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Contents

Session Four.
Hostile Takeovers in America:
Invasive Species in Wildlands and Waterways

Session Five.
NEPA After Thirty Years:
The Good, The Bad and The Ugly

Sustaining Oak Ecosystems in the Central Hardwood Region: Lessons from the Past—Continuing the History of Disturbance

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Oak savannas, woodlands and forests were dominant ecosystems throughout the central hardwood Region (CHR) before European settlement. Today, only 0.02 percent of the original oak savannas present at the time of European settlement remain, and bottomland hardwood forests have been reduced by 70 to 95 percent depending on the watershed (Nuzzo 1986, Sharitz and Mitsch 1993). This deforestation resulted largely from agriculture development.

Upland oak/hickory forests are still the major (54 million acres) forest type in the CHR. However, current disturbance regimes are driving forest succession to more shade tolerant species such as the maples and pioneer species such as yellow-poplar, especially on the more productive lands (site index = >60 feet, base age = 50) (Lorimer 1993). However, increased competition from shade tolerant trees and shrubs reduces oak regeneration potential even on drier sites. The inability of oak reproduction to compete and recruit into the overstory is the fundamental cause of oak sustainability problems in forested situations.

The primary factor leading to the successional displacement of oak has been a change in the historic disturbance regime that has altered the competitive relationship between oak and its associates. The widespread distribution and dominance of oak is a result of a long history of frequent fire, which peaked shortly after European settlement (Abrams 1992). Fire suppression has nearly eliminated wildfire as a forest disturbance since the 1930s, and the lack of fire is the most often cited cause of the recent oak regeneration problem, especially on high quality sites (Lorimer 1993).

The loss of oak forests in the CHR is a concern to resource managers and private forest landowners. Under current disturbance regimes, it appears that oak dominance will be increasingly confined to the less productive sites without human intervention through management. The more productive sites will succeed to other species, with a possible loss of species diversity, and loss of mast production that is important to so many wildlife species. Sustainability of oak ecosystems is predicated on an understanding of oak ecology and disturbance history, and it requires planned disturbances that favor oak regeneration and development.

Oak Regeneration Ecology

Oaks regenerate as new seedlings, seedling-sprouts and stump sprouts. Shoot growth of new seedlings (i.e., those that have not experienced shoot dieback) is relatively slow for most oak species, and hence, regeneration that relies mainly on new seedlings usually results in failure, even when abundant but small oak seedlings exist before overstory removal (Johnson 1993, Lorimer 1993). Successful oak regeneration is dependent upon there being an adequate number of large advance reproduction (primarily seedling sprouts that are present before overstory removal).

Oaks have evolved a regeneration strategy that relies on building large root carbohydrate reserves, at the expense of shoot growth, and a tremendous ability to produce new sprouts after death of the original shoot. Oaks are better adapted than many of their competitors to disturbances or environmental stresses that cause shoot dieback because they can repeatedly produce new sprouts (i.e., seedling sprouts) from the supply of dormant buds located at the root collar, which is often beneath the soil surface where buds are protected from fire or herbivores. Oak seedling sprouts with large root systems are able to grow rapidly in height after release from the overstory. In contrast, oak seedlings with small root systems are quickly suppressed by large shade tolerant (e.g., maples) saplings and fast growing shade intolerant (e.g., yellow-poplar) reproduction.

Oak reproduction is most competitive on sites with below average productivity that experience frequent disturbances such as fire and environmental stresses such as drought. On these sites and under these conditions, survival and growth of oak competitors are limited, as is overstory density, vertical structure of vegetation, biomass and leaf area. When light at the forest floor is adequate, oak advance reproduction can persist for decades (Merz and Boyce 1956). Oak seedling sprouts can accumulate with each good acorn crop, and grow in the understory of open-structured woodlands. These oak advance reproduction are able to develop large root systems that then can supply the energy for rapid shoot growth upon release from the overstory.

Today, oak forests on mesic sites do not usually regenerate to oak in the absence of disturbances that limit competing vegetation in both the understory and overstory. Without such disturbances, heavy shade (e.g., 1 percent of full sunlight) develops as shade tolerant canopies form in the understory. In this low light, oak advance reproduction does not grow well and does not survive. Abundant oak advance reproduction may result from a single good acorn crop, but large seedlings do not develop in the heavy shade. Those seedlings that do persist are small and have low regeneration potential. Thus, there are frequent and prolonged periods when there is little or no oak advance reproduction. Harvesting during these periods ensures that there will be fewer oak in the future forest.

