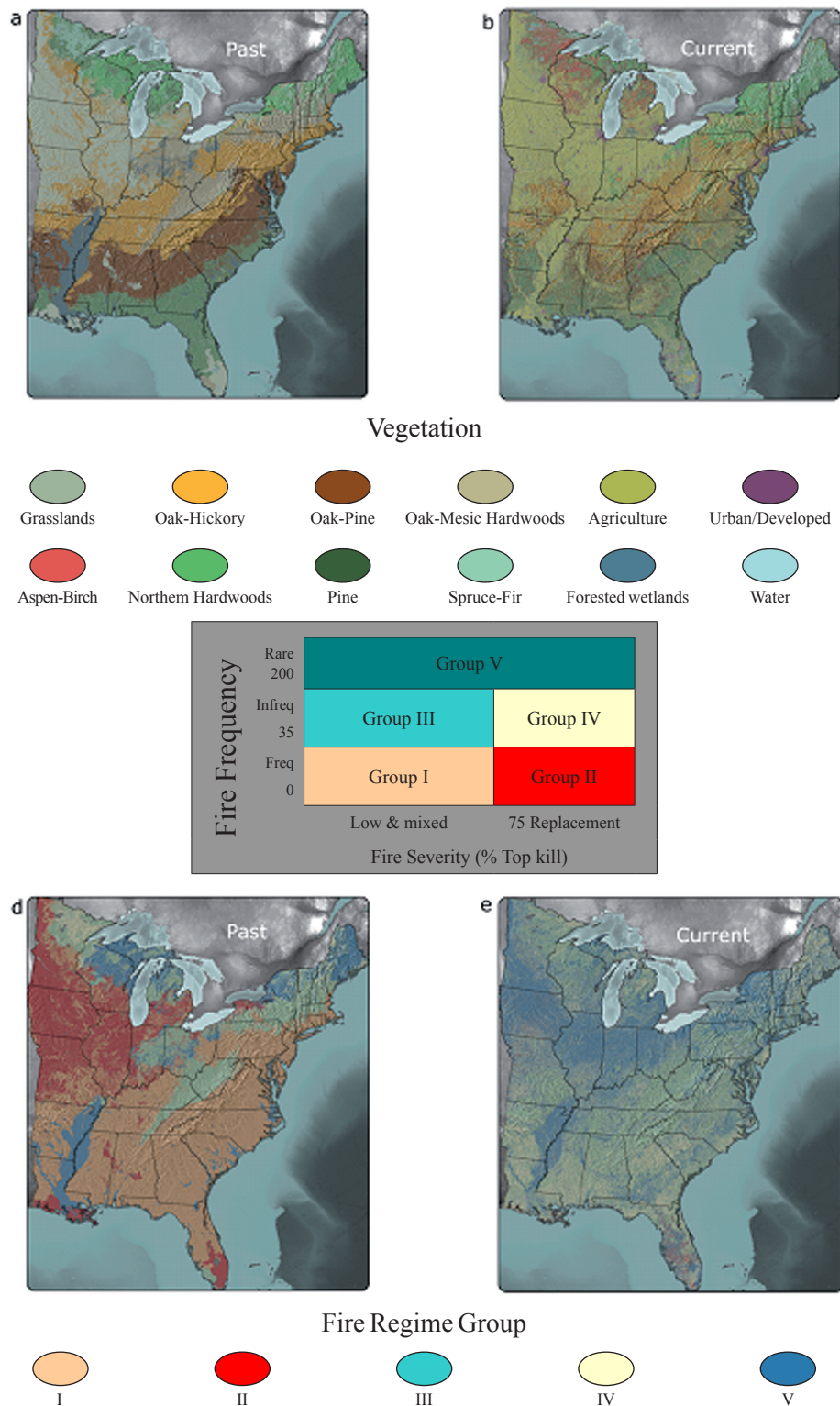


Figure 2. (a) Past (pre-European settlement) and (b) current vegetation mapped for the eastern United States. Past vegetation is mapped using the potential natural vegetation of Schmidt *et al.* (2002). The current vegetation is based on the Advanced Very High Resolution Radiometer and the National Land Cover Dataset. Fire regime groups (c) are determined by fire severity and frequency and are mapped as I (frequent, low to mixed severity), II (frequent, severe), III (infrequent, low to mixed severity), IV (infrequent, severe) and V (rare of any severity). The figure is from Nowacki and Abrams (2008) and is published with permission of the authors and BioScience.

dieback and sprouting, oak advance reproduction is able to grow to competitive sizes in well-lit understories, while fires concurrently reduce most woody competition. Thus, when any disturbance takes out overstory trees creating a large gap or patch opening, the large oak advance reproduction is better able to dominate the available growing space (Johnson *et al.* 2009).

