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Fire in Upper Midwestern Oak Forest Ecosystems: an Oak Forest Restoration and Management Handbook

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Cover: Spring prescribed burn in progress on sand savanna with northern pine and bur oak, Cedar Creek Ecosystem Science Reserve, Minnesota. Photograph by Kalev Jõgiste.

Abstract

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We reviewed the literature to synthesize what is known about the use of fire to maintain and restore oak forests, woodlands, and savannas of the upper Midwestern United States, with emphasis on Minnesota, Wisconsin, and Michigan. Included are (1) known physical and ecological effects of fire on oaks from acorn through seedling, established sapling, and mature stages of the life cycle; (2) the use of fire to modify competitive interactions between oaks and mesic forest species (e.g., maple), between oaks and pines, and between oaks and grasses; (3) interaction of fire with other disturbances such as windthrow and harvesting, invasive species, and deer browsing; and (4) climate change. Throughout the report, we discuss the advantages and limitations of fire use in oak forests. We incorporate lessons learned from long-term experiments with fire, from historical evidence of fire over the centuries, and processes in areas where natural disturbances occur. We provide a brief summary of the use of fire to restore mixed oak-maple forests, mixed oak forests, mixed pine-oak forests, and oak savannas, along with take-home lessons about the complex relationships between oaks and fire.

Keywords: Prescribed fire, oak forest, oak savanna, forest restoration, forest management, fire ecology.

Summary

Oak forests and savannas provide valuable ecosystem services, including timber production and wildlife habitat, so maintaining or increasing the abundance of oaks is a desirable goal for forest management in the Lake States of Minnesota, Wisconsin, and Michigan. Fire and climate played important roles in the development, maintenance, and geographical distribution of oak forests before and after European settlement. Changes in fire frequency and severity, shifting forest management practices, and invasive species have produced significant changes in forest structure and composition over the past century in many formerly oak-dominated ecosystems, such that long-term sustainability of oak forests is in doubt. Prescribed fire use or restoration of historical fire regimes may help to restore, maintain, or increase the dominance of oaks in these temperate deciduous forests, but efforts to restore oak forests using fire are constrained by social attitudes toward fire, and uncertainties about the frequency and severity of fires needed to reverse past changes. Efforts to restore oak ecosystems with fire may be further complicated by changes in atmospheric carbon dioxide concentrations, climatic changes, biological invasions (e.g., earthworms, buckthorn), and herbivore impacts, which may alter plant resource requirements, resource availability, biotic interactions, forest fuel dynamics, and potential fire behavior. The purpose of this document is to review and summarize scientific knowledge about the role of fire in oak forests, other factors that influence oak-fire relationships, and possible approaches for using fire in restoration-based management of oaks in temperate deciduous forests of the Upper Midwest and northeastern United States. We first introduce the concept of ecologically significant fire and review the mechanisms by which fire historically regulated the balance between oaks and other species at different life-history stages. We then review how different stand-development stages, exotic species, plant-animal interactions, and climate change can alter forest structure and composition, forest fuels, fire behavior and effects, and the potential effectiveness of fire as a restoration tool. We conclude by discussing approaches to restoring fire in a variety of contemporary oak forest types, including mixed oak forests, oak-maple forests, oak-pine forests, and oak savannas. A suite of oak forest restoration options are available to forest managers, including prescribed fire alone, prescribed fire combined with mechanical thinning, planting oak seedlings after removing competing vegetation, and deer exclusion. However, the effectiveness of different approaches will differ among biophysical and social settings, forest types, and forest management histories.

Historically, different fire regimes in place for centuries created a variety of oak forests and savannas. Burning frequently, every one or two decades, or once every several decades created savannas, oak forests, and mixed oak-maple forests or oak-pine forests, respectively. Many contemporary oak forests and savannas have been

through at least several decades of fire exclusion, and some invading maples have become large enough to resist fires, providing a permanent, and in many instances, undesired, seed source. A number of prescribed burns over time will be necessary to gradually push such forests back to a desired condition, especially because low-intensity spring burns are commonly done, and in many cases earthworm invasions have reduced the forest floor fuel loading, meaning that most fires carried out today have a relatively low intensity and small ecological impact. In most oak forests, understory shrubs, including invasive nonnatives, and shade-tolerant tree saplings create conditions unsuitable for oak establishment. In such cases, several burns in consecutive years may be needed to exhaust the sprouting ability of the shade-tolerant trees and shrubs, to create the open understory conditions lasting for several years that are needed for oak establishment. In oak savannas that have grown up into forests, without mechanical removal of some trees, several decades of frequent light to moderate burning is necessary to prevent oak reproduction (and also reproduction of mesic tree species on some sites) while tree density is gradually reduced by mortality of older trees.

The ecological impact of a prescribed burn can be considerably altered by manipulation of fuels prior to the burn. For example, pulling fuels away from the base of large oaks protects them from fire and maintains them as a future seed source, while piling fuels at the base of undesired trees like red maple (*Acer rubrum*) can be used to increase their chances of mortality. Other strategies such as timing fires to create ideal seed beds just before a bumper crop of acorns, to take advantage of a planned thinning, or after a chance wind-disturbance event, along with deer management after a fire, can all increase effectiveness of fires in regenerating oak.

Although oak forest management has been difficult in recent times owing to mesophication (the positive feedback cycle in which cool, damp, and shaded conditions and less-flammable fuel beds continually favor shade-tolerant species and inhibit shade-intolerant, fire-adapted species), increased deer populations, and a wetter summer climate, climate change is likely to be a positive factor for oak. Warmer summers and increased drought frequency will have a big negative impact on mesic species in the Lake States, and smaller negative or even positive impacts on oaks, throwing the competitive balance to oak's favor. A warmer climate may also promote oak invasion into the southern portion of the boreal forest. Therefore, fire management for oaks in the region is likely to become more feasible and more important.

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Introduction

Managing forests to maintain or increase the abundance of oaks is a desirable goal in many temperate deciduous forests of the upper Midwest and northeastern United States. Oak forests and savannas provide a variety of ecosystem services, including timber production and wildlife habitat. Oaks produce large quantities of acorns that are a major food source for many important wildlife species, including white-tailed deer, black bears, eastern gray squirrels and other rodents, and turkeys (Feldhamer 2002, Smith and Stapanian 2002, Steffen et al. 2002, Vaughan 2002) (common and scientific names of all plant and animal species mentioned can be found in the appendix). In addition to producing acorns, oaks provide other key wildlife habitat features such as cavity trees and dead wood (Healy 2002). Oaks attain large size and shed large quantities of leaf litter that heavily influence soil chemistry and ecosystem processes. Some oak species are long lived, with individual trees that are among the largest and oldest in the region, and many of the remnant old-growth forests of the Midwest are oak dominated (Frelich and Reich 2002). Thus, oaks are foundational species in ecosystem function across large landscapes.

In the upper Midwest (defined as Minnesota, Wisconsin, and Michigan for our purposes), oak forests currently are most dominant within a band several hundred kilometers wide that extends from northwestern Minnesota to southern Wisconsin, and southern Michigan (McWilliams et al. 2002). However, as the climate has warmed and cooled over the last 11,000 years since glaciers left the region, this band has shifted to the south and west during periods of relatively cool, moist climates, and to the north and east during times of relatively warm, dry climates (Umbanhowar et al. 2006).

Fire has been a major contributor to the development and maintenance of oak forests for thousands of years (Abrams 1992, 2002). Historically, the region of heavy oak dominance was bounded by grasslands with very frequent fires (generally 1- to 5-year return intervals) to the west, and mesic forests with infrequent fires (generally fire-return intervals of 100+ years) in the northeastern portion of the Lake States. Within this region however, topographic barriers to the spread of fire created local variability in fire frequency that, in turn, produced a mosaic of vegetation types that included prairie grasslands, oak savannas and woodlands, mixed-oak forests, and mesic deciduous forests (e.g., maple-basswood forests) (Grimm 1984, Williams et al. 2004). Fossil evidence of fire (charcoal) is often found together with fossil oak pollen in sedimentary sequences from basins in oak-dominated areas. Furthermore, it is known that human enhancement of fire frequency, such as burning by Native Americans, can convert mesic forest to oak forest or savanna (Clark and Royall 1995, Dorney and Dorney 1989). Hence, the oak-fire hypothesis—that periodic fires played an important role in the historical development and maintenance of oak

forests before and after European settlement and that fire regimes with a certain range of fire frequencies and intensities are needed to maintain oak—has been a mainstay of ecological theory for several decades (e.g. Abrams 1992, Collins and Carson 2003, Curtis 1959, Dey and Fan 2009, Johnson et al. 2009).

Changes in fire frequency and intensity since early settlement of the region have produced significant changes in formerly oak-dominated ecosystems (Nowacki and Abrams 2008). Harvesting and burning of mesic forests early in the settlement period favored oaks over more shade-tolerant but disturbance-sensitive species. In other areas, reductions in fire frequency—caused by fewer human ignitions, landscape fragmentation, and agricultural land conversion—led to the conversion of grasslands and oak savannas to closed-canopy oak forests and allowed shade-tolerant mesic species to invade and become dominant in formerly oak-dominated forests. As a result, high-quality oak savannas are now rare (Nuzzo 1986), and there is concern about increasing losses of oak-dominated forests and their associated ecosystem services, resulting from succession under continuing fire suppression policies and other factors (Nowacki and Abrams 2008).

Many forests formerly dominated by white oak or red oak have been invaded by maple in recent years, a process referred to as mesophication (fig. 1) (McEwan et al. 2011, Rogers et al. 2008). This mesophication process has been fostered not only by



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Figure 1—A mesophied northern red oak forest in southern Minnesota. Three sugar maple saplings stand in front of a large northern red oak.

fire suppression and exclusion, but by higher deer populations that prefer oaks over maples for winter browsing, a wetter summer climate in the last several decades, changes in the physical and chemical environment of the forest floor caused by maple invasion and, in some locations, invasive plant species such as buckthorn. All of these changes favor maple and other mesic-forest species like American basswood, which are more shade-tolerant than oaks, so that they may thrive in the now much denser forest understory. In particular, the more shade-tolerant red maple is expanding rapidly (Fei and Steiner 2009) and can tolerate many of the same environmental conditions as the oaks. This mesophication has many implications for the use of fire to restore oak that are discussed in this report.

The regeneration window for oaks (Johnson et al. 2009, p. 146), or the range of the light gradient over which oaks can successfully compete in the understory, is much narrower for the moist site conditions that have expanded to cover a larger proportion of the landscape owing to increasing understory density and the wetter climate of recent years. Under such conditions, larger gaps with relatively bright light are needed for successful oak recruitment. In other words, more forests are now in the “recalcitrant” category of oak reproduction accumulation, i.e., stands where shade and competition with mesic forest species prevent accumulation of large oak advance reproduction over successive acorn crops. And there has been a decline in the “ambivalent” or “intrinsic” categories of oak forests, where accumulation of large oak advance reproduction results in modest success on dry-mesic sites and high success on xeric sites (Johnson et al. 2009, p. 160).

The fire and oak hypothesis suggests that prescribed fire or restoration of natural fire regimes, particularly low-intensity surface fires, could be used to restore, maintain, or increase the dominance of oaks in the Midwest region. However, there are various constraints on the use of fire on modern landscapes, including continuing social bias favoring fire suppression, continued expansion of the wildland-urban interface, air quality laws, and lack of funding. Where fire can be used, it may not be effective for restoring oak dominance within typical management timeframes owing to persistence of large trees of mesic species that serve as local seed sources, feedbacks of mesic species on understory microclimate and fuels, persistence of exotic species associated with closed-canopy forests (e.g., buckthorn, earthworms), and resource constraints on understory oak regeneration and persistence (Johnson et al. 2009, chap. 3). Therefore, it won't be possible to restore oak forests to their previous status in all, or perhaps even many, cases using fire alone (Abrams 1992).

Efforts to restore oak ecosystems with fire may be further complicated by past and future changes in atmospheric carbon dioxide (CO₂) concentrations and climate. Climatic changes could assist in oak restoration if warmer temperatures produce more

favorable conditions for fire, if oaks are better adapted to warmer temperatures than their mesic competitor species, or both. Climatic changes are expected to shift the biogeographical distribution of biophysical conditions that historically favored oak dominance and persistence, which could create mixed responses within the current region of oak dominance. Changes in atmospheric CO₂ concentrations could also create mixed responses by altering the biophysical requirements of oaks and their co-occurring native species (Davis et al. 2007). Finally, climate change could introduce new (and changing) suites of co-occurring species as species migrate at different rates.

To some extent, changes in forest composition and structure proceed along a unique trajectory over time, and it may not always be feasible to maintain oak dominance (Frelich 2002). This is the dilemma of managing mid-successional forests. If there is no fire, the forest may succeed to species that are less desirable. If there is a severe fire, the current crop of mature oak trees may be damaged, although there is much flexibility in conditions between these extremes of fire occurrence in which oaks can be sustained. Fire also interacts in complex ways with deer, climate, soils, invasive species, and native competitors of oak at all stages of the life cycle from seedling to mature tree (Frelich and Reich 2002). A whole gradient of forest restoration options are available to oak forest managers, including planting oak seedlings after removing competing vegetation and fencing out deer until the saplings are beyond their reach; thinning to remove undesirable tree species combined with mechanical preparation of the soil surface; thinning combined with fire; prescribed fire alone; and no intervention, or “letting nature take its course.”

