Refining the Oak–Fire Hypothesis for Management of Oak-Dominated Forests of the Eastern United States

Mary A. Arthur, Heather D. Alexander, Daniel C. Dey, Callie J. Schweitzer, and David L. Loftis

ABSTRACT

Prescribed fires are increasingly implemented throughout eastern deciduous forests to accomplish various management objectives, including maintenance of oak-dominated (*Quercus* spp.) forests. Despite a regional research-based understanding of prehistoric and historic fire regimes, a parallel understanding of contemporary fire use to preserve oak forests is only emerging, and with somewhat inconsistent results. For prescribed fires to be effective, they must positively influence oak regeneration at one or more critical life stages: pollination, flowering, seed set, germination, establishment, seedling development, and release into the canopy. We posit that a simplistic view of the relationship between fire and oak forests has led to a departure from an ecologically based management approach with prescribed fire. Here, we call for a refinement in our thinking to improve the match between management tools and objectives and provide some guidelines for thinking more ecologically about when and where to apply fire on the landscape to sustain oak-dominated forests.

Keywords: oak-fire hypothesis, oak regeneration, forest management, oak ecology, prescribed fire

Forest managers working in oak-dominated forests throughout the eastern deciduous forest biome increasingly embrace prescribed fire among the silvicultural and restoration tools available for addressing a variety of management objectives. This growing acceptance and use of fire stems from a rapidly expanding research-based knowledge of prehistoric (Clark et al. 1996) and historic fire regimes in the region (Guyette et al. 2002, McEwan et al. 2007). This is coupled with mounting concerns about forest structure and compositional changes resulting from alterations to the historical disturbance regime (Nowacki and Abrams 2008), specifically regarding the lack of oak regeneration (Johnson et al. 2009). Consequently, national forest management plans throughout the region call for increased acreages burned (USDA Forest Service Daniel Boone National Forest 2005, USDA Forest Service Mark Twain National Forest 2005, USDA Forest Service Ozark-St. Francis National Forests 2005). Despite these trends, however, fire use as a forest management tool has often preceded research-based evidence for its effectiveness in accomplishing specific silvicultural and ecological objectives across the many ecological settings where oaks are dominant or prominent.

As public agencies and forest managers increase their burn acreage targets and personnel to accomplish more burning across the oak-dominated forest landscape, we think this is a good time to explore the physiological and ecological basis for using prescribed fire in eastern US oak forests. Prescribed fire in this region is used for multiple stated goals, including ecosystem restoration and oak regeneration. In this article, we address the limitations of using prescribed fire to sustain oak dominance across this land-

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scape and consider the stages during oak life history where fire could potentially be used as a tool to enhance oak regeneration. Finally, we provide some guidance for management considerations in the field.

The Oak–Fire Hypothesis: Issues in Contemporary Forests

The oak–fire hypothesis suggests that oak forests require periodic fire disturbances for their successful regeneration and conservation (Abrams 1992). This hypothesis stems from several lines of evidence. Oaks have physiological and morphological traits that suggest they are fire adapted, such as moderately high light requirements, a strong sprouting capacity, and thick bark. Paleoecological evidence points to a temporal co-occurrence of oaks and fire, and dendrochronological studies suggest oak regeneration problems began soon after the implementation of fire suppression. The current dialogue among forest managers and researchers suggests a somewhat simplistic expectation that because fire was present on the landscape historically and prehistorically and appears to be associated with oak prominence, prescribed fire applied to contemporary forests will yield a similarly positive association. Using fire effectively on today's landscape requires us to integrate all the accumulated knowledge about the ecology of oaks and their competitors, coupled with site-specific information, to determine the potential role of fire for sustaining oak forests. In addition, although fire may be an important element for managing forests to favor oak, the fire history literature reveals that oak recruitment to the overstory generally coincides with a significant fire-free interval (Dey and Guyette 2000, Dey and Fan 2009), suggesting the need to incorporate this equally important period of oak regeneration into management plans. Finally, we need to acknowledge that the effects of reintroducing fire into today's forests, after decades without fire, are unlikely to closely mimic the role that fire played in the past for a number of reasons.