Oak's resilience in the face of repeated fire is a result of a suite of traits that allow it to persist, and sometimes thrive, following fire. Initially, the dispersal and caching of acorns in mineral soil by small mammals and birds provides an advantage as the hypogeal germination of oaks often results in the root collar and dormant buds being buried in the soil. Because soil is typically a poor heat conductor, as little as 1.0 cm of soil can insulate the germinating acorn from fire's heat (Iverson & Hutchinson 2002, Boerner 2006). This benefit is enhanced in northern climates and high mountain elevations where soils are often frozen in the spring fire season. Following germination, oaks preferentially allocate carbohydrates to below-ground growth and these root systems are consequently insulated from the killing heat of fire by the soil (Kolb & Steiner 1990, Walters *et al.* 1993). With adequate light, oak seedlings can rapidly increase in basal diameter and build a relatively large root mass, characteristics that are positively correlated with sprouting capacity (Dey & Parker 1997, Brose 2008, Johnson *et al.* 2009). This high degree of sprouting capacity is critical as most juvenile trees (e.g., < 12 cm dbh) of all species are susceptible to being topkilled by surface fires (Waldrop *et al.* 1992, Barnes & Van Lear 1998, Brose & Van Lear 1998). Nevertheless, despite being topkilled following fire, oaks usually increase in relative abundance due to abundant resprouting from multiple dormant buds located near the root collar (Waldrop *et al.* 1992, Dey & Hartman 2005). Finally, oak trees typically have a thicker bark than most other hardwoods, making them relatively more fire tolerant than their associated species (Hengst & Dawson 1994).

Despite possessing a suite of traits that promote persistence following fire, fire can still be detrimental at certain stages in an oak's life cycle. The

heat of even low intensity surface fires is sufficient to kill half or more of the acorns that lie on the soil surface or are mixed in the leaf litter, and seed viability is significantly reduced in the surviving acorns (Auchmoody & Smith 1993, Dey & Fan, 2009). Oak seedlings that are less than 3 years old suffer high mortality (>70%) after a single low intensity dormant season fire (Johnson 1974, Dey & Parker 1996), in part because of thin bark and low root carbohydrate reserves in small diameter seedlings growing in a heavily shaded forest understory. Therefore, the season and frequency of fire in relation to acorn dispersal, seedling establishment, and rate of development influence the fate of oak reproduction and whether it is favored over its competitors. Ultimately, a sufficient fire-free period is required for growth (e.g., > 10 cm dbh) so that oak gains resistance to being topkilled by subsequent fires and can thereby recruit into the overstory. In Missouri, Dey & Fan (2009), estimated that this may take between 20 and 30 years for oak of average growth rate on most site qualities depending on the source of oak regeneration, i.e., seedling or stump sprouts. Such fire-free periods were not unusual in the Native American period (Guyette *et al.* 2002), but did not exist during the peak of European settler burning. It was not until the modern fire suppression era that many cutover and periodically burned lands began to mature into the oak dominated forests we see today.

Fire suppression has been a two-edged sword in eastern North American oak forests. Initially, the absence of fire permitted oaks to assume dominance. A long history of frequent fire had left oak in a highly competitive position because it is better adapted to fire than most species. Consequently, oak often became a major associate even on highly productive forest sites. Today's oak-dominated forests arose from savannas and open woodlands via tree ingrowth, abandoned cropfields and pastures reforestation, and cutover forests regenerating. Now, fire's absence is promoting succession to other species (Nowacki & Abrams 2008). Oak is replaced by shade tolerant species such as red maple (*Acer rubrum*) and sugar maple (*A. saccharum*) when forests are subject to small-scale natural disturbances or uneven-aged silviculture

(Schuler 2004). Many of the shade tolerant species that develop under oak canopies and replace oak under gap phase dynamics are widespread throughout the eastern United States and do commonly dominate in the absence of fire (Burns & Honkala 1990, Abrams 1998). In contrast, faster-growing species such as yellow-poplar (*Liriodendron tulipifera*), another widely distributed species in the eastern United States, often outcompete oak following large-scale natural disturbances or when even-aged silviculture is practiced (Johnson *et al.* 2009). Aspen (*Populus* L.) and birches (*Betula* L.) are fast growing pioneer species that dominate forest clearcuts and replace oak in the Lake States and other areas within their native ranges. On productive sites in the Mid Atlantic and southern Appalachian regions, oaks can be replaced by a diversity of hardwood species and future forest composition is determined by the suite of established species and type of disturbance.