The individualistic nature of plant communities over time and space, including forests, precludes the possibility of standardized/cookbook silvicultural or fire-use prescriptions that will be effective in all stands over an entire region. However, much information is available and presented here that can be blended with local foresters’ experience to get a picture of which options may have some success and how the level of effectiveness of various options is limited by the history of a given site, biology of the species present, and site conditions.

The purpose of this document is to review and summarize scientific knowledge about the role of fire in oak forests and other factors that influence oak-fire relationships, and to point out the potential positive effects and limitations of fire use in oak forests. Focusing on the Lake States of Minnesota, Wisconsin, and Michigan and adjacent areas, this review has a more northern bias than most of the existing body of literature on oaks and fire and therefore complements other classic and recently published reviews or large-scale studies of oak and fire (Abrams 1992, 2003; Arthur et al. 2012; Brose et al. 2013; Buchanan and Hart 2012; Dey and Fan 2009; Knoot et al. 2010; McEwan et al. 2011) from centers of excellence in research that

exist across the central U.S., including the Ozarks and Cross-Timbers (Oklahoma, Missouri, and Arkansas), Ohio River valley (Illinois, Kentucky, Ohio), southern and central Appalachians (Pennsylvania, West Virginia, North Carolina), and southern New England (Connecticut, Massachusetts). Oak is also important in much of the northern tier of states, and with a warming climate, oaks will potentially become an even more widespread forest type in the future. Therefore, interactions with the boreal forest and northern pine forests are also covered here.

We start by introducing and discussing the concept of ecologically significant fire and its importance in understanding oak-fire relationships and the potential for using fire to restore and maintain oak forests. We then review the mechanisms by which fire historically regulated the balance between oaks and other species at different life-history stages, and assess the continued relevance of those historical relationships for modern restoration-based management of oak forests. Next is a section on how fire interacts with multiple factors—including stand-development stages, exotic species, and plant-animal interactions—as every forest stand has several ecological processes happening at once that can work to enhance or diminish the desired effects of fire. Presentation of a case study that ties together multiple influences of fire on red oak—the most important oak species in northern forests—shows that red oak does respond to fire with good regeneration today under certain circumstances. We conclude with discussions of potential impacts of climate change on oaks and fire, a section on restoring fire in a variety of contemporary oak forests (with subsections on mixed oak, oak-maple, oak-pine, and oak savanna), and some conclusions or take-home lessons.

Ecologically Significant Fire in Oak Forests

A fire or series of fires that: (1) removes or reduces abundances of competitors of oak or keeps those competitors from entering the stand; (2) damages existing oak as little as possible; and (3) creates conditions for future recruitment of oak to the canopy, meets the definition of ‘ecologically significant’ for the purpose of restoring and regenerating oak. Ecologically significant fire is largely context-dependent because the factors limiting oak dominance and persistence vary among biophysical settings, stand-development stages, and forest types. For example, an ecologically significant fire for oaks in an oak woodland might have to eliminate duff so that germinating oaks can survive, and kill competing red maple saplings or understory shrubs. Removing overstory trees of mesic species and reducing total overstory canopy cover might also be required to remove competitors, promote persistence of overstory oaks, and facilitate seedling establishment in closed-canopy forests. Even if some oak seedlings are killed in a prescribed burn, it may still be possible to improve conditions for future oak recruitment (Simpson 2010). When restoring oak savanna that has grown into woodland, ecologically significant fire may include

purposefully damaging some mature oaks and eliminating some (but not all) oak reproduction to reduce overstory and midstory cover and promote the development of understory grasses and forbs that facilitate frequent, low-severity fires. Therefore, how fires damage trees and change fuel loadings for ecologically significant fires are two of the main considerations discussed below.

Tree Damage During Fires

Fires can kill trees by killing the root system, girdling the base of the tree, or completely scorching or burning through the crown. The root system can be damaged or completely killed by heat fluxes into the soil or by combustion of organic soils (Steward et al. 1990). However, in mineral soils it is uncommon for soil temperatures to rise to lethal levels below a depth of about 2 inches (5 cm), unless glowing combustion in microsites such as a pocket of deep duff, pile of branches, or hollow log lasts much longer than the flaming front (Dickinson and Johnson 2001). Combustion of organic soils is not usually an issue in oak ecosystems, but oaks often occur on rocky sites with shallow soils that could expose root systems to mortality during fires if fuels are heavy enough to generate long fire residence times and penetration of heat pulses deep into soils. A tradeoff exists between rockiness and the ability of the fire to spread. For example, extremely rocky sites have non-contiguous fuel beds that impede the spread of fire and cause patchiness in fire effects (Signell and Abrams 2006). Pockets of deep duff between rocks can support glowing combustion of long duration that may alternate with pockets that experience few fire effects. Patchiness in fire effects allows the coexistence of fire-dependent and non-fire-dependent tree species, such as found by Abrams et al. (1998) in Pennsylvania, where maple, basswood, and oak coexist. In contrast, moderately rocky sites may have contiguous duff and dry soils, allowing high soil temperatures during fires and more spatially homogeneous fire effects, especially across south-facing slopes. These variations in rockiness and the effects on fire behavior and tree species coexistence also occur across vast areas in Lake States oak forests in the Driftless area in Wisconsin, Minnesota, Illinois, and Iowa, and peninsulas and other rocky areas near the Great Lakes. Oaks also occur on deep sandy or loamy soils, where root death during fires is minor or spotty.

Fires girdle trees at the base by either burning through the bark to the cambium or by generating a heat pulse that penetrates through the bark and heats the cambium to a lethal temperature. Girdling will often simply top-kill oaks and other sprouting-capable hardwoods like basswood and sapling-sized maples, but will totally kill species unable to sprout from belowground, such as older sugar maples and conifers. Scorching the foliage via rising radiant and convective heat from surface fires will kill some trees, but others may persist by producing a new cohort of leaves from protected buds, by producing new branches and leaves through

epicormic sprouting, or through basal sprouting. Crown fire that directly chars the entire tree will generally kill conifers, but may only top-kill hardwoods (Michaletz and Johnson 2007). Crown fires and foliage scorch can occur in northern pin oak and mixed pine-oak forests on sand plains, leading to top-kill of the oaks, which commonly later resprout with multi-trunked trees.

Girdling of trees during low-intensity surface fires was also, under the oak-fire hypothesis, an important mechanism by which fire maintained oak dominance. Thick bark gives mature oaks more resistance to girdling than many of their thin-barked competitors (see box 1). In addition, oak seedlings and saplings often have higher rates of resprouting following top-kill than many of their more shade-tolerant competitors. Partial girdling during fire typically does not kill trees, but can

Box 1—Fire and cambial death at the base of trees

To kill cambium beneath the bark of a tree, the fire must either burn through the bark, or the radiant heat needs to penetrate the bark and bring the living cambial cells underneath to a temperature of 140 °F (60 °C) for at least a minute, or 158 °F (70 °C) degrees for a shorter time.

The time required for significant heat applied to the outer bark surface to reach and kill the cambium is related to bark thickness (Johnson 1992):

$$(1) Td = 2.9 BT^2$$

Where Td = time to cambial death (minutes) for radiant and convective heat applied to the outside surface of the bark, at standard ambient air and flame temperature (68 °F/20°C and 932 °F/500 °C, respectively), and BT = bark thickness in cm.

Using formula (1), we can fill out table 1—note that on warmer days this time would be slightly less, on cold days slightly more, and that bark moisture content and flame temperature will also vary somewhat from standard conditions under which this model was developed, depending on fuel structure, wind, time since last precipitation, and other local site factors including slope steepness and aspect.

Table 1—Time for cambial death (Td, minutes) at standard air and flame temperatures. BT = bark thickness

BT (cm)	Td (min)
0.5	0.73
1.0	2.9
1.5	6.5
2.0	11.6
2.5	18.1
3.0	26.1

produce fire scars that provide an entry vector for fungal pathogens that can damage or kill trees and increase susceptibility of trees to mortality in subsequent fires. In ecological restoration, fire scar creation may not be of concern, unless long-term retention of overstory trees is a concern. However, fire scars are not desired where oak is used for lumber.

Species and age-related differences in bark thickness and heat conductance among trees produce differences in tree mortality rates in response to fire. Since saplings and shrubs competing with oak—such as buckthorn, red maple, ironwood, and hazel—may have paper-thin bark, it is easy to discriminate against them in prescribed fires in mature oak forests, leaving the oak seed source and an open understory for oak seedling development. Note, however, that oak seedlings and saplings may also have thin bark and be killed or top-killed by a fire, and that a mature red maple or sugar maple may have bark thick enough so that it may not be killed by a fire without raising the intensity and duration of a fire to the point that some mature oaks would be killed as well (Hutchinson et al. 2005). Bark thickness differs among oak species as well as between oaks and maples; among oaks, bark thickness and tolerance to fire are generally ranked in this order: bur oak (most tolerant), black oak, white oak, red oak, and northern pin oak (least tolerant, Lorimer 1985).

Growing to a size that provides bark thick enough to resist surface fires is known as reaching a size refuge. This is related to growth rate, with fast-growing trees with wide rings having thinner bark. Larger trees usually have narrower ring widths and thicker bark and, in addition, the trajectory towards thicker bark with increasing size and age of trees varies among species. While all species have thin bark in the first few years as a sapling, a transition to thicker bark occurs at younger ages for fire-tolerant species such as bur oak, but may take a few decades for red oak, and several decades for species such as sugar maple, red maple, basswood, and eastern hemlock; and in a few species, the bark may never attain substantial thickness (e.g., beech). Large old maples and basswoods can reach a size at which bark thickness is equivalent to that of a mature oak, and be able to survive the same types of fires as oaks. Large trees of those species can also sustain fire scars and survive for decades after being scarred, thus exhibiting more tolerance of fire than their classification as ‘fire sensitive’ species implies. Fire-scarred sugar maple, yellow birch, and hemlock trees are common in unlogged forests such as the Porcupine Mountains Wilderness State Park, Michigan, where these species are mixed with fire-regenerated red oak (Frelich and Lorimer 1991, also see details under “A Case Study of Fire and Red Oak” below).

Some studies have used an alternative measure of fire effects on oak, namely the char height, or height of stem blackening, which is generally a surrogate for fire intensity and for the total amount of heat the tree experienced. In one study, a blackening height of 5 ft (1.5 m) led to 50 percent mortality of white oak of 5 in (12.7 cm) dbh (diameter at breast height), while 10 ft (3 m) of blackening was necessary to cause 50 percent mortality of 10-in (25.4-cm) dbh white oaks following dormant-season fires; the same numbers for black oak were about 3 and 6 ft (0.91 and 1.8 m) (Loomis 1973). Trees were much more sensitive to fire during the growing season, when blackening heights to cause 50 percent mortality were about half that of dormant-season fires (Loomis 1973).

Moving beyond individual fire effects, management of fire frequency may be important in managing oak forest ecosystems. Fire frequency influences the number of fires during the lifespan of a plant and the length of the recovery/growth period between fires. Fire frequency is often related to fire intensity and severity because of feedbacks on fuel type and quantity. Finally, fire frequency can influence plant nutrient availability through its effects on nutrient pools and cycling rates.

High fire frequencies place a premium on fire resistance or tolerance. High fire frequencies typically favor mature trees with thick bark that can protect themselves from injury. High fire frequencies can also favor trees and understory species with very high resprouting rates. In oak barrens in Minnesota, high-frequency prescribed fires (5 to 8 fires per decade) eliminated most non-oak species from both the overstory and understory, with understory oaks persisting as “grubs” through persistent sprouting after repeated top-kill (Peterson and Reich 2001). A problem with very-high-frequency fire regimes is that they prevent oak seedlings and sprouts from reaching fire refuge size. Occasional longer fire intervals are needed to allow oak reproduction to develop sufficient height and bark thickness to resist being top-killed by subsequent fires. Dey and Hartman (2005) found that larger black and white oak saplings (>4 in [10 cm] dbh) were very likely (80 to 90 percent) to survive (i.e., to resprout even in cases where the tree was top-killed by one or more fires) a single burn or 3 to 4 burns, while smaller saplings (1 to 2 in [2.5 to 5 cm] dbh) had somewhat lower survival rates (60 to 70 percent) after multiple burns. In Illinois, Bowles et al. (2007) found that 17 years of annual dormant-season burning eliminated most understory seedlings and smaller saplings (<2 in [5 cm] dbh), but caused loss of only 38 percent of larger saplings (2 to 4 in [5 to 10 cm] dbh), including a variety of non-oak tree species like maples and exotic buckthorn, apparently due to low fuel loads and low fire intensity.

Lower frequency fire regimes allow a wider range of species to persist, but may still favor oaks over competitors. Mean fire return intervals of 3 to 10 years provide longer periods for vegetation recovery and growth between fires and allow many sprouting woody shrubs and trees to persist in the understory. Longer mean fire return intervals will allow oaks, and perhaps some other species, to reach fire refuge size and eventually replace overstory trees killed by cumulative fire effects and other disturbances—details are given in the section “Fire as a Regulator of Oak Abundance” below.