Accumulation of large oak advance reproduction on mesic sites requires recurrent disturbances, which historically had been the role of fire before European settlement. Fire increases light at the forest floor by decreasing the density and size structure of woody species in the understory and by reducing overstory density. In the absence of periodic fires, mesic sites develop dense overstory canopies and complex vertical structure. Eliminating tall understory woody stems and reducing overstory density increases oak advance reproduction survival and growth (Lorimer et al. 1994, Larsen et al. 1997).

Stump sprouts are stems of reproduction that arise from overstory trees (stems ≥2 inches dbh) cut in a timber harvest, or topkilled by fire. Stump sprouts are the fastest growing form of oak reproduction. When growing in the open, oak stump sprouts have high probabilities of capturing growing space and maintaining dominance in the overstory. This growth advantage is due, in part, to a large root system that can deliver sufficient water, nutrients and other metabolites to the shoot.

The capacity for stump sprouting varies among species, and with tree size, age and vigor. It also depends on the season that the parent stem is cut. Most oak species have high sprouting potential (nearly 100 percent) for stems with diameters in the range from 2 to 8 inches dbh (5 to 20 cm) (Dey et al. 1996). Increasingly larger trees produce fewer sprouts, and oaks larger than 20 inches (51 cm) in dbh sprout infrequently. Sprouting potential and growth also decrease in older trees (Kozlowski et al. 1991). Cutting upland oaks during the dormant winter months results in higher densities of more vigorous sprouts per clump compared to trees cut during the growing season (Wendel 1975, Kays et al. 1985). Although they are the most competitive form of oak reproduction, stump sprouts should not be relied upon alone to sustain oaks in the future stand because the stocking of sprout producing trees is usually not high enough to maintain stand composition, unless the oak forests are young (e.g., < 60 years old) when harvested.

Disturbance History

Native American Fire

For 10,000 to 20,000 years, Indians used fire to influence forest composition and structure and the extent of grasslands in North America (Pyne 1982, Delcourt et al. 1993, Krech 1999). Indian fire favored the widespread dominance of (1) the oak woodlands and forests; (2) the eastern prairies, glades, and barrens; and (3) the oak and pine savannas. Many forests had an open, park-like appearance because of a long history of fires (Lorimer 1993). In the CHR, the cycle of fire determined the balance between tallgrass prairies, oak savannas, and oak woodlands and forests (Gleason 1913).

Frequent fires reduced the density and size of woody species in the understories of oak-dominated forests, increased the diversity in ground flora and favored the growth of grasses, legumes and other herbaceous plants (Wright and Bailey 1982). The overall effect was to promote the accumulation and growth of advance reproduction of the fire-adapted oaks by reducing understory competition and causing occasional overstory mortality, thus increasing light at the forest floor. Oaks often persisted as "grubs" in the understories of forests and savannas, as well as in prairies, glades, and barrens.

Variability in fire-free intervals was substantial, ranging from 1 to 70 years (Cutter and Guyette 1994, Guyette 1995, Guyette et al. 1999). This variability in fire frequency played a critical role in the regeneration and recruitment of species into the overstory because oaks require some fire-free period to develop enough resistance to burning injury before the next fire. During the longer fire-free periods, oak seedling sprouts were able to grow rapidly, increasing their ability to survive subsequent fires.

Low intensity surface fires were most common (e.g., every 5 to 15 years) in hardwood forests before the fire suppression period (Guyette and Dey 1997a, Sutherland 1997). These surface fires usually caused mortality of single or small groups of mature trees (Whitney 1994). Fire sizes were variable depending on the terrain, weather and fuel conditions. Fires spread without human suppression, burning out when they ran into natural fire breaks, the weather changed to rain or snow, or the fire encountered a less combustible fuel type.

Fires of moderate and greater intensity burned less frequently (e.g., every 40 to 50 years) and coincided with regional or subcontinental drought (Cwynar 1977, Guyette et al. 1999). Fires burned more extensively and caused greater mortality to overstory trees in drought years. Catastrophic fires intense enough to cause stand replacement were least common in eastern hardwood forests. The periodicity of severe, stand replacement fires is not well documented.

Fires were common in bottomland areas, and wetlands burned during drought periods. Europeans found large prairies and openings along the valleys of rivers, such as the Missouri and Mississippi, the result of Indian fires (Catlin 1844, Williams 1989, Nelson et al. 1999).