Forest structure has changed dramatically over the past 50 years in the absence of fire, i.e., stand density has increased, and shade tolerant trees and shrubs have formed mid and understory canopies that result in light levels as low as 1% of full sunlight at the forest floor (Parker & Dey 2008). In this heavy shade, acorns are able to germinate and seedlings develop; however, these ultimately die once acorn reserves are exhausted. For example, within 10 years of a good acorn crop the cohort of northern red oak *Quercus rubra* seedlings was nearly extinct and survivors had low regeneration potential (Loftis 1988, Crow 1992). Without adequate numbers of large oak advance reproduction, oak regeneration failure is all but certain because oak stump sprouting alone cannot sustain current oak stocking, for not all stumps produce sprouts (Dey *et al.* 1996a, Johnson *et al.* 2009).

SILVICULTURE FOR OAK REGENERATION AND RECRUITMENT

The sources of oak regeneration include seed, advance reproduction and stump sprouts (Johnson *et al.* 2009). Adequate seed production is fundamental for natural regeneration and large diameter mature oaks in dominant and codominant crown

classes are a prerequisite for good seed production in a stand. If overstory oaks are in decline or absent from the stand, then artificial regeneration is necessary to reestablish oak. Dey *et al.* (2008) provide a good review of artificial regeneration of oak in reforestation and afforestation situations.

MANAGING FOR OAK SEED PRODUCTION

Crown size, health, and class are major factors that influence acorn production (Downs & McQuilken 1944, Sharp & Sprague 1967, Sork *et al.* 1993). Dominant, healthy oaks with large, wide, and densely foliated crowns are most likely to reach their genetic potential to produce acorns and contribute to good acorn crops. Oaks in the intermediate and suppressed crown classes do not produce acorns.

At the beginning of the stem exclusion stage, i.e., sapling-sized stands, oak stocking and dominance can be improved by crop tree thinning to release desirable oak trees beginning at the time of crown closure in the stand (Miller *et al.* 2008). Oak crop trees can be released sufficiently to promote good crown development and dominance in the stand. The number of trees needing release depends on management objectives but an upper limit would be 150 oaks per ha, which would result in a fully stocked stand where oaks alone dominate the main canopy. Later in the stem exclusion stage, i.e., pole-sized stands, crop tree thinning may be used again to further ensure the presence of adequate large diameter, dominant oak in the overstory.

In more mature mixed-oak forests, the three-stage shelterwood method may be useful to promote acorn production and seedling establishment. The initial preparatory harvest is done to remove the seed source of undesirable species and to promote crown development in oaks. The intent is to enter a stand early enough to promote crown development and encourage acorn production. Therefore, the three-stage shelterwood should be initiated decades before the final regeneration harvest to allow time for crown development and account for periodicity in good acorn crops, which occur every 2 to 4 years on average depending on the oak species (Burns & Honkala 1990). Thus, the density of oak

advance reproduction can be enhanced by applying both crop tree thinning and the three-stage shelterwood to increase acorn production.

Another technique that should be considered in the understory re-initiation stage is site preparatory burning to enhance oak seedling establishment. A series of low-intensity surface fires conducted over several years are used to consume excessive amounts of leaf litter, partially control acorn insect pests, xerify the uppermost soil layers, remove the soil seed bank, and reduce understory shade (Barnes & Van Lear 1998). These effects create a more suitable environment for acorn germination and early seedling growth. In site preparatory burning, spring growing-season fires may create desirable understory conditions faster than dormant-season burns, because of greater control of non-oak competition. Once a good acorn crop is on the ground, burning should be delayed to avoid seed loss to fire and allow oak seedlings to build root mass, increasing their ability to sprout vigorously after the next fire (Auchmoody & Smith 1993, Dey & Hartman 2005, Brose *et al.* 2006).

IMPORTANCE OF OAK ADVANCE REPRODUCTION

Oak germinants have relatively slow shoot growth even in full sunlight. They are easily suppressed by competing vegetation during stand reinitiation. This is why regenerating stands with abundant but small oak reproduction (< 10 mm basal diameter) that establishes after harvesting succeed to species other than oak. When stands that are dominated by oak in the overstory and non-oaks (e.g., maples) in the mid and understory are harvested, prolific stump sprouting of the non-oaks readily outcompetes the smaller oak reproduction (e.g., Abrams & Nowacki 1992).

Although oak stump sprouts are the fastest growing and most competitive source of oak reproduction, the capacity of oak stumps to produce sprouts decreases with increasing tree diameter and age, and large overstory oaks commonly fail to sprout after harvesting (Dey, *et al.* 1996a, Johnson *et al.* 2009). Thus, the key to good oak regeneration is adequate numbers of large oak advance reproduction, and

this is most likely to occur when there is good acorn production capacity in moderately dense stands (e.g., basal area < 14 m² per ha in Missouri according to Larsen *et al.* 1997).