Fire may girdle a tree, or scar it by killing the cambium around only a portion of the basal circumference. Fire scars occur when larger trees are exposed to fires moving at moderate speeds, when vortices form on the lee side of the tree, creating flame duration that can be doubled or more compared to an average duration of flame exposure (Gutsell and Johnson 1996). Therefore, in a stand where mature trees have bark 1 cm thick, a flame front with general duration of 1.5 minutes might not kill the trees, but flame/heat duration could be 3 minutes on the lee side, and scar some of the trees. Once a tree is scarred, the callus tissue that rolls in from the sides during the tree’s attempt to cover the wound has thinner bark than the rest of the base of the tree, and therefore subsequent fires may be able to scar that part of the tree over and over.

Fuels that promote long-duration fires can also lead to scarring or mortality from basal scorch, even in very large trees with thick bark (fig. 2). These fuels can include down logs (especially if hollow), piles of twigs and branches lying near the base of the tree, a broken branch standing vertically against the lower trunk of the tree, a pile of duff material caught by the trunk on the upslope side, and accumulations of organic debris beneath the favorite perch of some wildlife species, such as a pile of acorn shells and twigs deposited by a squirrel. Branches can be deposited near the base of the tree during a storm or harvesting operation. For any of these cases, flame duration in a small pocket could easily be 30 minutes to a few hours—enough to create a fire scar from heat conducted through the bark, to burn through the bark, or perhaps even to burn through the base of the tree.

As previously mentioned, there is substantial variability among oak species and among individuals within species in their tolerance to fire. White oak and bur oak are more resistant to fire than red oak in two ways (Smith and Sutherland 1999). First, they are less likely to suffer a fire scar, and second, they are more likely to contain the spread of rot around fire scars. Northern pin oak, black oak, and red oak are more likely to rot at the base after being scarred and subsequently to blow down during a storm one to several decades later. Also, fires may have indirect effects on tree mortality. Peterson and Reich (2001) found that bur oaks had lower mortality



Kalev Jõgiste

Figure 2—A freshly formed fire scar at the base of a northern pin oak tree. The large accumulation of fuel near the tree was due to windthrow of another pin oak that had been fire-scarred several years earlier. Duration of flames from a prescribed fire at tree base was ca 15 minutes but was less than 1 minute elsewhere on this sand savanna at Cedar Creek Ecosystem Science Preserve, Minnesota (Frelich, personal observation).

at higher frequency of fire than northern pin oak on a sand savanna in Minnesota (as opposed to the expected higher mortality for higher fire frequencies). The likely cause was that pin oaks were getting taller than bur oaks and shading them out at low fire frequencies. High fire frequencies, on the order of 6 or 8 fires every decade for 4 decades, caused high mortality of the pin oaks, which then opened the canopy and lowered the mortality rate for bur oaks.

Various objectives, such as converting oak woodland to savanna, open grassland to savanna, sugar maple to sugar maple with some oak mixed in, or maintaining oak by getting rid of a maple or ironwood understory, will require different considerations when using prescribed fire. The physics of fire and bark thickness (described above) for the sizes and species of tree involved will determine whether it is possible to save desired trees while simultaneously eliminating undesired trees. If there is a large difference in tree size and bark thickness—e.g., 20-in [50-cm] dbh oaks with 4-in [10-cm] dbh red maple underneath—then it may be relatively easy to prescribe a fire that would at least top-kill the maples without much harm to the oaks. If bark thickness is almost the same, then creating differential mortality among species will be difficult or impossible.

Fuel Loads for Ecologically Significant Fires

To be ecologically significant, fire must, as described above, kill (or at least top kill) shrubs such as hazel and buckthorn, and seedlings/sapling of shade tolerant trees such as sugar maple, red maple, and basswood. Generating a flame with $>900^{\circ}\text{F}$ ($>486^{\circ}\text{C}$) heat that lasts long enough to kill unwanted species requires a certain fuel load on the forest floor, and contiguous fuel to carry the fire. Generally, if a fire has a flame length of 2 to 4 ft (0.6 to 1.2 m) and lasts for a minute or so as it passes by a given point, it could achieve selective kill of other understory species and leave mature oaks undamaged. Oak seedlings and saplings might also be top-killed, but if they are established as grubs, with a root at least 0.5 in (1.2 cm) thick at the root collar, they can resprout and grow rapidly using resources stored in the root system, and may perhaps outgrow sprouts of other species (Brose 2008).

If the fuel bed is not contiguous, or tonnage of fuel is too low, the fire may merely be a way to remove the duff, which might have some advantage in terms of producing seedbed conditions for oak germination, but would not necessarily set back shrubs and saplings of competing tree species enough to give oaks a window of time to become established. The fuel bed consists of duff, leaf litter (top layer of duff), fine twigs (10-hour time-lag fuel), and medium-diameter branches (100-hour time-lag fuels, 1- to 3-in [2.5- to 7.6-cm] diameter), with abundance of the latter especially important for fire intensity. Thousand-hour time-lag fuels (large snags and logs) are mostly not consumed in fires, and contribute to fire intensity to a moderate degree, although exceptions can occur, such as hollow coarse woody debris that has access by oxygen to the interior, creating a large surface area of burnable wood.

A variety of factors affect fuel bed accumulation and contiguity in oak forests. Fuels in eastern deciduous forests have higher decomposition rates than in western or boreal conifer forests, and therefore, amount of fuel available does not accumulate to huge tonnages over time; furthermore, fuel loads (duff, 1-, 10- and 100-hour) recover quickly—within a few years—after experimental fire (Graham and McCarthy 2006). Annual accumulation of 2 to 3 tons/acre [4.5 to 6.7 tonnes/ha] of leaf/litter fall is common in oak forests (Kaczmarek et al. 1995), and litter accumulation in the forest floor may be two to three times the annual litterfall. Lesser accumulations occur on mesic sites with exotic earthworm invasions, where decomposition of litter occurs faster than on dry and/or earthworm-free sites—see ‘Earthworm Invasion’ below. A survey of forest floor mass (Smith and Heath 2002) shows a mean of about 6.2 tons/acre (13.9 tonnes/ha; range 2.5 to 31 tons/acre [5.6 to 69 tonnes/ha]) in mixed hardwood and oak forests in the northern U.S. from

North Dakota and Missouri to the east coast. Fuel models for a variety of situations, including savannas with grass and shrub/grass fuels, and hardwood forests with forest floor litter fuel beds of various loadings, are summarized by Scott and Burgan (2005); discussion of how the models work to predict fire behavior for the case of oak forests is given by Waldrop et al. (2006).

Reports in the literature suggest that fires in oak forests have been ecologically significant when 1 to 6 t/ac (2.2 to 13.4 t/ha) of duff, 1-hour, 10-hour and 100-hour fuels are present and distributed in a contiguous manner (Chojnacky and Schuler 2004, Collins and Carson 2003, Dey and Hartman 2005, Kruger and Reich 1997). Even on sites without a contiguous fuel bed (e.g., sites where earthworms have eliminated the duff layer), the right amount and contiguity of fuel might occur after moderate-intensity windthrow, or after harvesting that deposits the needed amount of 1- to 3-in (2.5- to 7.6-cm) diameter (100-hour time-lag) fuels to the forest-floor fuel bed, especially if the burn is done in fall or early spring when leaf litter is also present. High-intensity fires may occur in heavy windfall or harvest slash, which may kill mature oaks and be difficult to control. If fireline intensity ($I = Kw/m$) is predicted to be >5000 , larger firebreaks and buffer zones with lower fuel loads than are usual for prescribed fires are needed. In such cases, water bodies or areas 50 to 100 ft wide [15.2 to 30.5 m] with fuel previously removed by a lower-intensity burn or mechanical removal are needed to ensure fire will not escape the prescribed zone, or to protect any desired residual trees.

Fires prior to the arrival of early settlers burned in oak savannas and forests with a wide variety of fuel loads, probably forming a mosaic of fuel loads across the landscape at spatial extents of 1000s of acres. Oak savannas that were burned every few years probably had low fuel loads of a few tons per acre composed of grasses and small shrubs, with low-intensity and short-duration fires (I in the range of 500 to 1000 Kw/m, 1-minute duration), leading to high levels of oak seedling death or top-killing of well established “grubs,” but little mortality of mature oaks. However, elsewhere, high fuel loads were created due to extensive areas of treefall slash from windthrow, ice storms, and passenger pigeon roosting areas, deep duff due to absence of invasive earthworms, and accumulation of woody growth due to less-frequent burning than on savannas. Such areas likely had high fuel loads equal to that of the tree-tops from seed-tree harvests—many tons per acre, with associated high fire intensities and long duration (I in the range of 5000 to 30 000 Kw/m, 5- to 10-minute duration)—killing mature trees and creating conditions for recruitment of even-aged cohorts of oak.

Fire as a Regulator of Oak Abundance

Historical Fire Regimes and Oak Versus Grass, Maple, and Pine

For centuries, or perhaps millennia, fire has modulated the interaction between oak as a dominant species and three main vegetation types: mesic forests of maple, hemlock, basswood, and yellow birch; cold-temperate and boreal forests of pine and spruce-fir; and grasslands, portrayed conceptually as the ‘Oak Triangle’ in fig. 3. Oaks occur within each of these three vegetation types (although only at the southern and eastern edges of the boreal and prairie biomes, respectively), with the abundance of oaks versus mesic tree species, pines, or grasses regulated by complex interactions with fire and soil type (Curtis 1959, Gleason 1913, Grimm 1984, Heinselman 1996).

There is abundant evidence, based on fire scar analyses, that fire frequency in oak forests of central North America has been much lower in the last century than in previous centuries, as fire return intervals from 4 to 16 years have increased to several hundred years (Dey and Guyette 2000a, 2000b; Shumway et al. 2001). McEwan et al. (2007) showed that the current mixed-oak canopy in Ohio and Kentucky was

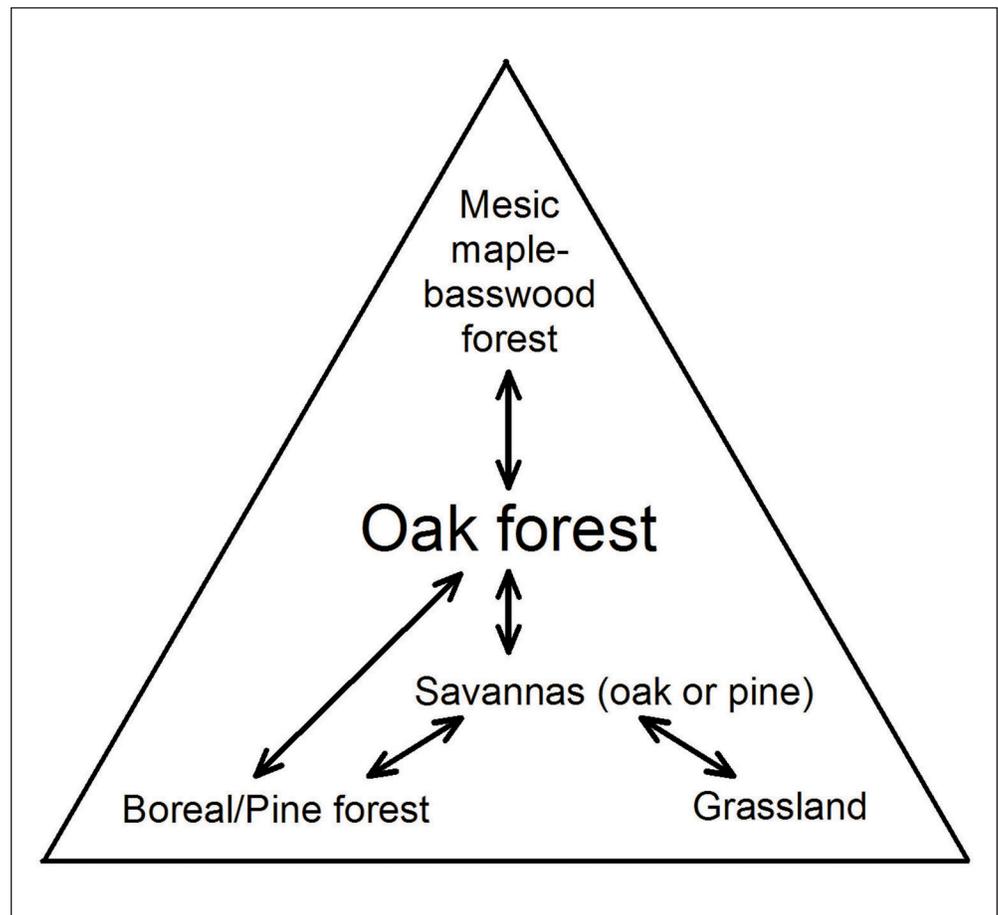


Figure 3—The Oak Triangle, showing the relationships between oak forests, oak savannas, mesic forests, and boreal/northern pine forests in the Lake States.

established during a period lasting several decades with fires approximately every 6 years (range 1.7 to 11.1 years among stands). Land clearing followed by frequent fires led to white and red oak establishment in the Ozark Mountains, followed by a period of fire suppression and no oak recruitment (Soucy et al. 2005). Arthur et al. (2012) emphasized that several short fire intervals followed by a longer interval (i.e., several short intervals of 2 to 5 years followed by a 20- to 30-year interval), would go a long way towards pushing back competition in forest understories and then allowing oaks to grow large enough to resist damage during the next fire that follows the long interval. This observation points out one aspect of the presettlement fire regime that variously benefitted oaks, grasses, or mesic tree species depending on the situation (see details below): over decades and centuries, fire regimes had great variability in intervals between fires.