Native American populations declined drastically due to European diseases during the 16th and 17th centuries. As many as 80 percent of the people in a tribe perished in disease epidemics (Williams 1989, Delcourt et al. 1993). The frequency of fire was greatly reduced during this period of low population (Guyette 1995, Guyette et al. 1999). Migrating Indian tribes, displaced from their ancestral lands in the East, carried fire back into areas of low population in the CHR, increasing fire frequency during the 18th century (Table 1). By the early 1800s, European settlers were pouring into the CHR.

European Fire

European settlers continued Indian burning practices, but often increased fire frequency and carried fire into more remote areas (Table 1). In general, fires burned most frequently during the period 1850 to 1930, when Europeans were busy converting the landscape into farms and villages (Pyne 1982). Fires, and now other forest disturbances such as grazing, logging, and fuelwood cutting, maintained the open, park-like character of the forests, with understories dominated by grasses and herbaceous plants. Frequent burning, grazing, and logging created forests of sprout origin dominated by oaks.

Fires burned extensively following wholesale logging of the forests. During this period, many of our most famous fires burned millions of acres of cutover forests and took the lives of many people in the Lake States. The cycle of

Table 1. Estimated annual wildfires per million acres based on fire histories in the Upper Current River watershed in the Missouri Ozarks for a range of average fire sizes (Guyette 1995).

		Average fire size acres (ha)			
		100 (40.5)	500 (202.3)	1,000 (405)	5,000 (2,023.5)
Period	MFI[a]	Fires per year per million acres			
Native American I (1581 to 1700)	15.8	632	126	63	13
Native American II (1700 to 1820)	8.9	1,123	225	112	22
European settlement (1820 to 1940)	3.7	2,703	540	270	54

[a] MFI = mean fire interval in years. Mean fire interval data for the Upper Current River watershed (approximately 1 million acres: 445,000 ha) represent the averages of 23 fire history sites.

logging and burning also greatly reduced the extent of pine forests in the CHR. After the mature, seed-bearing pines were harvested, intense slash fires and repeated burnings eliminated or greatly reduced the abundance of pine reproduction (Record 1910, Guyette and Dey 1997b). Oaks succeeded the pines and shade-tolerant mesophytic hardwoods (Abrams 1992). Oaks expanded their dominance on mesic, highly productive sites with frequent and widespread burning.

The widespread suppression of wildland fires began in the 1930s and 1940s in the CHR; however, in the Ozark Highlands wildland fires were common until the 1950s (Pyne et al. 1996). The amount of acres burned by wildland fires has dropped drastically over the past 100 years. At the beginning of the 20th Century, the fire rotation period was 90 years in Michigan and 50 years in Pennsylvania (Whitney 1994). During the initial period of European settlement in the Missouri Ozarks, mean fire intervals averaged around three years (Cutter and Guyette 1994). Now, the fire rotation period is estimated to be more than 700 years in Missouri (Table 2).

At the outset of the fire suppression period, modern oak forests developed rapidly across the CHR, replacing savannas, barrens and prairies, and dominating old fields and cutover lands. Oak advance reproduction in these systems grew quickly into closed canopy forests following the cessation of fire (Curtis 1959, Grimm 1984). However, with continued fire suppression, oak forests are being replaced by more shade-tolerant, mesophytic species such as the maples.

The Significance of Human-caused Fire

The balance between human-caused and natural fires is of importance in the debate about how we should conserve or restore our "natural" heritage. Natural fires generally refer to those that result from ignition sources other than human. Lightning is the primary ignition source of natural fires. Fire managers in Ohio, Missouri, Michigan, and other Midwestern states have observed that lightning causes 2 percent or less of all wildfires (Westin 1992, Ohio Depart-

Table 2. Estimated fire rotation periods for the modern period in eastern North America.