Contemporary oak forests differ from those of the past in structure and composition. Before European settlement and into the 19th century, oak forests experienced intermittent natural and anthropogenic disturbances, including pests and pathogens, grazing, ice storms, and fire (Abrams 1996). These disturbances would have created stands (or patches) of even, irregular, or uneven-aged forest structures, depending on their intensity and frequency. Because oaks have a relatively high light requirement (Johnson et al. 2009), seedlings could develop into large oak advance regeneration when fire and other land-use practices reduced stand density. Then, during sufficiently long fire-free periods, oak seedlings could recruit into the canopy. With the introduction of European settler fire, grazing, and logging, large advance oak regeneration was able to accumulate even on more productive sites so that, when permitted, it was able to recruit to dominance, thus forming our modern oak-hickory forests. On the more xeric sites of lower productivity (site index less than 14 m for oak), oak advance reproduction more naturally accumulates as larger seedlings (Johnson et al. 2009) because of site factors that limit stand density and the vigor of competing vegetation and drought effects that favor oak accession to dominance. Site quality also affects which oak species can accumulate as large advance reproduction. For example, the density of large advance regeneration of the more shade-intolerant oaks (e.g., scarlet oak [*Quercus coccinea* Muenchh.] and black oak [*Quercus velutina* Lam.]) increases with decreasing site quality (Kabrick et al. 2008). In the early 20th century, multiple and coincident disturbance factors such as loss of native fauna that were consumers of massive quantities of acorns (e.g., the passenger pigeon) and factors contributing to more open forest canopies, such as the loss of American chestnut (*Castanea dentata* [Marsh.] Borkh.), introduction of domestic livestock in forests and woodlots, and forest harvesting, all promoted the recruitment and dominance of oak in the overstory. Additionally, there is evidence that fluctuations over the past 100 years in the densities of white-tailed deer, an important herbivore throughout the eastern deciduous forest, are coincident with shifts in oak regeneration success (McEwan et al. 2011). More recently, however, the removal of disturbances through fire suppression and regulation of forest grazing has been linked to oak regeneration failure and a shift toward increased density of more shade-tolerant, "mesophytic" species (Nowacki and Abrams 2008). In these increasingly shaded understories, oak persistence and growth has declined, so large oak advance regeneration is often sparse or absent. Despite the variability in oak advance regeneration across the landscape, today's oak forests have more crowded mid- and understories dominated by shade-tolerant species such as red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marshall), and blackgum (*Nyssa sylvatica* Marshall; Abrams 1992). In some stands, species such as red maple have grown sufficiently large in the absence of fire disturbances to resist fire damage, but if top-killed by higher intensity fire, sprouting from root reserves is prolific (Blankenship and Arthur 2006).

The structure, composition, and flammability of fuels have changed in some systems. As fire frequency has declined across the landscape and savanna and woodlands have transitioned to forests, the abundance of grasses, forbs, and other fine fuels has decreased (Nowacki and Abrams 2008) and a subsequent modification of potential fire behavior, intensity, and severity has developed. Similarly, the proliferation of shade-tolerant hardwoods below oak canopies has decreased forest flammability because of differences in leaf litter structure and chemistry. Leaf litter of encroaching shade-tolerant species, such as red maple, decomposes faster than oak litter (Knoepp et al. 2005), potentially decreasing fuel loads. In addition, red maple litter retains more moisture than co-occurring oak species (Morgan Varner, pers. comm., Humboldt State University, July 7, 2011), potentially reducing flammability under environmental conditions typical on many sites. Leaf litter of red maple and other encroaching species also tends to lie flat on the forest floor rather than curled like oaks, allowing less oxygen to permeate the forest floor, further decreasing flammability. Smooth-barked species such as red maple may also reduce forest flammability because they funnel large volumes of stemflow near their boles, which may promote cool, damp conditions and create fuel discontinuity (Alexander and Arthur 2010), a significant limitation to the spread of prescribed fires in these forests (Loucks et al. 2008). These changes in species composition and consequent impacts of fuel type, abundance, and moisture have created a "mesophication" (sensu; Nowacki and Abrams 2008) of the forest that may make it harder to burn and manage with fire alone and has restricted the length of season when burning is feasible.

Burn policies for prescribed fire promote low-intensity fires because of safety concerns and logistical and infrastructure constraints. Contemporary prescribed fires