Fire intervals in the central United States have been influenced not only by climate, but also by anthropogenic factors. Guyette et al. (2002) showed that four stages occurred in Missouri oak woodlands/savannas. During the first stage, prior to extensive settlement of the area, anthropogenic ignitions were infrequent and resulted in low fire frequency. During the second stage when settlement was active, human ignitions were very frequent and fuel buildup became limiting. During the third stage, fuel fragmentation restricted fire spread, as large parcels of land were converted to agricultural land use. Finally, in the modern era, cultural practices such as fire suppression and decisions to carry out prescribed fire became the dominant factor in the fire regime. These stages also occurred in mixed pine-oak and northern hardwood-oak forests further north (Heinselman 1996), but were less accentuated due to the overall lower human populations, less conversion of land to uses other than forest, and colder climate with a shorter fire season.

Although aridity alone can preclude trees from grasslands, paleoecological studies show that frequent fires can also exclude trees from sites that are mesic enough to support tree establishment and persistence (Umbanhowar et al. 2006). In the Lake States, the climate can support trees on all but the most severe coarse sandy or rocky sites, and recruitment of trees on savannas has occurred even during some of the more severe droughts of the last century, as long as a sufficient fire-free interval allowed seedlings to grow large enough to resist the next fire (Ziegler et al. 2008). Therefore, fire regulates the balance between oak and grass, with high-frequency fire in the range of 1- to 5-year return intervals, when sustained over long time periods, leading to lack of oak recruitment and replacement by grasses with some shrubs (Hallgren et al. 2012, Peterson and Reich 2001). Frequent burning in nutrient-poor sand savannas can lead to lower nitrogen availability, enhancing dominance of grasses relative to oaks (Peterson and Reich 2001).

Variability in fire timing and spatial heterogeneity in fire intensity allow some oaks to persist in savanna vegetation types (fig. 4). In a savanna in southeastern Wisconsin, the mean fire interval over the last 200 years was 6.3 years, but fire intervals ranged 2 to 33 years, and the mean interval also changed among presettlement, settlement, postsettlement and modern eras (Wolf 2004). As an example of how variability in fire interval may work to allow oaks to persist on a savanna, consider the case where the mean fire return interval is 3 years, but it takes 7 years for an oak to reach a size such that it can persist through future fires (bur oak is best at this, it grows thicker bark early in life, but other oaks can also sometimes persist). Variability in fire intervals might lead to annual burns several years in a row, followed by 7 or 8 years without a burn, allowing oaks to get established, while maintaining a 3-year mean fire interval. Spatial heterogeneity such as that caused by gopher mounds that create mineral soil exposures of a few square feet in size, a large rock, or small wet area, or differences in slope and aspect might also allow some oaks to persist by creating small inclusions where fire intervals are longer than that for the area as a whole (Franklin et al. 1997).

Mean fire intervals in the range of 5 to 15 years usually lead to shrubby savanna-woodland vegetation types, often with hickories, elms such as rock elm and American elm, walnut, and basswood mixed with oaks on uplands, and cottonwood and red or silver maple mixed with oak in lowland savannas, depending on location relative to ranges of tree species (Curtis 1959; Dettman et al. 2009; Frelich, personal observation). The common view that savannas consisted of scattered bur

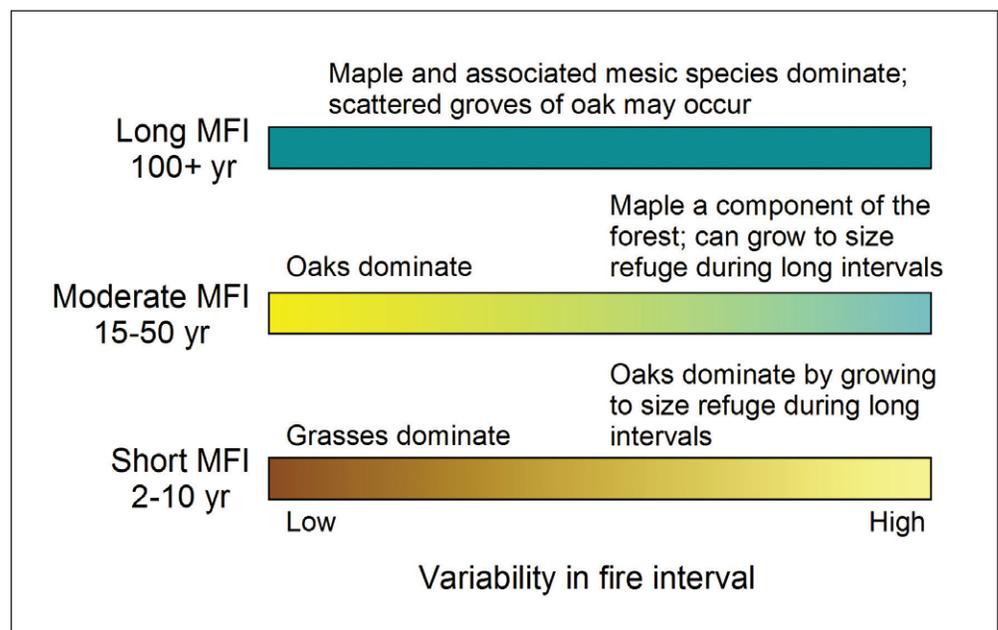


Figure 4—Relationship of mean fire interval (MFI) and its variability to oak.

oaks or just a few oak species over grasses is probably overly simplified (Dettman et al. 2009), except possibly for extremely nutrient-poor sites with coarse sandy soil such as those sites studied by Peterson and Reich (2001).

Moving to longer mean fire intervals (e.g., 15 to 40 years), variability works against oak whereas regular timing works in favor of oak (fig. 4). Here, fire regulates the balance between oaks and maples and other mesic forest species (Henderson and Long 1984, Holzmueller et al. 2009, Hutchinson et al. 2008, Lorimer 1985, McCarthy et al. 2001, McClain et al. 2006, Signell et al. 2005). Because it takes three to four decades for understory maple saplings to develop bark thick enough to resist a fire, a variation in fire interval causing a single 50-year interval, even if the mean interval is 20 years, will allow maples to establish and reach a size refuge, and shorter fire intervals going on for decades or centuries until the old maples have died would then be necessary to get rid of them unless they are mechanically or chemically removed. The power of fires every 10 to 20 years going on for centuries to favor oaks, as was the case on the landscape we inherited at the time of early settlement, should not be underestimated. Also not to be underestimated was the mass effect on the landscape of having large areas dominated by oaks, where maple seed sources were far away, so that even if some longer fire intervals occurred, maples would not necessarily have appeared. This situation is hard to create on the modern landscape.

Fire intervals on the order of a hundred years or more might allow scattered groves of oaks to appear within mesic forests, provided that the fires are intense enough to wipe out the maple regeneration layer and deer do not browse the oak seedlings (fig. 4). Because oaks that do get established can persist for 200+ years, scattered groves can easily exist across the landscape even in forests where average return times for fires are 500 to 1,000 years (Frelich 2002). However, note that dryness (as regulated by soil type, slope, and aspect), topographic roughness, settlement patterns, road networks, and presence of large tracts of public ownership can also lead to a mosaic of fire frequencies across the landscape (Yang et al. 2007), so that various mixtures of forest types, woodlands, and savannas may be present. In Minnesota and Wisconsin, regional water balance determined, at spatial scales of >50 mi (>80 km), where the prairie-forest border was located—with grasslands in areas where evapotranspiration exceeded precipitation and dense forests in areas with an excess of precipitation. At smaller spatial scales of 5 to 10 mi (8 to 16 km), the location of grasses and forests was fine-tuned by the presence of sandy soils, fire breaks (rivers and lakes) and topographic roughness (Danz et al. 2011). Grasslands and oak savannas occurred on flat, sandy outwash plains, rolling terrain to the southwest of fire breaks, and southwest-facing slopes (alternating with oak

woodlands and mesic forest on north and east slopes) in areas with dissected topography (Curtis 1959, Danz et al. 2011, Grimm 1984). Oak woodlands and savannas also occupied sites that could have supported forest but that were frequently burned by Native Americans, for example sites that are now occupied by the cities of Green Bay and Minneapolis (Berland et al. 2011, Dorney and Dorney 1989). Throughout the Eastern United States, a large proportion of white and red oak forest and savanna grew on sites that are capable of supporting mesic forest, but supported oaks owing to regular burning over centuries (Abrams 2003), although clearance and pasturing the land by settlers could also create savannas on lands capable of supporting forest (McEwan and McCarthy 2008).

Finally, pine-oak relationships can be somewhat regulated by fire, but climate is probably also important. Mature oaks in northern boreal-type climates (e.g., northern Minnesota) are short, and they are relegated to understory status in the southern margin of the boreal forest, and therefore produce few acorns. In slightly warmer climates (northern hardwoods of northern Wisconsin and Michigan), white and red pine forests have mixed fire regimes with high-intensity stand-initiation fires, moderate-intensity fires, and low-intensity fires every few centuries, every several decades, and every one to two decades, respectively (Frelich 2002, Guyette and Dey 1995). This mixed fire regime generally allows coexistence of red oak and white/red pines, all of which have thick bark when mature, so that they are capable of surviving fires even if scarred, and continuing to shed seeds for decades after a fire. There is no fire frequency that can eliminate oaks while allowing pines to dominate, but the opposite might occur. Oaks can resprout as grubs, and pines cannot, so in areas with very high fire frequency, pine reproduction will disappear (Blankenship and Arthur 2006, Chiang et al. 2005). Two high-intensity fires within an interval too short for pines to bear a seed crop (<10 years) could effectively wipe out pines while only top-killing oaks. Some pines could possibly withstand more drought than oaks, or more nutrient-poor soils than oaks, or deer might browse oaks more than pines, so that a combination of factors could drive forests towards dominance by pines in a climate where both oaks and pines can survive.

Northern pin oak and scarlet oak can be regenerated as even-aged coppice stands by crown fire as a result of marcescent leaves (dead leaves that remain attached through winter), which also protect the postfire stump sprout's terminal buds from browsing while they are less than 5 ft tall. Coppice stands with multiple trunks are expected and are sometimes mixed with jack pine on sand plains. This is one of the few examples of hardwood forest that supports high-intensity fire with even-aged stands, in the absence of major blowdown or logging. In contrast, most of the landscape on better soils would tend to support multiaged oak

savannas, woodlands, and forests, created by a disturbance regime that kills 10 to 30 percent of the trees within an acre every one to several decades, continuing over centuries. Some even-aged patches (tens to thousands of acres in size) would be present resulting from blowdown-fire combinations within these multiaged landscapes (Frelich 2002).

Logging of mixed white pine and oak forests during early settlement tended to work against the white pine, which cannot resprout and has no persistent seed bank. Red oak and other oaks regenerating after pine removal in a low-deer environment, sometimes with the help of site preparation from slash fires, created red oak forests that are common today across the northern tier of states in the Eastern United States and adjacent Canada (Leahy and Pregitzer 2003). Subsequent absence of logging or fire for several decades combined with increasing deer populations allowed establishment of maple and cherry understory seedlings, so that modern-day logging is accelerating succession towards mesic forest species on these sites (Abrams and Nowacki 1992). Pine can be removed from mixed pine-oak forests by two high-intensity fires in a short time or by logging of mature pines followed by a surface fire or slash fire that kills pine reproduction.

Burning Frequency and Competitiveness of Oak Regeneration in Forests

Oak sprouting and oak competition with other understory species have complex relationships with fire. Single burns may enhance reproductive success of oaks but create a short window of opportunity and allow mesic species to return within a few years (Brose 2010). Two or three reburns in successive years may be necessary to kill resprouting species such as hazel, buckthorn, or red maple, while possibly allowing oak grubs to survive and eventually be released (Blake and Schuette 2000, DeBord et al. 2011). Basically, this process of repeat burning has the objective of exhausting the below-ground storage of energy used to create resprouts—leading to death of the plants—and doing so for the undesired species but not for the advance regeneration of oak. This represents a fine line in the balance between oaks and other species (Blankenship and Arthur 2006, Bowles et al. 2007). The literature suggests that oaks in general are somewhat better adapted to survive repeat burning (Haney et al. 2008); however, repeat fires may also kill some oak seedlings and saplings, especially northern red oak, which has thin bark and relatively poor sprouting ability compared to other oaks (Collins and Carson 2003, Green et al. 2010). Another problem for multiple burns is the presence of sufficient fuel for ecologically significant fires during burns that occur within 1 or 2 years of the initial burn, especially on mesic sites with earthworms (see “Earthworm Invasion” below).

Even if successful, multiple burning may not create a long window of opportunity for regeneration of oak if mature trees of the undesired species are still present, as the forest floor seedbank could be readily restocked with maples, hazel, or buckthorn. In addition, the increased light levels associated with thinning of the forest midstory by repeated fires could also cause an increase in density of the herbaceous layer that can compete with oak seedlings at the germination and establishment phases (see “Competing Vegetation and Invasive Plants” below). Long windows of opportunity for oak establishment can be created if burns are successful at killing the seed-bearing individuals of undesired species, or if those species are removed mechanically prior to burning. Eliminating red maple by exhausting the energy of sprouting stems through repeated burns without killing regenerating oaks is difficult (Huddle and Pallardy 1999), and given the variability in the forest, probably not always achievable through burning alone, especially on mesic sites. Managers may have to settle for a forest with some red maple, ironwood, and other species mixed with oak.