In xeric forests of southern Michigan, Johnson (1992) observed that oak advance reproduction density increased with increasing basal area of large diameter oaks in the overstory, and height of oak advance reproduction increased with decreasing stand basal area. In xeric forests, oak advance reproduction is more likely to accumulate over successive acorn crops than it does in mesic forests. Likewise, Larsen *et al.* (1997) reported that the probability of large oak advance reproduction increased with decreasing stand basal area in xeric Missouri Ozark forests. In more mesic and productive forests, density of oak advance reproduction is also dependent on the density of large overstory oaks, but high seedling populations following good acorn crops do not accumulate over successive acorn crops in the deep shade of fully stocked forests (Loftis 1988, Crow 1992).

MANAGING FOR OAK ADVANCE REPRODUCTION

A primary limiting factor to oak advance reproduction survival and growth in forests is understory light levels below 5% of full sunlight, which is insufficient to meet the respiratory demands of many oak species (Hanson *et al.* 1987, Gottschalk 1987, Hodges & Gardiner 1993, Gardiner & Yeiser 2006). Oak seedling photosynthesis and growth improves significantly when light levels are increased to 20 to 70% of full sunlight (Ashton & Berlyn 1994, Gottschalk 1994, Gardiner & Hodges 1998, Parker & Dey 2008). Thus, the key to building populations of large oak advance reproduction is to provide adequate light to oak without aggravating problems from competing vegetation that will also respond to the increased light. Increasing light from 5% to 20% of full sunlight benefits both oak and its shade tolerant competitors (e.g., sugar maple; Parker & Dey 2008). Continued increases in light above this level further improve oak growth but not that of shade tolerant competitors because they are now light saturated. However, increasing light up to full sunlight

begins to benefit shade intolerant species such as aspen (*Populus* L.), birch (*Betula* L.), yellow-poplar, and increasingly Tree-of-Heaven (*Ailanthus altissima*) in some areas.

Increasing light for oak advance reproduction requires reducing tree stocking and shrub density. It is accomplished by timber harvesting, thinning to remove the midstory, control of troublesome species in the ground flora, or combinations of these practices. Increasing understory light by midstory removal has been shown to significantly improve the survival and growth of oak advance reproduction. Several studies from throughout the region have found that thinning from below alone can increase light to 9 to 16% of full sunlight (Lorimer *et al.* 1994, Miller *et al.* 2004, Motsinger 2006). In all cases, these increases in light significantly improved the survival and growth of oak advance reproduction.

The density of mid and understory woody or herbaceous vegetation can be reduced by mechanical cutting, herbicide application or prescribed burning. Herbicides are the most certain method for killing competing vegetation (Kochenderfer *et al.* 2001). The challenge in using herbicides though is that the chemicals that are effective in killing oak's competitors also kill oak. Care must be taken in application, which increases the cost of this method. Mechanical cutting can be done by hand or machine. Machine work is more indiscriminate in what is cut and may adversely affect oak reproduction. Regardless of method, cut stems have a high probability of sprouting, and under moderate to low stand density conditions sprouts can rapidly grow to their pretreatment heights in a matter of a few years. Low intensity prescribed burns can reliably girdle or kill trees less than 12 cm dbh, but most larger trees survive intact with only minor stem wounding (Waldrop *et al.* 1992, Barnes & Van Lear 1998, Dey & Hartman 2005). Cutting larger trees followed by burning in subsequent years is effective for reducing stand density and controlling sprouting hardwood stumps. Care must be taken not to kill the desired residual overstory trees especially during the first burn when fuel loading from thinning may be high.

Maintaining an intact main canopy can be used to control growth of competing vegetation while increasing light to oak advance reproduction. On good to high quality sites in the southern Appalachian Mountains, Loftis (1990a) recommended this approach to increase light to oak by removal of the midstory and intermediate and suppressed overstory trees, a thinning from below that does not create large openings in the main canopy. He showed this to be an effective method for controlling rapidly growing yellow-poplar while simultaneously improving the survival and growth of northern red oak advance reproduction.

OAK REGENERATION METHODS

There are some guidelines for assessing oak regeneration adequacy in certain regions, e.g., Dey *et al.* (1996b) for the Missouri Ozarks and Brose *et al.* (2008) for the Mid-Atlantic Region, but this information is lacking for many other oak ecosystems. In general, significant reductions in overstory density are necessary to increase light to 30 to 70% of full sunlight and quickly promote the growth of oak advance reproduction. Of the traditional regeneration methods available (Smith *et al.* 1997), the clearcut, shelterwood, and group selection methods are most often used to regenerate oak.