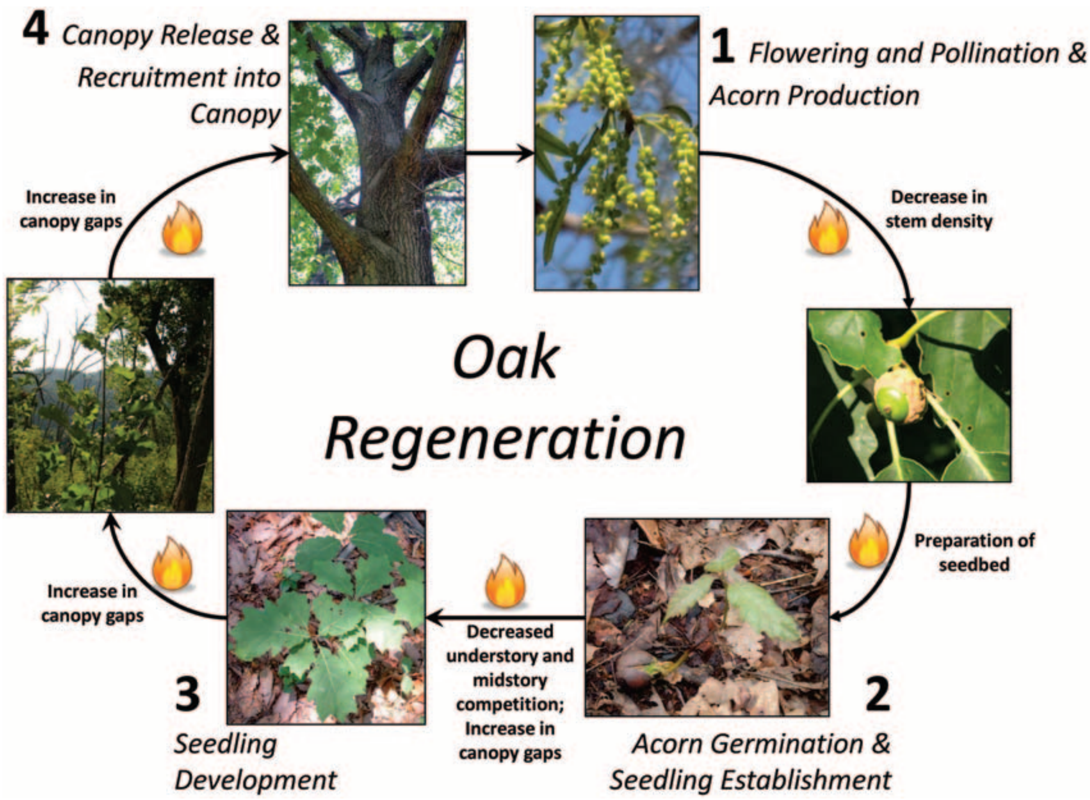

Figure 1. Illustration of the key life stages for oak regeneration: (1) flowering, pollination, and acorn production; (2) acorn germination and seedling establishment; (3) seedling development; and (4) release from overstory competition and recruitment into the canopy. The text in bold provides descriptions of the processes by which fire disturbance may influence oak regeneration success.

are managed to minimize escapes and air-quality problems in a highly inhabited landscape and often fail to create long-lasting increases in understory light necessary for oak development. Burning under conditions needed to produce more intense fires often conflicts with the readiness needed for wildfire suppression during higher fire danger periods, creating another limitation to higher-intensity fires. In contrast, fires ignited by prehistoric humans or natural ignitions would have burned indiscriminately, and in years of unseasonal drought would have been more likely to cause substantial overstory mortality leading to stand replacement in extreme cases. Differences in fire implementation between contemporary prescribed fires and past fires are likely to produce differences in fire behavior with concomitant differences in ecological effects.

Oak forests exist on a wide range of sites in the eastern United States. This great environmental variability is revealed, in part, by the diversity of oak species (approximately 30) dominating this region for nearly 10,000 years (Abrams 1996). Across climatic, topographic, and edaphic gradients, these forest communities differ not only in the suite of oak species present but also in the array of competitor tree species. Determining a fire regime (frequency, intensity, severity, and seasonality) needed to sustain oak is difficult because response to fire varies among species and life stages, and site-specific forest composition, structure, and environmental conditions influence fire behavior and, hence, severity. This makes it more difficult to translate the findings and experiences of researchers and managers working in sites in different ecoregions.

How Could Fire Promote Oak Regeneration at Different Life History Stages?

Against the backdrop of these limitations to using fire effectively to manage contemporary oak forests, it is useful to consider at what stages in the development of a cohort of oak advance regeneration fire could potentially enhance oak regeneration success (Figure 1). The general process of successful oak regeneration is well understood: (1) mature oak trees produce an acorn crop after successful flowering, pollination, and acorn development; (2) new seedlings become established from viable acorns; (3) seedlings develop in the understory; and (4) oak advance regeneration is released from overhead competition and competes successfully with other regeneration. In addition to this pathway for oak sexual reproduction, asexual reproduction via stump sprouting can be an important source of regeneration, potentially relevant in stages 3 and 4 mentioned previously. To understand how fire could influence this process, we need to think specifically about each life stage and consider whether and under what circumstances there is a potential role for fire, with or without other silvicultural tools, to improve the success of oak regeneration in the stand. For each regeneration stage highlighted in Figure 1, we draw on the existing literature to highlight the conditions necessary for oak to grow into successive stages. We then discuss our current understanding of fire effectiveness for creating those conditions.

Flowering, Pollination, and Acorn Development

Few studies address the factors influencing the first steps in oak regeneration: oak flowering and pollination, and acorn production. However, it has been shown that weather conditions are likely an important factor in flowering and pollination success (Sharp and Sprague 1967, Cecich and Sullivan 1999) and that variation in acorn production is strongly related to total production and survival of female flowers (Sork et al. 1993, Cecich and Sullivan 1999). Because acorn production is strongly influenced by tree vigor, a consequence of nutrition and photosynthetic capacity (Kozlowski and Pallardy 1997), researchers have examined the influence of species, tree size, and basal area on acorn production. Greenberg (2000), studying the factors causing variation in acorn production among five species of southern Appalachian oaks, largely confirmed what is generally known about oak acorn production: (1) acorn production among different species tends to peak in different years (Beck 1977); (2) individual trees vary tremendously in acorn production, with "good" producers consistently producing larger than average acorn crops compared with "poor" producers (Greenberg 2000); and (3) individual tree size can be an important factor in acorn production, with larger diameter, full-crowned and dominant trees generally producing more acorns, but tapering off in large-diameter trees and with age (Downs and McQuilken 1944, Greenberg 2000). Where nitrogen is limiting to forest growth, nitrogen fertilization may contribute to increased flowering and acorn production (Callahan et al. 2008).