Fire Season

Fire season can be an important factor influencing oak regeneration through its effects on acorn development, deposition, and germination, and subsequent oak establishment. Fire season interacts with regeneration phenology to determine direct effects of fire on acorns and seedlings. Fire season also alters the importance of plant-animal interactions such as the caching of acorns by squirrels. Finally, fire season may influence the relative abundance and dominance of oaks and competitor species through previously mentioned differential fire effects on regeneration and survival.

A recent meta-analysis of 32 prescribed fire studies conducted across eastern North America over the last several decades showed that prescribed fire can be successful as a tool for site preparation for oak seedlings and for release of well-established oaks (Brose et al. 2013). Growing-season fire (between beginning of spring leaf expansion and autumn leaf abscission) was found to be more effective at giving oak the advantage over other hardwoods, especially if it occurred several years after a reduction in overstory density. Apparently, growing-season fire is better at setting back mesic hardwood regeneration than dormant-season fire, consistent with predictions that follow from an examination of physiological response of oaks and other hardwoods to the heat of fire (Abrams 1996, Romero et al. 2009). Analysis of lightning-strike activity and precipitation suggests that natural ignitions are most likely to occur during the growing season in Ohio (Petersen and Drewa 2006), and if this pattern holds for most of the range of oaks, then combined with experimental evidence, there is a strong suggestion that growing-season fires should be considered in the mix along with dormant-season fires for oak forest restoration.

Damage and mortality to acorns can be high for autumn fires for white oaks (which germinate in fall) or during the entire fall-winter-spring dormant period for red oaks (which germinate the following spring). Greenberg et al. (2012) found that acorns on the surface of the leaf litter suffer high mortality rates during dormant-season prescribed burns, but that those acorns deep in the duff or mineral soil often survive owing to insulating properties of the litter/soil. In contrast, growing-season fires probably have little impact on developing acorns held high in the canopy, with the possible exception of acorns developing on oaks that are intermixed with pines, where crown fires may occur.

In presettlement forests, natural fires in mid summer could have been quite intense if they interacted with unsalvaged slash from windfall and passenger pigeon damage. White oak acorns falling during the following autumn would have landed on a litter layer thinned by fire, making penetration of the germinating radicle into mineral soil possible, and would have been covered by the following autumnal leaf litter as well, helping the acorns escape detection by deer and keeping the acorns moist during germination. Most prescribed burns today have difficulty recreating these conditions as a result of the conservative nature of burn prescriptions that do not allow fires to take place with very low-humidity and high-wind conditions during severe droughts—conditions during which natural fires made their large runs with high intensities likely to kill species that compete with oaks. Although they would have had immediate negative effects on oaks, oaks were more poised to regrow vigorously in such postfire conditions. It may take many low-intensity spring prescribed burns to equal the effect of one high-intensity mid-season wildfire, or to come close (as their effects will never quite match those of the single hot fire).

Multiple Factors Interacting With Fire

Regenerating oak requires managing the interplay between oaks and competing vegetation at the seedling, sapling, and mature stages of the oak life cycle. Success of oak regeneration is likely to be context-specific owing to the unique combination of variables present on a given site (Brose et al. 2013, Dickie et al. 2007). A thin leaf-litter layer and higher canopy openness created by prescribed fires were the most important factors predicting success of white oak seedlings in experiments on the Cumberland Plateau (Royse et al. 2010) and Piedmont of South Carolina (Wang et al. 2005). Increased soil nutrient levels after prescribed burns further enhance oak seedling growth in productive forests (Scharenbroch et al. 2012). These conditions last for a short time after a fire and interact with predation on acorns, herbivory, stand development, competing understory vegetation, and invasive species, as explained in the following subsections.

Plant-Animal Interactions

Acorn predation—

Acorn mortality occurs from insects that use acorns as habitat (weevils and galls) and from animals that eat acorns on the ground (deer, bears, turkeys) or pick acorns from trees and cache them for later use (squirrels and blue jays). A combination of acorn weevils (*Curculio* spp.), pip galls (cynipid wasps), and consumption by squirrels, chipmunks, mice, turkey, deer, and bears, can destroy most acorns in an oak stand (Bellocq et al. 2005, Marquis et al. 1976). McShea and Schwede (1993) found that deer ate 70 percent of marked acorns placed in the forest during mast-fall and squirrels and chipmunks also consumed 61 percent of acorns later in the season, so that predation on acorns significantly limited oak reproduction during low mast-producing years. In contrast, a study of acorn consumption comparing forested landscapes with woodlots in an agricultural landscape found that deer consumption of acorns was relatively small when agricultural foods such as soybeans and corn were available (Nelson et al. 1988). Brose (2011) reported on the fate of red oak acorns after a bumper crop in Pennsylvania. Overwinter survival of unburied acorns was only 20 percent owing to desiccation, insect infestation, disease, and consumption by wildlife, while 80 percent survival occurred for acorns buried in leaf litter. Thus, burying of acorns by squirrels probably leads to survival of those acorns that squirrels fail to relocate later.

Despite predation on acorns, germination of oak seedlings is still found in many forests. Passenger pigeons no longer consume the huge quantities of acorns that they once did (Ellsworth and McComb 2003), so that squirrels, turkeys, deer, and bears have probably increased use of acorns. It is likely that the masting pattern of oaks evolved to super-satiate acorn predators every few years, so that a number of acorns go on to germinate regardless of the species consuming acorns.

Herbivory—

One of the most significant bottlenecks in the life cycle for most oaks is likely that deer eat seedlings a few years after germination, when they are between 6 in and 5 ft tall (15 cm to 1.5 m)—susceptibility to browsing usually starts during the second or third year after germination. Oaks are favored species by deer, especially red oak (fig. 5). A study of red oaks in Pennsylvania (Brose 2011) found that survival for 8 years after acorns were produced was strongly affected by deer as well as level of understory density and shade. Seedlings that germinated inside a deer fence with partial shade had 56 percent survival after 8 years, while those exposed to deer and dense shade had only 2 percent survival. If fencing is used to control deer impacts on oak seedling mortality, 2 years of fencing has been found



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Figure 5—A northern red oak receiving insufficient sunlight to make any progress in height growth due to deer browsing.

to be ineffective and 6 to 7 years of protection from deer and an understory environment without dense shade are needed for oaks to grow beyond the reach of deer (Yuska et al. 2008). However, rapidly growing oak seedlings can outgrow deer. If an oak seedling/sapling puts on 1 to 3 feet (30 to 91 cm) of new growth with a thick leader (at least 1/4 in diameter [0.63 cm]), then deer are likely to take only part of the new growth; thus the sapling can make several inches of upward growth progress every year, and will eventually reach a height where it is beyond the reach of deer. In a dense-shade situation, or in small gaps, the leading twigs of oaks are thin and deer can take the entire twig, effectively creating a hedge that is chopped off at the same height year after year until the sapling dies. Thus, oak saplings with more light are more likely to outgrow deer (Lorimer et al. 1994). Resistance to browsing will eventually develop through natural selection and spread throughout oak populations, as there is variability in palatability within natural populations. However, this will take several generations, and in the very long meantime, deer can give the advantage to ironwood, red maple, sugar maple, pines, and other species that are either not palatable or that have an excellent ability to grow rapidly, or resprout repeatedly after burns or browsing (Matonis et al. 2011).

Earthworm invasion—

There are no native earthworms in most of the northern hardwood region, and European earthworms have invaded most of the landscape of Wisconsin, Minnesota, and Michigan. Changes caused by earthworms can influence fire behavior and intensity and the forest floor environment experienced by oak seedlings.

Earthworms are important soil ecosystem engineers and because they can alter soil community composition, nutrient availability, and the structure of soil itself, these abundant and keystone detritivores may have large invasion impacts. Invasive earthworms occur throughout the world (Frelich et al. 2006, Hendrix et al. 2008) and are recognized as one of the most important environmental issues of our time (Sutherland et al. 2011). Invasive earthworms change soil structure and function by consuming the organic horizon (or leaf litter), increasing bulk density and mixing of the mineral horizons (Alban and Berry 1994, Hale et al. 2005) and consequently affecting nutrient and water cycling in the soil (Bohlen et al. 2004, Costello and Lamberti 2009, Hale et al. 2005). These changes to the soil environment have been shown to produce many ecological cascades that affect native plants and animals, as well as facilitate invasive species that compete with native species (Heimpel et al. 2010, Nuzzo et al. 2009). Earthworms can affect native plants in many ways, including (1) ingesting seeds; (2) eating germinating seedlings; (3) influencing symbiotic fungi that plants need for germination and growth; (4) changing the physical characteristics of the seedbed that affect germination; (5) changing the nutrient status of the soil, often decreasing availability of nitrogen (N) and phosphorus (P) to plants; (6) changing the water balance of the soil, drying the A horizon; (7) changing the competitive balance among plant species; and (8) interacting with insects and mammalian herbivores that affect plant growth (Eisenhauer et al. 2009, 2010; Fisichelli et al. 2013; Hale et al. 2005, 2006, 2008). Negative impacts of earthworms on rare plants and native plant species richness have been shown (Gundale 2002, Holdsworth et al. 2007), as have decreases in tree growth (Larson et al. 2010).

The two most relevant changes for oak forests caused by earthworms are their impacts on the understory environment, including competing vegetation, and on the forest-floor fuel bed. Forest-floor conditions created by earthworms favor germination of graminoids in general (grasses and sedges, Eisenhauer et al. 2009), and also favor other invasive plant species (buckthorn and garlic mustard, Knight et al. 2007; Nuzzo et al. 2009; Van Riper et al. 2010). See details in “Competing Vegetation and Invasive Plants,” below. Exotic and native slugs as well as the exotic European earthworm, the nightcrawler, are direct predators on germinating seedlings; they eat developing leaves (cotyledons) of germinating plants (Eisenhauer et al. 2010). However, no studies have been done to quantify these effects on oaks.

Invasion of European earthworm species, especially the detritivore species, nightcrawlers and leaf worms, is having a large impact on the duff portion of fuel loads in deciduous forests (Frelich et al. 2006). This impact varies by stage of invasion (box 2), from thick duff at stage 2 to almost no duff at stage 5. Much of the Midwestern landscape far from metropolitan areas and waterways used for fishing (which are the origin points for earthworm invasion fronts) is in stages 2 through 3 of invasion, with a thinned but still contiguous leaf-litter (duff) layer, making it easier to apply a prescribed fire than at later stages of invasion. However, it seems likely that all areas with productive oak forests will eventually progress to stage 5 of invasion—which can occur on loamy-sand soils with up to 85 percent sand (Holdsworth 2007). High stages of earthworm invasion are unlikely in unproductive northern pin oak forests and savannas on pure sand.

Box 2—Stages of earthworm invasion

Earthworm invasion occurs in five stages (Loss et al. 2013; fig. 6):

Stage 1—earthworm-free, with thick duff and fresh litter, fragmented litter and humus layers.

Stage 2—the duff-dwelling species Small Leaf Worm is present, but duff is still thick.

Stage 3—the leaf worm (a strong detritivore capable of consuming the entire duff layer) is present, and usually more than one species of angleworm, which live in the top 15 in (38 cm) of soil, grazing on organic matter in the A and B soil horizons. In stage 3, the litter layer is substantially reduced in mass and thickness but is still contiguous and may still carry a fire, although the amount of fuel may not support ecologically significant fire intensities until after leaf fall.

Stage 4—there are heavy infestations of the leaf worm and angleworm species, and the nightcrawler invasion has begun, with patches of bare mineral soil forming by mid-summer.

Stage 5—the terminal stage of invasion. The nightcrawler, a detritivore that eats freshly fallen litter, is the dominant species, and commonly the litter layer disappears by mid summer, so there is no permanent duff layer. Instead, the duff layer exists temporarily from fall to spring, with much lower mass and potential to support an ecologically significant fire than sites at stage 3 or lower of earthworm invasion. At this stage, there may be a large accumulation of twigs (10- and 100-hour fuels) that otherwise would have been embedded in the duff where they would have rotted away (Frelich, personal observation). However, no studies have been published on the characteristics of these fuel beds in earthworm-infested areas, and it is not certain if they are contiguous enough to carry fire.



Figure 6—Forest floors of (A) Stage 1 of earthworm invasion—earthworm-free; note thick and contiguous duff; (B) Stage 5 of earthworm invasion at midsummer—note the low fuel loading and discontinuity of the duff.

For the large majority of oak forests now in stage 3 of invasion, the duff is likely thin enough for successful oak germination, having a positive effect on oak germination in the absence of fire. On the other hand, the earthworms have done only half of the work accomplished by fire—fire creates a litter layer of reduced thickness that oaks prefer and kills shrubs and competing tree seedlings. Earthworms do this first half, namely creating a thinner organic layer, sometimes eliminating the need for scarification or fire for the purpose of creating an ideal seedbed. However, earthworms do not duplicate the second part of fire effects, namely killing saplings of trees such as red maple and understory shrubs.