If the density of large oak advance reproduction is adequate, then clearcutting is a viable regeneration method. Naturally occurring large oak advance reproduction is most likely to be found on xeric sites where drought and other environmental factors restrict oak's competitors more so than the drought tolerant oak (Johnson *et al.* 2009). Clearcutting on high quality, mesic sites accelerates the loss of oak to succession by other species because oak advance reproduction is often absent or has low regeneration potential due to its small size. Oaks can be favored after clearcutting by periodic prescribed burning (e.g., every 3-5 years) following the recommendations of Brose *et al.* (2006).

The shelterwood method is highly recommended to increase the size of oak advance reproduction (Loftis 1990b, Spetich *et al.* 2002, Johnson *et al.* 2009). Light levels under shelterwoods may range

from 20 to 60% of full sunlight depending on the density and spatial arrangement of the shelterwood. In mature hardwood forests, harvesting to leave 60% stocking, removing 50% of the initial basal area or reducing crown cover by 30% can produce about 50% of full sunlight in many forest types (Schlesinger *et al.* 1993, Gardiner & Yeiser 2006, Parker & Dey 2008).

Higher residual density shelterwoods can be used to control fast growing competitors (Loftis 1990b), or prescribed fire and herbicides can be used to favor oak reproduction over competing vegetation. Either one can be applied during the shelterwood period, or after removal of the shelterwood. Prescribed burning has advantages when trying to reduce high densities of small diameter stems, but it can have adverse affects on the density of small oak advance reproduction.

Brose *et al.* (1999a, 2006) and Brose & Van Lear (1998) have developed an approach of using the shelterwood method in combination with prescribed fire. Fire is generally first used 3 to 5 years after the first shelterwood cut (50% residual basal area) to control competition. The delay is to permit small oak seedlings to grow in diameter and develop root mass before burning. A second fire is optional depending on oak's free-to-grow status, which should be monitored during this critical period of regeneration.

Moderately intense fires during leaf expansion in the spring cause the most change in species composition and favor oak (Brose & Van Lear 1998, Brose *et al.* 1999b). However, less intense fires and burning in other seasons are possible depending on the management objectives and degree of competition control needed to free the oak regeneration. If fire is applied during the shelterwood stage, care must be taken to avoid loss of overstory trees. Also, burning may cause browsing problems by white-tailed deer because they will repeatedly feed on the sprouting regeneration, so some measures of deer control may become necessary. Finally, prescribed fire may cause problems with native and non-native invasive species because some of them

are well-adapted to fire disturbances and thrive after burning in more open stand conditions.

Group selection openings that are at least 1-tree height in diameter, based on the height of the adjacent dominant mature trees, provide adequate light for development of oak advance reproduction (Fischer 1981). It is often necessary to control shade tolerant mid and understory trees and shrubs before or during creation of the group openings. Fire is less useful in these applications because many group openings are small and scattered in a matrix of forest that is harvested by the single-tree selection method. This makes it hard to burn the group openings without burning the rest of the forest, which would not be desirable in the single-tree selection area. Herbicides or mechanical cutting to control unwanted woody species are better alternatives, though cutting alone will lead to prolific sprouting that must be managed with additional treatments. Group openings can be overrun with fast growing shade intolerant species such as yellow-poplar (Weigel & Parker 1997, Jenkins & Parker 1998). For oaks to be competitive and reach a dominant crown position in this situation, competing vegetation must be controlled.

IMPLICATIONS OF SILVICULTURAL ACTIONS FOR NON-TARGET COMMUNITIES

Silvicultural practices used in oak management also affect the composition of non-target organisms in the herbaceous layer, and in avian, herpetofauna, and mammal communities (Table 1). There is growing recognition that sustainable forestry should consider the impact of silvicultural practices on patterns of overall biodiversity and the mechanisms that influence these patterns (Roberts & Gilliam 1995, Brown 1997, Hunter 1999, Lindenmayer *et al.* 2000). Understanding silvicultural impacts on non-target species in eastern North American oak ecosystems is particularly important as these forests contain among the highest levels of diversity and endemism in North America, making the region a global temperate biodiversity hotspot (Kiestler 1971, Ricketts *et al.* 1999, Whigham 2004, Kier *et al.* 2005, Gilliam 2007).