The factors affecting oak flowering and acorn development are not easily altered through management. Nonetheless, two potential roles for prescribed fire occur at this life history stage. Based on our current understanding, the greatest influence on acorn production would likely be achieved through manipulation of stand density to enhance crown development and potential for acorn production. Thinning to release individual tree crowns can increase acorn production (Healy 1997), but thinning effects can be inconsistent because of genetic variability among trees to produce acorns and the inability to identify good producers during thinning, especially in younger, immature stands (Healy 2002). If good acorn producers can be identified based on a known history of seed production, thinning nonoaks by mechanical methods can help to improve acorn production. Relying solely on fire to reduce stem density for the purposes of improved acorn production would be unlikely to produce predictable results, given the highly stochastic nature of this process. However, thinning and dormant-season burning treatments in oak forests in southeastern Ohio suggested treatment differences in the impacts on acorn production (positive response to "thin + burn") and seed size (positive response to "burn only"), and different responses among species (positive treatment response for chestnut oak (*Quercus montana* Willd.) but not black oak (Lombardo and McCarthy 2008). Conversely, burning can lead to a decline in crown vigor (Arthur, unpublished data, Mar. 2012) that may lead to declining health and lower acorn production, despite the fact that opening the canopy might be expected to increase radial growth (Rentch et al. 2002) and potentially acorn production (Downs and McQuilken 1944, Greenberg 2000). Finally, although burning can lead to a temporary increase in site nutrition including nitrogen availability (Blankenship and Arthur 1999), which could potentially increase acorn production (Callahan et al. 2008), there is also evidence that a frequent fire can lead to long-term reductions in nitrogen availability (Hernandez and Hobbie 2008).

Acorn Germination and Seedling Establishment

Oak success at the acorn germination and seedling establishment stages is also influenced by multiple potential limitations: herbivory (including mammals, birds, insects, and pathogens), litter depth, competition, and seedling nutrition. The leading limitation among these may be herbivory, because in any given year, most of an acorn crop can be lost to herbivory (Bellocq et al. 2005). Thus, it is in mast years that oak seedlings establish in significant numbers (Johnson et al. 2009). Management to improve the rate of acorn germination and seedling establishment may therefore have the greatest impact when applied with explicit attention to mast production.

Herbivory by insects and soil-dependent biota (such as bacteria, fungi, and nematodes) has a significant impact in rendering acorns nonviable (Johnson et al. 2009). Insect predation of acorns is common and well documented, with weevils a common predator, leading to nonviable seed or low-vigor seedlings (Gibson 1982, Lombardo and McCarthy 2009). There has been speculation that spring fires could decrease weevil and other insect populations by disrupting the life cycle portion spent in the soil (Wright 1986). However, experimentation with fire to reduce weevil herbivory on acorns has not consistently yielded reductions in insect populations (Lombardo and McCarthy 2009). Rodents and other small mammals, as well as deer and birds, can consume a large proportion of the acorn crop (Johnson et al. 2009), negatively impacting oak germination and seedling establishment. However, acorn burial by some animals offers some measure of "escape" from consumption. As a result, the relationship between fire and herbivory is likely complex, having the potential to reduce herbivory by organisms that spend all or part of their life cycle in the soil but, conversely, potentially increasing the possibility of consumption if too much of the litter layer is removed.

Litter depth can influence oak germination and seedling establishment in two additional ways. For acorns to remain viable, their moisture content must remain above 40% for white oak species (*Leucobalanus* spp.) and 25% for red oak species (*Erythrobalanus* spp.; Korstian 1927) and is best maintained when seeds are buried in mineral soil or deep within the organic layer. Buried seed is also better insulated from the heat of fire (Cain and Shelton 1998, Iverson and Hutchinson 2002), although even low-intensity surface fires can destroy half or more of an acorn crop (Dey and Fan 2009). Conversely, although some litter can protect acorns from desiccation during winter, too much litter impedes root penetration into underlying soils and can lead to long, weak stems as new seedlings grow up through thick litter layers. For these reasons, fire can benefit oak seedling establishment by reducing the thickness of deep litter layers (Abrams 2005, Royse et al. 2010), as long as acorn desiccation does not become problematic. However, only a small body of research has directly examined the influence of forest litter on the germination and establishment of oak species in this region (Garcia et al. 2002, Kostel-Hughes et al. 2005), and few studies have examined fire (Wang et al. 2005, Royse et al. 2010). In addition, variability across the range of oak-dominated forests in the region, as well as climate variability, leads to a gradient of decomposition rates and litter depths that should be incorporated into our understanding. Additional research is needed to determine whether fire timed to acorn production could enhance germination success and seedling establishment, a prospect that will be challenging to implement in any case.