Stand Development

Stand structure and development have a large impact on success of oak seedlings. The intensity of shade and abundance of competing understory species varies as stands develop. A large peak in light levels occurs during establishment after stand-leveling disturbance, dense shade occurs during the even-aged, stem-exclusion stage of development, and an increase in light occurs during canopy breakup and the transition to the uneven-aged stage, although understory shrubs and shade-tolerant tree species can also increase. Modification of stand structure and canopy shading are therefore important in restoration-based management of oak forests, and fire is an important (but not all-powerful) tool for managing stand structure and canopy shading.

Shade tolerance varies among oak species, but in general, oaks are less tolerant of shade than their competitor species. However, not all shade is the same, and under certain conditions, oak species can be surprisingly tolerant of shade. Several studies provide evidence of growth prior to releases from suppression that are slow, approximately equal to suppressed sugar maple and hemlock on mesic sites—and such periods of suppression prior to release can last 40–90 years—even for species such as red oak, black oak, and white oak (Rentch et al. 2003). However, this occurs in forests with oak-dominated canopies and open understories (Povak et al. 2008), which have light levels much higher than either mesic maple and hemlock forests or oak forests invaded by buckthorn (fig. 7). Unfortunately, red maple, ash, and other moderately shade-tolerant tree species can also grow in open oak understories.

Old even-aged stands and stands in transition to uneven-aged canopies, with a high density of overstory oak trees and understory shade-tolerant trees such as red maple, have little or no successful oak regeneration. Burns in such stands will not be successful at allowing oaks to establish unless the understory layer is removed, so that light levels increase (Signell et al. 2005). In contrast, the disturbance regime of presettlement forests of the central and Eastern United States included patches of



Alex Roth

Figure 7—Oak regeneration can tolerate open understory conditions (foreground) better than dense understories (background). A mixed red and white oak forest in Minnesota is shown with an invading front of understory buckthorn, which has remained green into November.

trees killed by passenger pigeons, blowdown, and fire, leading to multiaged stands with more widespread and larger gaps across the landscape than those that form in the even-aged stands that are common today (Buchanan and Hart 2012). Although some larger gaps are created by natural disturbances in the contemporary forests by wind, ice storms, insects, and disease, many stands today have relatively small, ephemeral gaps because canopy trees dying from self-thinning in even-aged stands have small crown diameters. The resulting gaps can be filled both by lateral expansion of the surrounding trees and rapid upward growth of advance regeneration of shade-tolerant species. Thus, smaller gaps tend to favor recruitment of shade-tolerant mesic species such as maples over oaks (Cowell et al. 2010, Fei and Steiner 2009). In a mixed forest in Ohio, large gaps that formed after prescribed burns had killed shade-tolerant advanced regeneration were much more effective at recruiting white oak saplings than gaps created in unburned forest (Hutchinson et al. 2012). In this case, even though shade-tolerant species also germinated after the gaps were created, the fact that the larger advanced regeneration of shade-tolerant species had been killed by burning gave oaks a chance to compete, probably leading to co-dominance by oaks and shade-tolerant species, and at least maintaining the oak component of the stand for several more decades.

Competing Vegetation and Invasive Plants

A variety of understory vegetation can compete with oak seedlings for light, nutrients and water, from the germination through seedling-establishment stages of the oak life cycle (Bowles et al. 2007). Large-seeded species like oaks are more resistant to competition shortly after germination than small-seeded species, because the energy stored in the acorn may allow the seedling to grow above herbaceous vegetation (Flory and Clay 2010). However, dense understory vegetation in forests or grasses in savannas that are taller than oak seedlings can still be significant competitors (Davis et al. 1999). Grasses and leaf litter can also form contiguous fuels and carry fires that kill small oak seedlings.

There is a complementary relationship between understory herbaceous and woody vegetation. In forests with a dense shrub and sapling layer, the herbaceous layer tends to be sparse, whereas without the woody layer, the herb layer can be dense and relatively tall. It is difficult to obtain forest floor conditions with sufficient light for oak seedling growth, but without a dense layer of either herbaceous or woody vegetation. Deer influence the balance between woody and herbaceous understory vegetation; if deer suppress the woody vegetation through winter browsing, then the herbaceous layer becomes denser (Abrams and Johnson 2012). In general, however, woody understory vegetation has a more negative effect on oak regeneration than herbaceous vegetation (Brudvig and Asbjornsen 2008, Brudvig et al. 2011), so that fire and other management actions should generally be directed at controlling woody understory vegetation.

There are cases where some species of oak seedlings compete better (or are at least associated) with certain types of low shrubs and herbaceous vegetation. For example, in Pennsylvania white oak regeneration was most abundant on plots with moderate blueberry or huckleberry cover (and it is interesting to note that oaks and blueberries are both adapted to fire), whereas red maple was associated with eastern hayscented fern (Fei et al. 2004). Such relationships probably also exist in other areas, but have not been systematically studied across the region.

Some herbaceous and woody understory species that compete with oak seedlings have a seed bank that is a historical legacy of past management (Ashton et al. 1998). Graminoids (grasses and sedges) and shrubs, such as raspberries and blackberries, are especially common in the seedbank of oak forests (Aikens et al. 2007, Schelling and McCarthy 2007). For example, red raspberry is a buried seed species with long-term seedbanks in the soil. Seeds that have been in the soil since widespread land clearance during early settlement may still be viable when the forest floor is exposed to light. This legacy is continued each time the seeds are germinated and allowed to progress to seed-set, by a management action or fire that

disturbs the duff and kills woody vegetation, creating a mineral soil seedbed with enhanced light at the forest floor (Schelling and McCarthy 2007). Perhaps trying to germinate them and then reburn after a short time—prior to seed-set—so that the seed bank is exhausted would reduce their abundance, giving the edge to oak seedlings. On the other hand, dense raspberry and associated herbs and shrubs that are common on many sites after prescribed fires or silvicultural treatments might help hide small oak seedlings from deer.

A number of exotic herbs and shrubs have invaded oak woodlands and forests in the Midwest, including reed canary grass, garlic mustard, Tatarian honeysuckle, and common buckthorn. Although the invasive shrubs are known to have large negative impacts on oak regeneration, there seem to be no systematic effects for exotic herb impacts on oak seedlings (Abrams and Johnson 2012, Davis et al. 2012). Reed canary grass on nutrient-rich sites may be an exception, as it reaches high densities and is relatively tall for an herbaceous plant (often 3 to 4 ft [0.91 to 1.2 m]) (Dettman and Mabry 2008). Although fire can reduce reed canary grass density, it does not eliminate it, and other control measures may be needed (Dettman and Mabry 2008). This grass is commonly associated with lowland sites; however it is also favored on nutrient-rich upland sites with silty soils near the prairie-forest border, where it can become abundant after silvicultural treatments and prescribed fires, competing with oak seedlings (Frelich, personal observation).

Invasive earthworms also influence competing vegetation in complex ways. They reduce density of understory vegetation in very low-light conditions, but promote sedge mats or lawns in forests with moderate light levels, and the density of these lawns can be enhanced by deer grazing (Holdsworth et al. 2007, Rooney 2009). These lawns also compete with oak seedlings, although in this case, the short heights of the sedge (less than 1 ft [30 cm]) would be relatively easy for the oak seedlings to overcome using energy stored in the acorn. Research needs to be done—it is not clear what the impact of sedge lawns on oaks seedlings will be (Rooney 2009). If the sedges turn out to be detrimental, they could be treated with herbicides for temporary reduction while oak seedlings are established. Sedge mats might also be contiguous enough to carry fire when they dry down in the fall. If so, then the positive effects may outweigh the negative effects. Also, factors that have a negative impact on oaks and other species but more negative against other species than against oaks, can have a net positive effect for oak. One possibility here is that the sedges might work against maple more than against oak, thereby being a negative factor on growth for seedlings overall that creates a net positive effect for oak.

An adaptive management or even experimental approach may be necessary to establish the best system to manage competing vegetation within a multi-factor environment in each landscape unit. It may never be possible to provide a prescription that will work everywhere at the regional scale, or even the ecological section/subsection scale. Competing vegetation seed bank, deer density, deer browsing preferences, stand development, and effects of invasive species vary locally. Fire will affect and interact with these factors differently, leading to individualized effects across the landscape.

A Case Study of Fire and Red Oak

Among the oak species present in the Midwest, red oak is an especially desired species. It grows fast, and over the northern portion of the region it is the only oak species that produces high-value timber products. It also has the most ambiguous relationship with fire in that although it needs fire to become a dominant tree, fire can also, under some circumstances, work against it (Collins and Carson 2003). It is the oak species least tolerant of high fire frequency, has the poorest ability to resprout after fire, and is perhaps the oak species most likely to persist in the absence of fire, although sometimes at low abundance. Red oak does well when a period of frequent burning is followed by a few decades without fire (Arthur et al. 2012).

Red oak dominance in many regions today is probably a “one-time deal,” owing to the historical dynamics of the passenger pigeon, Native American burning, settlement effects, and deer. Frequent burning by Native Americans to purposely favor white oak (Abrams 2003), consumption of red oak acorns by the now extinct passenger pigeon (Ellsworth and McComb 2003), and frequent prairie fires in areas near the prairie-forest border maintained white oak and bur oak as dominant species in oak woodlands and savannas prior to early settlement. After settlement, Native American burning and passenger pigeon effects disappeared or were greatly reduced, and an episode of landscape clearing and burning followed by farm abandonment in an environment with few deer allowed massive recruitment of red oak across much of the Midwest and northeastern United States, over a period ranging from the late 1800s to the mid-1900s (McEwan et al. 2011).

In many areas, the environment is no longer suitable for red oak recruitment owing to increasing deer browsing and mesophication of the forest, including dense understories of shrubs and maple allowed by fire exclusion and a recently wetter summer climate in the region (Abrams 1992). A century of fire exclusion and poor recruitment has led to an almost complete takeover by mesic forest species on sites with good soils (Aldrich et al. 2005). Earthworms, human dispersal, and human disturbance to the environment also facilitate the spread of invasive shrubs such as common buckthorn and Tatarian honeysuckle (Nuzzo et al. 2009), which form

very dense understories even in stands without native maple or hazel understories. Although red oak seedlings and saplings can tolerate the shade of an open understory for several decades, they cannot tolerate shade in an understory with a shrub and sapling layer (Crow 1988).

Prescribed burns do not always allow red oak recruitment to the sapling layer or eventually to the canopy (Collins and Carson 2003). For a prescribed burn to do that, it must reduce the litter layer and eliminate competing vegetation such as shrubs and saplings of other species for a long enough period for the oaks to reach the canopy, often in the presence of deer. Although removal of litter and low vegetation competition after a prescribed fire often lasts long enough for seedlings to become established (Albrecht and McCarthy 2006), it is difficult to achieve an increase in light availability for another decade or longer as oak saplings grow upwards, unless the prescribed fires are accompanied by formation of some gaps large enough so that they do not close in by lateral expansion of mature trees before new oak saplings reach the canopy (Alexander et al. 2008). Thus, taking advantage of wind disturbance, mortality owing to old age, or thinning, by combining gap formation with prescribed burning is likely to yield better results for canopy recruitment (Brose et al. 1999, Rentch et al. 2003).

Consumption of acorns by deer, bears, squirrels, turkeys and other birds, and acorn weevils and galls is important today, but not the limiting factor for red oak. Many acorns are buried or cached by squirrels, blue jays, and other animals, and not all are retrieved, so that many acorns can survive predation by animals that eat them on the surface of the soils (such as deer) and go on to germinate (Garcia et al. 2002, Haas and Heske 2005, Johnson and Webb 1989). Adequate germination does occur across the range of red oak, but browsing by deer and slow growth rates owing to unsatisfactory understory environments are now widely limiting recruitment into the overstory. Mixed forests of red oak with white oak, sugar maple, basswood, or white pine (depending on location) are probably more achievable than red oak-dominated forests.

In spite of the foregoing difficulties, red oak can have a positive relationship with fire, and still does recruit in areas with suitable conditions. It is instructive to examine those few areas where red oak is still able to regenerate in the last several decades and today. One such area is the unlogged forests of the Porcupine Mountains Wilderness State Park, Michigan. This site is in a mesic forest climate, with generally high-quality soils that support sugar maple, hemlock, basswood, and yellow birch (a few oak stands also occur on rock outcrops, mentioned below). The park lies beyond the range of white and black oak, so that red oak is by far the most important oak species. Surface fires of natural origin have continued to occur and have burned

portions of the park during the last century (Frelich and Lorimer 1991). These surface fires have removed the duff layers, killed some overstory sugar maple and hemlock trees (or burned through areas with moderate-intensity windfall of the maple and hemlock), creating large gaps with light levels equivalent to shelterwood harvests with bare soil seedbed. Because the interior of the Porcupine Mountains is in the Lake Superior snowbelt, there is little overwinter deer browsing on red oak—deer leave the area during the winter and migrate to lower elevation areas near Lake Superior where snow is less deep. By the time deer return to the upland hardwood forest in the spring, they have switched their diet to grazing on herbaceous plants. In addition, because the area was never logged, it is without the legacy effect of the settlement-era seed bank of raspberry, reed canary grass, or other shrub and herbaceous competition, and there has been very little intrusion of invasive species. Also, the carpet of maple seedlings usually present in such forests is wiped out by fire and takes a decade or more to reestablish (an example of this outside the Porcupine Mountains is given by Albrecht and McCarthy 2006), giving oaks plenty of time to recruit to the large-sapling size class after fire. The net effect is groves of red oak currently ranging in age from 40 to 200 years old, interspersed with sugar maple and hemlock in parts of the park prone to these fires—generally upland areas with significant lightning-strike frequency, deep duff (which helps carry the fires) owing to lack of earthworm invasion, and occasional summer drought, above the Lake Superior coastal fog belt (fig. 8; Frelich 2002). There are also occasional red oaks within mesic forests that become established in treefall gaps without fire (Collins and Carson 2003,



Lee Frelich

Figure 8—Groves of northern red oak embedded within a sugar maple-dominated forest in the Porcupine Mountains Wilderness State Park, Michigan. In this May photograph, the dark color of oaks without leaves stands out against the light green of sugar maples with expanding leaves.