Within the range of silvicultural practices possible, tree harvesting and prescribed fire represent the most common anthropogenic disturbances employed in contemporary oak silviculture in eastern North America (see above). Although a general deficiency of literature on the impacts of these practices on non-target communities precludes a full understanding, we briefly review the available literature and draw generalizations regarding the general impacts of these two practices on non-target species. We urge the reader to examine specific reviews on these topics for a more comprehensive examination of these impacts (e.g., herbaceous plants: Battles *et al.* 2001, Roberts & Gilliam 2003, Whigham 2004; herpetofauna: Russell *et al.* 2004, Renken 2005; birds: Annand & Thompson 1997; and mammals: Kirkland Jr. 1990). As more knowledge is gained on the response of non-target species to oak management practices, land managers will be able to develop prescriptions that balance timber-oriented goals with biodiversity goals (Zenner *et al.* 2006).

HERBACEOUS LAYER COMMUNITIES

The response of the understory plant community to silvicultural practices is largely determined by the degree to which these practices alter forest canopy structure, the forest floor environment, and the survival and recruitment of understory

vegetation (Roberts 2004, 2007). Generally speaking, harvesting operations most strongly influence overstory canopy structure and openness and have less impact on the forest floor and extant vegetation (Roberts 2007). The bulk of evidence from second-growth forests strongly suggests that timber harvesting results in short-term increases in the abundance (e.g., cover, biomass, density) of understory plant species, while species richness and diversity either remain the same or more typically increase (reviewed by Battles *et al.* 2001, Roberts & Gilliam 2003, Rowland *et al.* 2005, Moola & Vasseur 2008). The neutral to positive effect on diversity is attributed to high survival of resident species and recruitment of new species following disturbance. The increases in overall abundance and recruitment are driven by 1) increased resource availability, 2) the creation of germination microsites, and 3) direct and indirect germination cues for seed-banking species. Typically, gains in species richness and diversity are short-lived (10 to 20 years) as the stands proceed from the establishment into the thinning/stem exclusion stage, but begin to increase again during the understory re-initiation and old-growth stages (Peet & Christensen 1988). Conversely, while harvesting impacts on species richness may be relatively minor, evidence does show that harvesting can greatly alter patterns of species dominance. At times, these shifts

Table 1. Effects of common silvicultural prescriptions on non-target organisms in oak forest ecosystems. Arrows denote whether the preponderance of evidence in the literature suggest impacts are positive (↑), negative (↓), or mixed (↕). In all cases, the literature suggests impacts are transient and tend to disappear as the stand structure reestablishes.

Species Group	Prescribed Fire	Shelterwood	Clearcutting
Herbaceous	↑ ¹	↑, = ¹	↕ ² , ↑ ³
Avian	↓ (Shrub nesters) ³ ↑ (Ground nesters) ³	↑ ¹	↓ ² , ↕ ³
Herpetofauna			
Amphibians	=, ↓ ³	=, ↓ ³	↓ ³
Reptiles	↑ ³	=, ↑ ³	↑ ¹
Mammals	=	=	=

1 Effects on both richness and abundance

2 Effects chiefly on richness

3 Effects chiefly on abundance

are readily apparent, as ruderal, shade-intolerant species and/or undesirable, non-native invasive species expand and dominate the understory (reviewed by Bashant *et al.* 2005, Royo & Carson 2006). Other shifts are more subtle, as a few uncommon, microhabitat-specialists may decline or become locally extirpated as a result of direct mortality, demographic stochasticity, or alterations of their microhabitat (Meier *et al.* 1995, Jolls 2003). For these species, recovery may proceed at a much slower pace.

In contrast to harvesting, the primary impacts of fire on herbaceous layer communities of oak forests are mediated via disturbance effects to the forest floor instead of the forest overstory. Low-intensity prescribed fires, which cause little or no overstory tree mortality, may influence herbaceous layer communities by 1) reducing the dominance of fire-susceptible woody vegetation, 2) facilitating germination of seed-banking species by reduction of leaf litter and chemical cues (e.g., nitrate, smoke), and 3) increasing resource availability (nutrients and light) (Hutchinson 2006). The application of prescribed fire to oak forest understories results in increases in herbaceous layer species abundance and diversity (Elliott *et al.* 1999, Kuddes-Fischer & Arthur 2002, Hartman & Heumann 2004, Hutchinson *et al.* 2005, Royo *et al.* 2010). Post-fire conditions have also been shown to increase productivity and seed production of common perennial forbs in oak forests (e.g., Boerner & Huang 2008). Direct mortality of resident herbaceous species is usually negligible as most fires are of fairly low intensity and are conducted during the dormant season (Hutchinson 2006). While spring growing season fires can favor oak regeneration more than dormant season fires (Brose & Van Lear 1998), very little is known about the effects of these fires on herbaceous layer vegetation.