Fire has the potential to significantly alter the regeneration pool of seedlings and sprouts via heat-induced mortality or combustion of existing seeds and seedlings, seedbed preparation for new seedlings, and stimulation of the sprouting response of fire-damaged or top-killed plants. Hence, in addition to the fire effects on the stages of oak regeneration, it is important to consider fire effects on potential competitors at the germination and seedling establishment stage. Unfortunately, there is a paucity of research examining the effects of fire on species composition at this stage, and what is available is somewhat contradictory, suggesting the need for more research at sites with varying conditions because the importance of this source of new competitors is highly site specific. It is well known that some shade-intolerant species, such as yellow-poplar (*Liriodendron tulipifera* L.) and black birch (*Betula lenta* L.), produce high numbers of wind-dispersed seeds (Weigel and Parker 1997, Jenkins and Parker 1998) that easily germinate in postfire soils and also exhibit rapid shoot growth in high light conditions, becoming increasingly competitive with oak as overstory density declines (Dey and Parker 1996). Schuler et al. (2010) found that fire can reduce abundance and alter species composition of the seed bank directly, although after two prescribed fires, the seed bank was still an abundant regeneration source for tree species that are oak competitors. Variability in fire effects on species composition of new germinants partly reflects the preburn seed bank composition. For example, in the relatively xeric Ozark Mountains of Arkansas, Schuler and Liechty (2008) found that prescribed fire led to increases in some species but decreases in others, with very low abundance of tree species germinating from the seed bank with and without fire.

The variability in germination and establishment found among different studies and sites may in part result from differences in the reproductive "strategies" of the species present. Highly fecund species that produce large to very large seed crops, exemplified by red maple, provide a constant source of new germinants and seedlings regardless of fire treatment. Species that remain viable in the seed bank for several years, such as yellow-poplar, may show reduced numbers of seedlings after multiple fires, as the seed bank becomes depleted. Oak competitors with strong root bud sprouting responses to disturbance, such as sassafras (*Sassafras albidum* [Nutt.] Nees.; Bosela and Ewers 1997), may lead to high seedling densities on sites where it is present. Hence, fire's potential effects on oak competition must be evaluated in the context of the species already on a site, as well as the extent, frequency, and intensity of the fires themselves.

Seedling Development

The growth and development of oak seedlings is primarily a function of light availability. In general, oak seedlings grow best when understory light is at least 5% of full sunlight, with maximum growth occurring at 30–50% of full irradiance (Ashton and Berlyn 1994). Irradiances of 10–15% full sunlight have been shown to improve oak seedling growth in a number of forest types, including Wisconsin oak-maple (Lorimer et al. 1994), central Appalachian hardwoods (Miller et al. 2004), and Mississippi River bottomland hardwoods (Motsinger et al. 2010). Many contemporary mature stands have light levels well below (less than 2%) the level needed to promote oak seedling growth (Jenkins and Chambers 1989, Lhotka and Lowenstein 2009), often because of the development of a midstory of shade-tolerant species in the absence of fire (Lorimer et al. 1994, Abrams 2005, Nowacki and Abrams 2008). Oak seedlings in such low-light forest understories may have little to no growth and a seedling population that establishes after a good acorn crop may plummet to extinction in less than 10 years (e.g., Loftis 1988, Crow 1992). Thus, one way prescribed fire could potentially promote oak seedling development is through top-kill of saplings and midstory trees, which are typically shade tolerant, thereby reducing competition for understory light.

There are several reasons to think that oak seedlings would be more resistant to mortality from prescribed fire compared with most competitor species. With hypogeal germination, oak dormant buds are often below the soil surface, where they are better protected from fire damage, and with sufficient light, they can develop a large root system that facilitates regrowth after top-kill (Brose and Van Lear 2004). In contrast, many oak competitors have epigeal germination, which tends to expose dormant buds to high burn temperatures (Brose and Van Lear 2004), and a nonconservative growth strategy, which promotes shoot over root growth (Lorimer et al. 1994). Thus, oak seedlings top-killed by fire are more likely to survive through resprouting compared with most competitor species (Kruger and Reich 1997, Brose and Van Lear 1998), and competitor mortality should increase as fire frequency increases because of reduced levels of stored carbohydrates in rootstocks after repeated shoot dieback.

Although fire may increase light availability and reduce densities of competitor seedlings, oak seedlings' competitive status still may not improve (Alexander et al. 2008, Green et al. 2010), in part because the light increase is relatively small and only short-lived. This is because low-intensity prescribed fires generally cause little mortality of overstory trees, often reducing stand basal area by less than 5% (Dey and Fan 2009), and small canopy gaps quickly reclose after prolific resprouting of competitor species that were only top-killed (Chiang et al. 2005, Blankenship and Arthur 2006) or lead to only small increases in canopy openness (Hutchinson et al. 2005, Alexander et al. 2008). Low-intensity fires consistently top-kill hardwoods below 10-cm dbh and a significant proportion of those between 10- and 20-cm dbh, including the oaks (Waldrop et al. 1992, Dey and Hartman 2005, Green et al. 2010). After decades of fire suppression, however, competitors often exist as larger saplings, poles and sawtimber-sized trees that are sufficiently large to resprout with vigor after top-kill. For example, although red maple is especially susceptible to fire mortality when small (Iverson et al. 2008), this species becomes increasingly resilient with increased size (Ward and Brose 2004) and can resprout even after several burns (Chiang et al. 2005, Blankenship and Arthur 2006). Furthermore, some competitor species in the seedling stratum, such as sassafras, resprout prolifically from clonal ramets after fire damage and exhibit increased density and growth even after repeated fires (Dey and Hartman 2005, Alexander et al. 2008). Thus, careful consideration of the size, resprouting capacity, and light requirements of potential recolonizers of the postfire stand must be considered before using prescribed fire as a tool to promote oak seedling development.