Frelich 2002). In addition, red oak in the Porcupine Mountains can coexist with mesic forest species in areas of rocky terrain where there are microsites not quite suitable for dominance by the mesic species but that allow persistence of oaks, which then also serve as seed sources for gaps and nearby burns, as described by Frelich (2002) and Abrams et al. (1998).

Thus, we know that red oak today is capable of reproduction given the right conditions, but that these conditions are not as common across the landscape as they were during the early 1900s (Crow 1988). This case illustrates the usefulness of natural areas, where we can learn from intact natural processes that lead to regeneration of desired tree species. Conditions that now occur in the Porcupine Mountains were unwittingly created on a massive scale by the settlement of eastern North America, so that red oak forests were created over vast acreages during the late 1800s and early 1900s. We have taken that situation with abundant and now aging red oak stands as normal, but in fact, as explained by McEwan et al. (2011), this may be a unique situation in the last several centuries, and it may not be possible to for red oak dominance to continue without alteration of landscape conditions.

Oak and Climate Change

An increase in mean annual temperature of about 5 °F (2.8 °C), along with a slight increase in precipitation, is expected in the western Great Lakes Region by 2069 (Galatowitsch et al. 2009). The increase in precipitation is unlikely to balance higher evaporation, so the net impact will likely be towards a drier climate. The net effect is equivalent to a latitudinal shift such that a given location will experience climates currently prevailing 250 to 300 mi [400 to 482 km] to the south-southwest (Galatowitsch et al. 2009).

In the northernmost region of occurrence for the oak species group, including northern Wisconsin, upper Michigan, northern lower Michigan, and northeastern Minnesota, oaks could benefit substantially from a warmer climate. Here oaks compete with boreal conifers, red, white, and jack pine on sandy or rocky sites, as well as mesic northern hardwoods on sites with deep, loamy soils. Oak in these locations—as demonstrated by a modest increase in importance value (the average of relative density and relative volume in a stand)—has already begun a slow expansion during the last two decades (Fei and Yang 2011). Limits to oak growth imposed by a short growing season and extreme winter minimum temperatures will lessen over time in these areas as the climate warms, allowing oaks to better compete with boreal species and northern pines. Northern hardwoods including oaks can outgrow boreal species as understory saplings, when mean summer temperatures (June, July, August) exceed ca 64 °F (18 °C), although deer browsing can raise this threshold to

68 °F (20 °C) (Fisichelli et al. 2012), owing to deer preference for hardwoods over white spruce and balsam fir as winter browse. Thus, increasing deer populations in the far north may retard the expansion of oak into the boreal forest.

As the climate warms, much of the Midwest could enter a postmesophication era, where maples may no longer have the advantage as a result of longer summer dry periods and warm early springs (Belden and Pallardy 2009, Fei et al. 2003). Longer summers and more frequent droughts in this northern region will narrow the niche of sugar maple and associated species along a soil-moisture gradient, confining them to progressively more silty/clayey soils, while expanding the niche of oak onto sandy loams now occupied by mesic forests (Bapikee 2013). The effectiveness of fire in favoring oaks will also increase as the warmer climate begins to work in concert with fire to favor oaks over mesic tree species. A warmer climate is also likely to favor increasing proportions of oaks in oak-pine mixtures on sandy soils. We can deduce this from the existing gradient of decreasing pine abundance from north to south across the Midwest, as shown by Curtis (1959).

At the same time oak has been expanding in the northernmost region of occurrence, it has been declining along the prairie-forest border region that cuts northwest to southeast across Minnesota and Wisconsin into northern Illinois, Indiana, and southern Michigan (Fei and Yang 2011). A century of fire suppression, fragmentation of the landscape, wetter summers for the last few decades, dense understories, and high deer populations have allowed mesophication of oak forests, typified by invasion of sugar maple, basswood, and other mesic forest species (McEwan et al. 2011). This trend is likely to reverse with a warmer climate, although the magnitude of reversal will depend on the extent to which the other factors mentioned above continue to work against oak. Deer, in particular, are likely to be a major force opposing the expansion of oaks, although their impacts will vary with deer density across the landscape and will eventually be overridden at some level of climate warming that disfavors mesic tree species. Thus, the postmesophication era will play out differently across the landscape, creating a mosaic of differential oak success potential, because factors that oppose the general trends toward oaks caused by a warmer climate vary at the spatial scale of stands to ecological sections.

It is not certain at this point whether a warmer climate will cause the region dominated by oak to simply shift north, losing out to grasses along the southwest and replacing mesic and boreal forests in the north, as opposed to causing wider ecotones within which oaks will be mixed with grasses and mesic/boreal forest trees. Iverson et al. (2008b) suggested that the oak-hickory forest type will expand into the current northern hardwoods and boreal forests without retraction along the southwest part of the range, while Frelich and Reich (2010) point out that a number

of factors (drought, fire, windstorms, insect pests, diseases, invasive species, and deer) other than climate change may work against trees, magnifying the impacts of climate change. Matthews et al. (2011) have made an early attempt to model how multiple factors may affect tree species abundance in the region as the climate warms. The latest available maps of change in abundance across the Eastern United States for tree species of interest are available in Prasad et al. (2007 to ongoing). Managers can use these maps to see how dominant tree species may potentially change by the end of the century for low and high climate change scenarios.

Most analyses of future climate point to a longer fire season. However, it is unknown how this will affect the number of days that meet conditions for prescribed fire. A larger number of days on which fire could occur throughout the year could be counterbalanced by an increase in number of days where fire weather conditions are too severe for prescribed fire. This could also lead to more wildfires that may reduce the need for prescribed fires. We don't have the ability to model future fire behavior in the oak region as can be done for the boreal forest, where much more research has been done on how climate will affect future fire frequency and intensity in a changing climate.

Restoring Fire in Contemporary Oak Forests

Forest managers are basically trying to push succession ahead, keep it the same, or push it backward. Maintaining existing oak ecosystems generally requires maintaining the current successional status (i.e., stopping forward movement), and fire is a tool that can do that alone or in combination with harvesting. A thinning-fire combination can prevent succession, possibly keeping the forest at an early- to mid-successional state, which is generally the goal of oak management. Such combinations of disturbance may even set succession back—generally the goal for mixed oak and maple stands. Although it is not possible to create perfect conditions for oaks everywhere within one site, or on all types of sites across the landscape (Iverson et al. 2008a), there are a number of factors that affect oak regeneration at various stages from germination, establishment, and recruitment. The list of factors varies from region to region and stand to stand. It is up to the manager to create the relevant list for a given stand and push as many factors as possible in favor of oak. Fire will also affect these factors and have direct effects on oak, as summarized nicely by Johnson et al. (2009, p. 157).

Mixed Oak Forests

In parts of the upper Midwest, it is possible to maintain a mixture of oak species. Mixtures of northern red, white, and black oak are possible in southern Wisconsin, Minnesota, and Michigan. Mixtures of red, bur, and northern pin oak are possible in the southern boreal region of northern Minnesota. The advantages of mixed oak

forests are mast in different years, so that acorns as a food source for wildlife will be more even over time, and supporting a greater diversity of ecosystem processes and habitat structures. To enhance all oaks, fire can play a role in limiting understory density, especially density of mesic species like maple and shrubs.

Several factors have moderate to pronounced differential effects among oak species:

- Among oak species, deer will work against red, black, and northern pin oaks relative to white and bur oaks.
- South aspects will generally support more oak species (white oak, northern red oak, black, and bur oak) than north aspects (generally only red oak).
- Varied gap sizes will take advantage of differential shade tolerance among oaks. Northern pin oak and black oak require more light than northern red oak, with other oak species intermediate in shade tolerance.
- Higher fire frequencies favor white oak and bur oak, while lower frequencies favor the red oak group.
- The continued spread of oak wilt would favor the white oaks over the red oaks.

Oak-Pine Forests

There are two types of oak-pine covered here: (1) jack pine–northern pin oak on sandy soils, which has some features analogous to sand savannas of pin oak, bur oak, or black oak; and (2) red and white pine mixed with northern red oak on dry-mesic sites.

The main complicating factor in managing fire in oak-pine mixtures is that the fuel structure will support high-intensity fires. Particularly in northern pin oak–jack pine on sand, it is hard to control the fire frequency, as uncontrollable wildfires are common, and prescribed fires are risky, owing to the fuel loading on the forest floor, low heights to canopy base, and low foliar moisture content (including marcescent leaves of pin oak during the dormant season), all increasing the chance of a surface fire becoming a crown fire. These forest types require high-intensity disturbance to regenerate, like boreal forest. This is a problem, as most of the areas with oak-pine forest in the Midwest are also in a wildland-urban (WUI) interface (see “Wildland-Urban Interface” section below), with small towns and cabins embedded in the forest. High-intensity fires are also possible in white/red pine and northern red oak forests, owing to dense brush and sometimes balsam fir in the understory.

For a single high-intensity fire, oaks will resprout and initially overtop pines after fire, but that situation will reverse a decade later when pines put on more height growth. If a prescribed burn is done within a few years after a high-intensity wildfire, when all seeds of pine have either germinated or died, but there is no seed crop on the young pines, the young pines may be killed, virtually eliminating pines from a stand.

Oaks farther from pines in high-intensity fires are less likely to be killed during fires (Johnson et al. 2009). Therefore, if coexistence of pines and oaks is desired, especially in the jack pine–northern pin oak type, a mosaic of forest types may work better than having pines and oaks mixed together at the scale of individual trees.

For other situations where the structure allows prescribed fire due to higher canopy base heights and relatively low canopy bulk density, including many red oak mixtures with white and red pine, it is relatively easy to manage the balance between pine and oak. Following in concept the example of land use by early settlers that created now-mature northern red oak forests (see “Historic Fire Regimes and Oak Versus Grass, Maple, and Pine” above), cutting pine followed by burning to remove duff and brush will likely allow establishment of a new cohort of oaks.

Light conditions are generally conducive to oaks on the jack pine-pin oak sand sites. However, on account of fire suppression, red pine, white pine, and red oak forests today often have dense understories of hazel, red maple, and balsam fir. This understory interferes with oak and pine reproduction and, like red maple removal in mesic forests, burns during 2 or 3 consecutive years are required to eliminate it.

Oak-Maple Forests

In managing for mixed oak-maple composition, the goals are usually to stop any further advance in, or reduce the dominance of, maples and other mesic species in the forest. The oak component will mostly be composed of northern red oak across the northern part of the region, but could include white oak and black oak in the southern part of the Lake States or northern pin oak to the west. On north- and east-facing slopes, maintaining an oak component in mixture with maple is probably all that can be accomplished—if one or two cohorts of oak are recruited into the canopy each century, coexistence can be maintained. The manager should decide under what conditions it is practical to fight maple, versus when it is futile, or perhaps even work with maple. It may be prudent to wait and see if climate change begins to help push the successional trajectory of the forest away from maple. On south- and west-facing slopes, it is much easier to create or maintain oak dominance by using fire.

Low-intensity fire can make positive contributions toward these goals by:

- Removing a carpet of sugar maple seedlings that often exists.
Reestablishment of a dense carpet may take a decade or more.
- Killing maple saplings with thin bark up to 3 to 4 in dbh (7.5- to 10-cm).
Fires in 2 or 3 consecutive years may be necessary to kill resprouts of red maple, which can outgrow red oak in some cases.
- Removing the duff layer, providing a 1- to 2-year window of opportunity for oak seedlings to germinate, especially if the fire is timed to match a mast year for acorn production.

Killing large red and sugar maples with fire is difficult, as they can develop thick bark. Therefore, rapid restoration to oak could be accomplished by a combination of thinning to remove maple or discrimination against maple during a burn by piling fuel against the base of maple trees to kill them and reduce future maple seed input. A slower restoration could be achieved by prescribed burns every several years to prevent a maple seedling layer from becoming established, while waiting for fire-scarred large maples to rot at the base and fall over.

Complicating factors can include earthworms that remove the duff layer, making it difficult to run a fire through a stand, even though this situation may also help acorn germination. Winter deer browsing also works in favor of maple, as oaks are generally more preferred by deer than sugar maple. Larger gaps (500 to 2000 ft² [46 to 186 m²]) created by windthrow, selection cutting, or thinning, followed by fire, will allow oaks to grow faster than maples and even to outgrow deer in some cases. Fuels from thinning or windthrow may allow a much higher-intensity fire than could ordinarily occur in this forest type, which would have a much higher efficacy in favoring oaks over maples, but have the downside of more restrictive prescription conditions and fire/smoke management.