Following fire, the structure and composition of the forest herb-layer community is driven by species possessing vigorous post-fire persistence (e.g., resprouting of woody species, re-emergence of herbaceous species from belowground structures) and recruitment (e.g., germination of seed-banking species) mechanisms (Schiffman & Johnson 1992, Roberts 2004). A few of these are rapidly growing,

shade-intolerant species that may temporarily dominate much of the forest understory and potentially interfere with hardwood regeneration (Royo & Carson 2006) while others may be species that are absent or infrequent in the stands prior to burning and are of conservation priority (Hutchinson 2006, Royo *et al.* 2009). Indeed, Royo *et al.* (2010) suggested the re-introduction of fire to historically fire-prone systems may benefit uncommon herbaceous species that rely on a long-term seed dormancy for persistence because continuing fire suppression leads to an impoverishment of the seed bank (e.g., Keeley *et al.* 2005). By providing a recruitment and reproductive burst that replenishes seed banks, prescribed fire not only promotes current plant diversity, but may also sustain diversity over a much longer term.

Increasingly, overstory disturbance and fire are being used together in oak forest management (e.g., shelterwood-burn treatments, Brose *et al.* 1999a, Van Lear & Brose 2002) and research must elucidate how both factors operate alone and in tandem, with respect to herbaceous layer communities. This interaction between overstory disturbance and understory fire may influence understory plant species to a far greater degree than either disturbance in isolation. Evidence from the few existing studies that manipulate both factors suggests the establishment pulses afforded by fire are often constrained without the increased understory light levels resulting from overstory manipulations (Hutchinson & Sutherland 2000, Franklin *et al.* 2003, Phillips *et al.* 2007, Royo *et al.* 2010). Although only one of these studies employed a shelterwood harvest (Franklin *et al.* 2003), results from experiments that combine burning with either understory thinning (Phillips *et al.* 2007) or experimentally created canopy gaps (Royo *et al.* 2010) provide corroborating results that synergies between both treatments yield the greatest increase in herbaceous layer cover and richness.

AVIAN COMMUNITIES

Forest bird communities are shaped primarily by stand structure, as well as species composition and landscape context. Species present within a stand vary with canopy openness and understory density (Crawford *et al.* 1981). Therefore, as with

herbaceous plants, avian responses to silvicultural practices depend largely on how those practices alter forest structure, composition, and landscape character (Thompson *et al.* 1995). Any changes resulting from timber management practices are likely to favor some species and be detrimental to others. A substantial body of work has been published on the effects of various silvicultural practices on avian abundance and diversity in eastern North American oak forests; much less attention has been given to understanding the effects on critical demographic parameters such as reproductive success and survival (Thompson *et al.* 1995, Sallabanks *et al.* 2000).

Generally, opening the forest canopy and subsequent understory growth favors some birds but reduces habitat suitability for others. A suite of birds specializes in early successional woody habitats, and will occupy a site for 10-15 years following overstory removal. Many of these early successional species also will use the dense understories that develop in thinned, shelterwood cut, or two-age stands (Annand & Thompson 1997, Baker & Lacki 1997, King & DeGraaf 2000). Dense understories also benefit shrub-nesting forest birds, but tend to be unsuitable for many ground-foraging species (Augenfeld *et al.* 2008). Most canopy birds increase in abundance following partial opening (Rodewald & Smith 1998, Ross *et al.* 2001). Overall, most studies have reported little difference in avian species richness, abundance, or diversity between uncut oak stands and stands opened to varying degrees. Where differences were detected, all three measures peaked at intermediate disturbance levels, as are typically produced in shelterwoods (Annand & Thompson 1997, Wang *et al.* 2006).

Few studies have assessed the effects of silvicultural treatments on nest success or brood parasitism, factors that generally have the greatest impact on population trajectories. Often landscape context appears to have more influence on demographic parameters than does stand structure (Rodewald & Yahner 2001). Within primarily forested landscapes, silvicultural treatments have shown little or no effect on nest success or brood parasitism rates of forest birds (Annand & Thompson 1997, King & DeGraaf 2000, Powell *et al.* 2000).

Ground fires produce a temporary reduction in the density of understory vegetation as well as depth of litter. The effects of prescribed fire are most evident immediately after burning takes place but abate quickly (Dennis 2002). The most consistent response by birds to fire in oak forests is a short-term decrease in shrub-nesting species due to the loss of suitable nesting substrate, often accompanied by a concomitant increase in ground-nesting species (Aquilani *et al.* 2000, Artman *et al.* 2001, Dennis 2002, Blake 2005).