Prescribed fire applied repeatedly may eventually create canopy openings of sufficient size to support oak seedling development, although there is limited evidence of this occurring (Hutchinson et al. 2005, Alexander et al. 2008) except in combination with the formation of natural canopy gaps (Hutchinson et al. 2012). Even if the necessary understory light environment is achieved with prescribed fire, this does not guarantee that an oak seedling will have the ability to respond. Oaks must be relatively large (basal diameters of more than 1.9 cm [0.65 in.]; Brose et al. 2006) before burning to be competitive postfire. In addition, oak seedlings residing in the understory in a suppressed state for considerable periods (such as those in many of today's stands) may be physiologically unable to respond to light increases, even high light provided by a release (Dillaway et al. 2007), although there may be an improvement in physiological status (Alexander and Arthur 2009). Furthermore, although oaks can develop large root systems and have protected basal buds, small oak seedlings often die when burned (Johnson 1974, Alexander et al. 2008). Thus, a prefire assessment of the size of oak regeneration on site is critical and may provide some idea of whether oak seedlings have the capacity for rapid shoot growth after an increase in understory light.

Another approach for improving oak regeneration is to use prescribed fire combined with more precise silvicultural techniques. Several studies have shown that a combination of thinning and prescribed fire can increase light and decrease competition. Although the benefits to oak regeneration are variable, depending on the amount of thinning and length of time between thinning and burning (Brose and Van Lear 1998), the effects may nonetheless be lasting (Brose 2010). Responses also vary with site index (with little effect on mesic sites; Iverson et al. 2008) and may occur after a lag effect of several growing seasons after repeated fire (Albrecht and McCarthy 2006, Iverson et al. 2008). Although difficult to manage for or predict, multiple prescribed fires preceding canopy gap formation resulting from white oak (*Q. alba* L.) decline led to abundant white oak regeneration in a central hardwood forest (Hutchinson et al. 2012), simultaneously showing the complexity of developing viable management approaches and the potential importance of combining fire with other methods. Overall, the variability in oak seedling response to prescribed fire, used alone or in combination with other techniques, clearly indicates that we still need improved species-specific ecophysiology standards related to forest structure, light levels, and growth for eastern oak species and their competitors, as well as improved understanding of the direct effects of fire on tree seedlings.

Release from Competition and Recruitment into the Canopy

A primary limitation to oak recruitment into the canopy is low light availability due to a partial overstory. Relatively low levels (more than 5 m^2/ha) of overstory dominants uniformly spaced over an area can significantly reduce seedling survival, growth, and diversity with effects most pronounced with shade-intolerant species (Miller et al. 2006). Moderate- to high-density overstories exceeding 14 m^2/ha basal area significantly suppressed larger (more than 1 m tall) oak reproduction density compared with clearcutting (Larsen et al. 1997, Kabrick et al. 2008) and decreased the survival and growth of oak stump sprouts growing beneath a partial overstory (Dey et al. 2008, Atwood et al. 2009). Thus, one way prescribed fire could be used to enhance oak regeneration during this life stage is to reduce competition and open up the canopy. However, the use of fire to provide sufficient light (30–50% or more of full sunlight) for oak recruitment into the overstory requires high-intensity fires that cause mortality of large overstory trees, and most prescribed fires are not conducted under the conditions (warm, dry weather with high fuel loads) necessary to do so. Even if high-severity fires were implemented, managing fire in a way that gives much control over the spatial arrangement of canopy openings is complicated for a variety of reasons. Notably, fire effects on individual overstory trees partially depend on microsite variations in topography, fuel location and arrangement, and fire behavior (Whelan 1995, DeBano et al. 1998), and interactions between fire intensity and tree characteristics (i.e., species, size, and physiological activity) influence the probability of tree mortality (Whelan 1995, Brose and Van Lear 1998). Other methods such as regeneration cutting and chemical or mechanical thinning are more effective than fire for controlling stand structure to manage understory light.

If fire can be used to release oak reproduction from canopy competition, what is the length of the fire-free period necessary for recruitment? It is useful to think of the time it takes for a tree to attain a minimum diameter that confers some resistance to cambial damage and subsequent top dieback from fire because resistance to fire damage increases exponentially with increasing diameter (Hengst and Dawson 1994, Bond and van Wilgen 1996). We have previously established that low-intensity surface fires can cause top-kill in most hardwood species in trees less than 15 cm in diameter, including oak species. Using this as a threshold indicating some fire resistance and lower probability of top-kill, local diameter growth rates can be used to estimate the time it takes for a tree of a given species to achieve this diameter. For example, in Missouri, the average diameter growth for codominant white oak saplings (2.5- to 8-cm dbh) growing in a regenerating clearcut is 3.8 cm in 10 years on sites with average site index of 19 m (Shifley and Smith 1982). At this rate, it takes 33 years for a white oak sapling to attain 13-cm dbh and have a good chance of surviving a low-intensity surface fire. Diameter growth rate will vary by site quality, and any addition of overstory competition will reduce diameter growth rates in oak reproduction, more so with black oak and scarlet oak than white oak, thereby increasing the time it takes to gain sufficient size to avoid damage by fire. If the regeneration source is oak stump sprouts, then the time it takes to reach a fire threshold diameter will be less than that of advance regeneration because oak stump sprout initial diameter growth is substantially greater. For example, Dey et al. (2008) reported that oak stump sprouts in Missouri Ozark clearcuts grew to an average of 7.8-cm dbh for scarlet oak, and 5.8 cm for black oak and white oak in 10 years. However, as with seedling origin reproduction, overstory densities that averaged 15 m^2/ha significantly reduced oak stump sprout diameter growth, and oak stump sprouts averaged only 1 to 2-cm dbh after 10 years.