Region	Fire rotation period	Reference
Missouri Ozarks	715 years	Westin 1992
Pennsylvania	910 years	Whitney 1994
Lower Michigan	1,400 to 2,000 years	Whitney 1994
Southern Illinois	900 years	Haines et al. 1975

ment Natural Resources 2000, Michigan Department Natural Resources 2000, Tennessee Forestry 2000). From another perspective, lightning causes less than 1 fire per 1 million acres (400,000 ha) annually in the CHR, based on weather and fire records from the past century (Schroeder and Buck 1970). Thunderstorms occur on average 30 to 50 days each year over much of the CHR (Baldwin 1973). The highest occurrence (50 to 70 days per year) of thunderstorms is in the southwestern portion of the region. Most thunderstorms in the CHR are accompanied by heavy rainfall, which reduces the likelihood of fires spreading from lightning strikes. Also, lightning-caused fires are less likely to spread in the summer, when vegetation is in leafout and fuels have high moisture contents. In contrast, humans have caused an average of 105 fires per year per 1 million acres (400,000 ha) in southern Missouri (1970 to 1989), which includes one of the largest contiguous forested areas in the CHR, the Ozark highlands.

How has the role of humans as ignition sources changed since the Native American period? Although documented fire histories are rare in eastern North America, we do have a wealth of information on historic fire regimes in the Missouri Ozarks. Within the Upper Current River watershed, which encompasses some 1.1 million acres (445,000 ha), Guyette (1995) reconstructed fire histories for 23 sites distributed throughout the area. The composite fire history for all these study sites is presented in Table 1 by historic period. The Native American I period refers to a time when Indian populations were decimated by diseases introduced by Europeans. Fire was less prevalent (mean fire interval [MFI] = 15.8) in the Ozarks than later periods. Human populations began to recover during the Native American II period due to increases in local populations and immigration of eastern tribes. Coincidently, fires burned the Ozark forests more often. The greatest period of fire activity was during initial settlement of the Ozarks by the Scotch/Irish and other European settlers beginning in the 19th century.

Historic levels of fire occurrence are substantially greater than the rate of natural fires caused by lightning in the Missouri Ozarks (Table 1). Based on Guyette's (1995) data, a range of average fire sizes from 100 acres (40 ha) to 5,000 acres (2,023 ha) was used to estimate annual fires per 1 million acres (400,000 ha), and to evaluate the contribution of humans to the overall frequency of fire. It is difficult to establish actual fire sizes in the past, however, we do know that fires in the Missouri Ozarks averaged 100 acres (40 ha) in size during the early stages of fire suppression (1930s to 1940s) (Westin 1992), and that average fire size was certainly larger than this when fires burned freely. The high level of fire activity in historic times (Table 1) relative to the background level of lightning fires is largely a result of human ignitions. Widespread use of fire by Native Americans and early European settlers is well documented, and it is unlikely that the level of lightning has changed much in the past 400 years. In the absence of humans, natural fire would have shaped the development of vegetation in the CHR and provided opportunities for oaks to persist. However, the current abundance of oak and other fire dependent genera would not exist if it were not for human-fire.

The Need to Manage Oak Forests

Today, humans start most of the wildfires in the CHR, as they did in the past, but the area burned annually has been dramatically reduced by effective detection and suppression programs. Over the past 30 years, the number of human-caused wildfires in forest protection districts has been relatively constant in such states as Missouri, Ohio and Tennessee, where on average from 1,000 to 3,000 wildfires burn per year. The number of wildfires can double in a drought year. What is notable is that within the past 70 years, average fire size has been drastically decreased from about 100 acres (40.5 ha) to just 10 acres (4 ha) or less.

In the absence of fire, disturbances that result in small openings in the forest canopy accelerate succession to shade tolerant species. How private landowners harvest their forest has a tremendous effect on the sustainability of oak forests because they own most of the forest lands in the CHR, and provide the bulk (e.g., 90 percent) of the annual hardwood production (Birch 1996). Unfortunately, most of the harvesting is done without any forest management plan. Although it is difficult to quantify the amount of timber harvested by regeneration method, common harvest techniques on unmanaged private land include selective cutting or high grading and diameter limit cutting. These rogue harvest practices create small gaps in the overstory canopy, which usually do not favor oak development, especially on the more productive sites. Harvest by these methods often results in understocked stands of reduced quality and value.

With the suppression of wildland fires, wind has become one of the last natural forces capable of altering forest character on a landscape basis (Greenberg and McNab 1998). Wind storms create regeneration opportunities by the windthrow of a single or several overstory trees, or by catastrophic loss of the overstory over larger areas. The small scale disturbances are by far the most common form of wind damage, regardless of forest type. These gaps range in size from 0.01 to 0.1 acre (0.004 to 0.04 ha) (Runkle 1982, 1990, Lorimer and Frelich 1994).