From a conservation perspective, silvicultural treatments to promote oak are likely to have strongly beneficial effects on avian populations. In eastern North America, a much higher proportion of the bird species of disturbance-dependent habitats have exhibited population declines than have species associated with mature forest interiors or generalist species (Brawn *et al.* 2001). Such species (e.g., cerulean warbler *Dendroica cerulea*) generally increase in abundance and frequency following silvicultural treatments that open the canopy (Ross *et al.* 2001, Hamel 2004). Also, oak forests tend to support greater abundances of most bird species in all seasons in relation to comparable maple-dominated forests (Rodewald & Abrams 2002).

HERPETOFAUNA COMMUNITIES

Amphibians are moisture-dependent and will respond negatively to any disturbance that increases the aridity of their habitat over the long term (Russell *et al.* 2004). Generally, amphibian abundance on the forest floor decreases after all levels of harvest intensity relative to levels in uncut stands; such changes tend to be short-lived (DeMaynadier & Hunter Jr 1995, Harpole & Haas 1999, Knapp *et al.* 2003, Patrick *et al.* 2006). Although, abundances can remain depressed for at least 15 years after harvests are completed, they generally return to pre-treatment levels within 20 to 25 years (Ash 1997, Duguay & Wood 2002). In contrast, almost all published studies on the effects of prescribed fire on amphibians have reported little or no change in abundance or species richness (Ford *et al.* 1999, Russell *et al.* 2004, Renken 2005, Greenberg & Waldrop 2008). These results may be due to the low-intensity of most prescribed fires, which leave

refugia for amphibians in the form of moist litter and coarse woody debris, and keeps humidity-holding canopies intact (Renken 2005).

Unlike amphibians, reptiles tolerate reduced humidity well, and often prefer areas with at least partial sunlight on the forest floor. In addition, their prey often occur at higher densities in early-successional habitats than in uncut forest (McLeod & Gates 2009). Although poorly-studied, published work documents either no significant change in reptile communities (Ford *et al.* 1999) or increases in reptile numbers following silvicultural treatments that open the canopy (Perison *et al.* 1997, Shipman *et al.* 1999, Keyser *et al.* 2004, Greenberg & Waldrop 2008).

MAMMAL COMMUNITIES

Populations of small mammals display inherent variability over spatial scales similar to those at which forestry is typically practiced (Bowman *et al.* 2000). Not surprisingly, most studies of the effects of silvicultural practices, including fire, on small mammals in eastern North American oak forests have shown few changes to community structure or abundance (Kirkland 1990, Ford & Rodriguez 2001, Keyser & Ford 2005, Matthews *et al.* 2009, Zwolak 2009). Treatments that open canopies and promote understory growth can favor certain taxa, such as aerial-foraging bats and larger predators (Litvaitis 2001, Owen *et al.* 2004).

Overall, silvicultural practices to promote oak regeneration have few short-term negative impacts on vertebrate diversity, abundance, or species richness. Long-term impacts are almost entirely positive because of the high value of oak forests to wildlife relative to alternative forest types (McShea *et al.* 2007, Rodewald 2003).

CONCLUSIONS

Sustaining oak forests requires active management because oaks are adapted to frequent disturbances that give them an advantage over competing vegetation. Today, common silvicultural practices can

be used to regenerate oak and promote its dominance. The timing and combination of treatments must take into account the current regeneration potential of oak and its competitors. Oak's prominence in the future forest is largely determined by the composition and structure of the forest at the time of regeneration. The regeneration potential of oak in a stand is the product of contributions to stocking from seedlings, advance reproduction and stump sprouts. But, having an abundance of large advance reproduction is key to successful oak regeneration. Thinning and shelterwood methods are effective when combined with treatments to control competing vegetation, in that they provide adequate light to oak reproduction. Prescribed burning is an increasingly common tool for controlling oak's competitors.

Silvicultural manipulations that change the stage of forest development, for example, from mature to regenerating forest, differentially promote some flora and fauna species over others. The overall consensus is that regeneration of oak forests has negligible to positive effects on species in the short-term. Any negative impacts to native diversity associated with forest regeneration should be mitigated. However, in the long-run, sustaining healthy oak forests provides benefits that outweigh any short-term impacts associated with regeneration. Flora and fauna of oak forests have persisted for thousands of years in the face of frequent disturbances that resulted in the dominance of oak in eastern North America. Due to a lack of management and selective cutting, an emerging conservation issue today in heavily forested landscapes in eastern North America is the predominance of closed-canopied, mature forests and lack of early successional forests. Application of even-aged silvicultural systems that favor oak across the landscape provides crucial early seral habitat to many species of conservation concern and ensures mast production into the future. Silvicultural treatments that emulate natural disturbances will have minimal negative consequences on other biota of oak ecosystems.

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