Thus, a fire-free period of 10–30 years will be needed for oak to grow large enough to survive additional fires, depending on site quality, competition, and long-term retention of overstory trees. These long fire-free periods are commonly found in the fire history records of eastern hardwood forests (e.g., Guyette et al. 2002, 2006). During the mid-19th to early 20th centuries, European settlers caused fires to be more consistently frequent, which prevented recruitment into the overstory. Today, managers often restore prescribed fire into forests based on the reported mean fire-free intervals in published fire histories. Thus, e.g., areas are burned every 3–10 years, a common mean fire return interval in the eastern United States (e.g., Guyette et al. 2002, 2006). This overly simplistic approach may work initially to gain benefits by returning fire to forests, but in the long run, fire management plans must

Table 1. Questions to ask about the status of oak regeneration and of competing species at each life stage to determine the potential role of fire in achieving the desired ecological effect.

Life stage	Questions
Flowering, pollination, and acorn production	**Are there large seed-bearing trees in which their canopy position could be enhanced by a reduction in stand density?** YES: Fire may have the potential to reduce the density of competing fire-intolerant trees. NO: Fire may not be useful to address this goal. CONSIDERATIONS: The risk is the concurrent loss of oaks by fire mortality. Thus, a reduction in stand density may be best achieved through silvicultural techniques that more specifically target nonoak trees such as mechanical or chemical thinning and timber harvesting.
Acorn germination and seedling establishment	**Is forest floor depth limiting to seedling establishment?** YES: Fire could enhance acorn germination by consuming a portion of the forest floor and preventing acorn desiccation prior to germination. NO: Fire may not be useful to address this goal.
	Is the litter layer sufficiently dry to be consumed by fire? YES: Plan burning when conditions are conducive to forest floor combustion. NO: Delay fire until litter dries out.
	Is the forest floor covered with leaf litter from species known to have flammable litter? YES: Plan burning when conditions are conducive to forest floor combustion. NO: Fire may not be useful to address this goal.
	Can fire be timed to coincide with seed dissemination of competitor species, but not oaks, thereby reducing competition? YES: Time fire with this goal in mind. NO: Fire may not be useful to address this goal.
	Was there a recent oak mast crop? YES: Delay fire to avoid burning acorns. NO: Not a consideration for decision to burn.
	Is there evidence of a mast crop in the canopy? YES: Consider timing burning to precede mast crop where forest floor depth is potentially limiting to acorn germination or to set back competitors. NO: Not a consideration for decision to burn.
Seedling development	**Is stand density limiting light to oak in the understory?** YES: Fire could reduce mid- and overstory competitors and provide increased light to oak seedlings. NO: Fire may not be useful to address this goal.
	Are oak seedlings present in the understory in significant numbers and sizes to survive fire? YES: Fire could reduce competitors while allowing oaks to resprout. NO: Fire may not be useful to address this goal. CONSIDERATIONS: If existing oak seedlings are of sufficient size to survive multiple fires, repeated fire may be useful to control competitor species. Oaks need adequate light to grow between fires.
	Are dominant oak competitors in the understory in sufficiently small numbers and sizes to be killed by fire? YES: Fire may reduce competitor abundance, but will only have positive implications for oak regeneration if oaks are of sufficient size and numbers (see previous question). NO: Fire may not be useful to address this goal. CONSIDERATIONS: If competitors are likely to resprout, consider repeated burning or other alternatives to burning such as cutting and herbiciding to reduce competition.
	Do competitor species have a seed bank strategy? YES: A single fire may "release" these species leading to an abundance of newly germinated seedlings that will compete with oaks. NO: Not a consideration for decision to burn. CONSIDERATIONS: Repeated fire may be useful to "release," but then kill, newly germinated competitor seedlings.
	Are there large competitor species that will likely survive multiple fires and continue to contribute to the seed and seedling banks regardless of repeated burning? YES: Fire may not be useful to address this goal. NO: Not a consideration for decision to burn. CONSIDERATIONS: Thinning or timber harvesting may be good alternatives to reduce the density of seed bearing competitors.
Release from competition and recruitment into the canopy	**Is oak advance regeneration present in sufficient number and size to achieve desired stocking after fire?** YES: Consider using fire to reduce stem density and increase light. NO: Not a consideration for decision to burn.
	Is fire capable of creating canopy gaps? YES: Fire could provide increased light necessary for oak release. NO: Fire may not be useful to address this goal. ALTERNATIVE: Mechanical or herbiciding methods may be used to open gaps.
Maintenance of oak dominance	**After burning, are oaks maintaining dominance in the canopy, and are they present and developing in the understory?** YES: Continue monitoring to insure oak regeneration success. NO: Consider use of fire or other means of thinning or crop tree release and competitor suppression.

allow for recruitment of oaks to the overstory by withholding fire for a longer period.