The annual rate of small canopy gap formation in old-growth forests ranges from 0.4 to 2.0 percent for a variety of temperate hardwood forests (Runkle

1990). At these rates of canopy gap formation, complete overstory turnover can occur in < 250 years. For mesophytic hardwood old-growth forests, rotation periods range from 50 to 250 years for disturbances that cause small canopy gaps (e.g., 0.1 acre:0.04 ha) (Table 3). Shade tolerant species dominate regeneration in these small canopy gaps.

Storms such as tornadoes and thunderstorms that cause large scale windthrows are rare. Tornadoes can cause catastrophic damage in forested landscapes, although their damage is usually localized, and effects only a small proportion (e.g., < 0.04 percent) of area in the CHR (Jamison 1978). Thunderstorms can produce severe vertical winds known as downbursts, and multiple downbursts can collectively cause damage over a large forested area. However, the frequency of storms that cause large-scale forest damage is low, resulting in extended rotation periods at the landscape-level (Table 3). Shade intolerant, pioneer species often dominate regeneration in these larger windthrow areas.

Conclusion

Oak species are adapted to thrive in environments characterized by periodic disturbances such as fire, drought and herbivory. Disturbances that cause repeated shoot dieback favor oaks over their competitors. Historically, frequent fires created open forest conditions by limiting the development of a shade tolerant subcanopy and by reducing overstory stocking, which allowed the shade intolerant oaks to persist and grow as large seedling sprouts, and to accumulate as advance reproduction in the understory. Upon subsidence of the disturbance, large oak seedling sprouts grow vigorously and are able to dominate growing space made available by the past disturbance.

Many oak forests have developed shade tolerant understories and increased overstory stocking over the past 70 years of fire suppression. The resulting low light condition at the forest floor limits oak regeneration and promotes the dominance of the shade tolerant species. Subsequent timber harvesting, regardless of method, releases the shade tolerant advance reproduction. In larger harvest areas, fast growing species such as yellow-poplar dominate the regeneration. Oak advance reproduction is either lacking or is too small to compete well.

For thousands of years, humans have been instrumental in creating the disturbances that have favored the development of our oak forests, primarily through the use of fire. More recently, timber harvesting, open range grazing and other commercial uses of the forests have added to the array of disturbances that favor oak dominance. But fire suppression and the virtual elimination of fire from the forests has radically altered forest successional processes to the detriment of oak and the benefit of it's competitors.

Table 3. Rotation periods[a] for wind disturbances in common forest types of the eastern United States. Disturbance type is catastrophic winds that cause stand regeneration unless otherwise noted.

Rotation period in years	Forest/disturbance type	Region	Reference
50 to 250	Old-growth mesophytic hardwoods; small canopy gaps	Eastern U.S.	Runkle 1982, 1990
1,200	Hemlock/white pine/northern hardwoods; more than 2.5 acres	Michigan and Wisconsin	Canham and Loucks 1984
2,900	Hemlock/white pine/northern hardwoods; more than 2,500 acres	Wisconsin	Canham and Loucks 1984
300	Old-growth hemlock/northern hardwoods; disturbance that destroys 30 to 50 percent of canopy	Michigan	Frelich and Lorimer 1991
1,500	Old-growth hemlock/northern hardwoods; disturbance that destroys more than 60 percent of canopy	Michigan	Frelich and Lorimer 1991
5,600-6,000	Old-growth hemlock/northern hardwoods; tornadoes with greater than 75 mile per hour winds	Wisconsin and Michigan	Frelich and Lorimer 1991
1,000-2,000	Hemlock-white pine/northern hardwoods	Pennsylvania and New York	Whitney 1990
2,000	Central hardwoods, tornadoes	Indiana	Whitney 1994

[a] Rotation period is the time required for an area equal to the size of the study area to be affected by a specific disturbance regime. For a given region, it is the inverse of the percentage of area affected on a yearly basis by a specific size and type of disturbance (Whitney 1994).

Planned and repeated human disturbances are necessary to sustain oak forest ecosystems. Silvicultural practices that regulate overstory stocking, limit shade tolerant understories and promote accumulation of large oak advance reproduction are key for the maintenance of forest composition and diversity. Timber harvesting in combination with understory competition control using prescribed fire, herbicides or mechanical cutting can be used to create favorable stand structure for development of oak advance reproduction. Underplanting oak seedlings in shelterwood understories can expedite the development of large oak advance reproduction. Landowners must adopt oak regeneration as a management objective and be willing to invest in appropriate silvicultural practices needed to sustain oak.

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