Oak Savanna

Three different goals occur: (1) restore savannas that have “grown up” into oak forests back to savannas; (2) introduce scattered oak trees into open grasslands to create savannas (this latter goal often occurs on recently abandoned farmland); and (3) maintain the rare existing savannas, preventing invasion by shrubs and trees. Most oak-dominated landscapes originally had a mosaic of stands with various degrees of canopy closure, and given the mosaic of environmental variables that influence favorability to trees versus grass, such as soil type, slope, and aspect, a mosaic of woodland, shrubby savanna, and grass with scattered trees may be more realistic than all savanna.

Regular fires every 2 years are generally required to maintain grasses (Considine et al. 2013), which in turn provide the necessary continuity of fuel for fires to spread at an intensity that will top-kill oak seedlings (Johnson et al. 2009). Spatial and temporal variability of fire allow occasional recruitment of oaks (black oak, northern pin oak, bur oak, and white oak) to a size where they can survive the next fire. Only a handful of oaks need to be established and recruited to the canopy each decade, even on a 10-ac (4-ha) tract of savanna, to maintain a savanna level of tree cover.

Restoring “grown up” savannas requires one of two strategies. The first is to maintain a high fire frequency for several decades, during which older trees die without successfully reproducing, leading to reduced tree density over time. In the second, thinning is followed by a relatively high-intensity fire to create a large,

quick push towards savanna conditions, followed by frequent low-intensity fires for maintenance. Recent case studies support these strategies. Haney et al. (2008) found that a single high-intensity fire had a larger impact on restoring savanna conditions on a black oak sand savanna than several lower intensity burns over 20 years, whereas Peterson and Reich (2001) showed that 40 years of almost-annual burning accomplished the same goal on a sand savanna with northern pin oak and bur oak (fig. 9). Brudvig et al. (2011) found that mechanical removal of woody vegetation followed by maintenance of an encroachment-free state by frequent prescribed fires and promotion of diverse understory plants native to oak savanna constituted an effective strategy for restoring the desired savanna vegetation.

Note that older trees in the red oak group (northern pin and black oaks) will rot around a fire scar and eventually fall down. Therefore, continuation of high-frequency fire for several decades will lead to more dominance by bur and white oaks, as was the case for areas frequently burned by Native Americans. Pushing fuel that will burn for a long time (several 1- to 3-in diameter [2.5- to 7.6-cm] pieces of wood and duff) up against the bases of trees you want to remove, or pulling such fuels away from the trunks of trees you want to save, as a prefire treatment could be very effective. This could be done in combination with a harvest that would supply movable 1- to 3-in (2.5- to 7.6-cm) diameter fuel. Or, if timing of a prescribed burn can be flexible, a prescribed fire within a year or two after a windstorm or ice storm that provided copious fuels on the forest floor that could be manipulated may lead to maximum fire effect. In any case, a goal of getting fire to last for 12 minutes or more at the base of larger trees that are marked to be killed would be effective for a bark thickness of 0.75 in (2 cm). Good models do not yet exist for predicting fire duration, so local experience needs to be developed.

For restoration of trees in grassland, there are two factors to take into account. First, competition with grasses for natural regeneration or planted oak seedlings will be severe (Davis et al. 1999); removal of the sod or use of mulch or mats to keep grasses at bay around seedlings may be needed. Second, lack of mycorrhizae could be an important limiting factor for tree establishment (Dickie et al. 2007). Thus, supplements of forest soil to reintroduce mycorrhizae and protection from deer and competition with grasses and forbs may be needed for oak establishment. Establishment in this context means that oaks are tall enough to be above heights that deer can reach, above the heights of grasses and forbs, and large enough in diameter and bark thickness to withstand any future fires. Once this size is reached, the tree and grass mixture can be maintained by frequent fire, and given the long lifespan of many oak species, only a few new trees need be recruited per acre per decade to maintain the tree component.



Figure 9—Prescribed fire in a pin oak–bur oak sand savanna, Cedar Creek Ecosystem Science Reserve, University of Minnesota. A. Spring burn in progress. B. Four decades of almost-annual burning has allowed substantial progress toward restoration of oak woodland to savanna, with death of pin oaks due to rotting basal fire scars (note fallen pin oak on left) and release of old bur oaks. Photos: Kalev Jõgiste.

The Wildland-Urban Interface (WUI)

The region with highest oak abundance also corresponds to areas with high density of human settlement. Suburban and second-home development has spread into many oak forests and savannas throughout the Midwest. Therefore, where prescribed fires occur and where the smoke goes have become issues in the use of fire for oak management. For a review of these issues, and models available to help manage smoke distribution during fires, see Achtemeier (2009). High-intensity fire with a strong updraft may take smoke higher into the atmosphere so that level of exposure to smoke for local residents may be minimal. Similarly, fires conducted during windy days have a higher dilution factor as wind spreads the smoke. Intensity and windspeed, however, are two factors that must have strict limits for any prescribed fire. The types of fires commonly prescribed in oak forests generally have smoke close to the ground with limited dilution by wind. Furthermore, being in a Wildland-Urban Interface also restricts the range of fire prescriptions that are acceptable, because higher intensity fires that may be desired to kill late-successional and invasive species, require wider firebreaks, hold over longer, and generate more smoke than low-intensity grass fires. Consequences of an escape are much larger than for fires not occurring in a Wildland-Urban Interface. Therefore, wind direction and speed and fuel conditions for fire prescriptions may be quite restricted. This may necessitate greater reliance on mechanical treatment than fire, as the prescriptions necessary for ecologically significant fire may not be possible.

Conclusions—Some Take-Home Lessons

1. Do not underestimate the legacy effects of long-term fire regimes that were in place prior to or during early settlement, where decades to centuries were available to create oak-dominated stands (McEwan et al. 2007). It probably will take a long time to reverse the effects of several decades of fire exclusion that have led to today's conditions in many oak forests.
2. The impact of several burns in a short time is generally underestimated, and potential for a single burn overestimated, especially in the context of a forested site that has experienced fire exclusion for several decades to a century. Also, the impact of variation in return intervals between fires in moderating the competitive balance among oaks and other tree species has been underestimated. The concept of cumulative disturbance severity tells us that either several burns or one burn with very high intensity would be necessary to push a forest (where fire has been excluded) back to a condition where future low-intensity fires would be effective in maintaining desired conditions.

3. The needed cumulative disturbance severity to push successional status of oak-maple forests back to oak may also have to be achieved by some combination of mechanical treatments and fire. If maples and other mesic species have reached a size refuge (thick bark resistant to fire effects), only continued high-frequency fire that prevents regeneration until the old trees die will remove those species from the forest. The old mesic trees could die from natural causes such as rotting from fire scars leading to blowdown, although a silvicultural treatment designed to favor oaks could also be helpful for both forests (Brose et al. 2008) and savanna restorations (Brudvig and Asbjornsen 2008).
4. Learn to predict when mast years will occur (a function of size of oak flower crop, weather, and time since last mast year; Sork and Bramble 1993, Sork et al. 1993) and time fires so that they create optimal conditions for a large crop of oak seedlings, and cause minimal damage to the acorn crop itself.
5. Take advantage of windthrow and ice storms. Use crowns on the ground as buffers against deer if practical. Windthrow and fire interaction could also be used to carry out a prescribed fire with higher than usual intensity if adequate fire breaks and other aspects of the local situation allow.
6. The balance between relative sprouting ability of smaller trees of species you want to disfavor (red maple, sugar maple, and others) and oaks is an important consideration, especially as it relates to the number of burns needed to kill undesired species while allowing oaks to survive. Northern pin, bur, white, and black oaks will fare better in this balance than red oak. It may not be a bad thing to have some basswood, red maple, ironwood, or other species mixed in with oaks. It is probably almost impossible to adjust the sequence of events (in terms of silvicultural method followed by burning) that will create perfect conditions for oaks only.
7. Oak seedlings that are well established, to the point of a grub with significant underground stored energy, will more likely survive top-killing by fire, and resprouts will be poised to grow rapidly. Therefore, an effective strategy is to use prescribed fire several years after a canopy disturbance (whether a silvicultural treatment such as thinning or windthrow), so that postfire oak seedlings will resprout vigorously. Oaks can take advantage of single-tree sized gaps, but only if advance regeneration of mesic tree species like maple is not present. Otherwise, larger gaps are needed.

8. Altering the fuel structure may help tremendously in increasing the effectiveness of a prescribed burn, possibly mimicking the effects of a more severe fire than was actually carried out. This objective of increasing the effect of a prescribed fire may be achieved in several ways; for example, by altering fuel structure to kill oaks (to restore forest to savanna) or to save oaks and kill other tree species (to restore a maple-oak forest to higher percentage of oak).
9. Learn about germination ecology of competing shrubs, trees, and herbaceous species; there is always the possibility of inventing unique ways to discriminate against them, and in favor of oak. Try to exhaust the seed bank of undesired species. Competition varies tremendously across the range of oak in the Midwest, and studies have not been done that show how to vary management activities to regenerate oak under all conditions across the landscape.
10. Mesophication, also called mapleization of oak forests in some areas, has occurred owing to the wetter summers of recent years, reduced fire frequency and intensity, and faster litter decay (Nowacki and Abrams 2008). This leads to less-intense fires, possibly too low in intensity to have a significant ecological effect. However, this situation may start to reverse with a warmer climate and higher drought frequency, which would start to favor oak over maple.
11. A number of changes have occurred in the environment in the last several decades, including earthworm invasion, sedge mats, invasive plant species that change understory density, deer grazing, and climate change. These multiple factors often have both positive and negative impacts on oak, and numerous interactions with fire. Also, their occurrence varies locally and regionally throughout the oak-forest region.

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Metric Equivalents

When you know:	Multiply by:	To find:
Inches (in)	2.54	Centimeters (cm)
Feet (ft)	0.305	Meters (m)
Miles (mi)	1.609	Kilometers (km)
Acres (ac)	0.405	Hectares (ha)
Square feet (ft ²)	0.0929	Square meters (m ²)
Tons (ton)	0.907	Tonnes or megagrams
Tons per acre	2.24	Tonnes or megagrams per hectare
Degrees Fahrenheit	0.56(°F – 32)	Degrees Celsius

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Appendix: Common and Scientific Names

Common name	Scientific name
Vertebrate animals:	
Bear (American black bear)	<i>Ursus americanus</i>
Blue jay	<i>Cyanocitta cristata</i>
Deer (white-tailed deer)	<i>Odocoileus virginianus</i>
Squirrel (eastern gray squirrel)	<i>Sciurus carolinensis</i>
Passenger pigeon	<i>Ectopistes migratorius</i>
Turkey, wild	<i>Meleagris gallopavo</i>
Invertebrate animals:	
Nightcrawler	<i>Lumbricus terrestris</i>
Leaf worm	<i>Lumbricus rubellus</i>
Small leaf worm	<i>Dendrobaena octeadra</i>
Angleworms	<i>Aporrectodea</i> and <i>Octolasion</i> spp.
Herbaceous plants:	
Garlic mustard	<i>Alliaria petiolata</i>
Hayscented fern, eastern	<i>Dennstaedtia punctilobula</i>
Sedge	<i>Carex</i> spp.
Reed canary grass	<i>Phalaris arundinacea</i>
Shrubs:	
Blueberry, lowbush and sour-top	<i>Vaccinium angustifolium</i> and <i>A. myrtilloides</i>
Buckthorn, common	<i>Rhamnus cathartica</i>

Common name	Scientific name
Hazel	<i>Corylus cornuta</i> and <i>C. americana</i>
Honeysuckle, Tatarian	<i>Lonicera tatarica</i>
Huckleberry	<i>Gaylussacia baccata</i>
Raspberry and blackberry	<i>Rubus</i> spp.
Red raspberry	<i>Rubus ideaus</i>
Trees:	
Ash	<i>Fraxinus</i> spp.
American basswood	<i>Tilia americana</i>
Birch, yellow	<i>Betula alleghaniensis</i>
Cherry	<i>Prunus serotina</i>
Cottonwood	<i>Populus deltoides</i>
Elm	<i>Ulmus</i> spp.
Elm, American	<i>Ulmus americana</i>
Elm, rock	<i>Ulmus thomasii</i>
Fir, balsam	<i>Abies balsamea</i>
Hemlock, eastern	<i>Tsuga canadensis</i>
Ironwood	<i>Ostrya virginiana</i>
Hickory	<i>Carya cordiformis</i> and <i>C. ovata</i>
Maple	<i>Acer</i> spp.
Maple, red	<i>Acer rubrum</i>
Maple, silver	<i>Acer saccharinum</i>
Maple, sugar	<i>Acer saccharum</i>
Oak	<i>Quercus</i> spp.
Oak, black	<i>Quercus velutina</i>
Oak, bur	<i>Quercus macrocarpa</i>
Oak, northern pin	<i>Quercus ellipsoidalis</i>
Oak, red	<i>Quercus rubra</i>
Oak, scarlet	<i>Quercus coccinea</i>
Oak, white	<i>Quercus alba</i>
Pine	<i>Pinus</i> spp.
Pine, jack	<i>Pinus banksiana</i>
Pine, red	<i>Pinus resinosa</i>
Pine, white	<i>Pinus strobus</i>
Spruce, white	<i>Picea glauca</i>
Walnut, black	<i>Juglans nigra</i>

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