Management Applications and Other Issues

As the use of prescribed fire in oak-dominated forests of the eastern United States increases, land managers need to ask precise questions about the specific goals of burning in a particular landscape or forest stand. When the goal is to enhance oak regeneration and oak dominance, focusing on the oak life history stages that could be enhanced by fire, as well as the life histories of competing species, can help to hone fire effectiveness in accomplishing the stated objectives. Conversely, when prescribed fire has been applied and has not achieved the stated objectives, managers should ask, "Why isn't fire promoting oak regeneration in this stand?" It is increasingly clear that the application of fire to oak forests as a coarse tool often does not achieve the desired objectives, at least in the short term, and simultaneously can damage residual trees necessary for future acorn crops. Thus, stands in which fire can improve the competitive status of oak regeneration should be targeted for prescribed burning over those where the fire's potential role is unclear. Although Brose et al. (2008) have developed detailed guidelines for using the decision support system, SILVAH, to guide managers in making decisions aimed at developing oak seedlings capable of recruiting into the canopy, our goal, here, is to engage readers in thinking about the potential roles of fire in oak ecology.

A better understanding of how to use fire in eastern oak forests to accomplish management objectives would come from a balanced and analytical approach that considers the potential ecological effects of fire. This would require four components:

- A better understanding of the physiology and ecology of the species being managed, both the desired species and the key competitors.
- Improved knowledge of when to apply fire in the life cycles of oaks and the key competitors for various stages of stand development.
- Whether managing at the stand or landscape level, development of specific management goals and silvicultural prescriptions that are based on the current stand and site factors that identify other important factors that could affect seedling regeneration and development and that state the future desired condition, all of which are then used to guide the fire management plan and burning prescription.
- Increased skill in using fire to increase consistency in attaining desired results.

Our goal in this article is to encourage managers and researchers considering using prescribed fire for oak regeneration to ask a series of questions, in a site-specific context, to determine whether prescribed fire has the potential to improve the competitive status of oaks (Table 1). Managers and researchers should be able to identify the expected mechanism by which prescribed fire *could* enhance the regeneration of oak in a particular stand. For example, if there are oak trees in the stand producing viable acorn crops, is there a need to reduce the depth of the leaf litter? This approach will be most relevant when smaller stands are being managed, but it still requires attention to operational considerations.

Clearly, using fire to promote oak regeneration in this region is complicated because prescribed fire is being conducted across increasingly large areas, presenting unique constraints and concerns. For example, the USDA Forest Service, which conducts most of the forest burning in the region, is often limited by resources and staff to burn the acreage called for by forest plans (e.g., Mark Twain National Forest). Furthermore, fire management officers and silviculturists often do not stay long in the same position, leading to shifts in expertise and ability to implement management goals on the landscape. Burning windows in this forest region are often short, unpredictable, and require considerable monitoring to determine when conditions are right. To address these limitations, we need a rapid response system of sufficient capacity to accomplish the level of burning desired or identified in forest plans. Optimization analyses are needed to identify key areas for fire use on the landscape, taking into account site productivity and the role of fire in specific landscape positions, as well as the ability to conduct prescribed fire, operations and logistical constraints, and ownership. Because most of the oak resource is owned by private landowners and landscapes are comprised of mixed ownerships, there is a need to address state laws, training, and insurance issues to facilitate burning on private lands in an integrated landscape approach that is not present in most states. Work is ongoing to remedy some of these limitations to the use of fire in the various states, but more progress is needed.

Furthermore, we must acknowledge that fire alone is not a "silver bullet" for enhancing oak regeneration regardless of site quality, and in many instances, fire use may be constrained or simply impossible. As such, future research should investigate the effectiveness of silvicultural practices such as forest harvesting and herbiciding as fire surrogates for speeding structural and compositional transition. When fire is the only feasible management tool available, repeated fire may provide a suitable means for improving oak regeneration. However, there remains a relative dearth of information on the long-term ecological consequences of (and capabilities for) repeated burning and whether fire applied repeatedly can be used to achieve the effects that can be accomplished using fire coupled with cutting and herbiciding, such as a reduction in the sprouting response of shade-tolerant species and greater light availability for oak seedlings. Furthermore, there may be instances where oak regeneration problems stem from issues unrelated to competition and understory light, such as increased herbivore population (e.g., white-tailed deer), which prescribed fire may be unable to address.

As fire is increasingly used in eastern forests to achieve a variety of management objectives, there are additional fire effects on the landscape that require consideration. From an ecological perspective, fire is an ecosystem process with numerous interconnected implications for plant successional dynamics, soil nutrient availability, carbon sequestration, and water and air quality. As such, management objectives must be considered in concert with fire's many other roles and scales of implementation. More studies are needed to address the consequences of long-term and frequent fire use on biodiversity, species invasions, air and water pollution, soil fertility, and potential interactions with and feedbacks to climate change. There is also a need to understand the ecological and social tradeoffs inherent in the implementation of fire use on the landscape. These factors all require additional study in the context of landscape use of fire and its multifaceted effects on ecosystems.

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