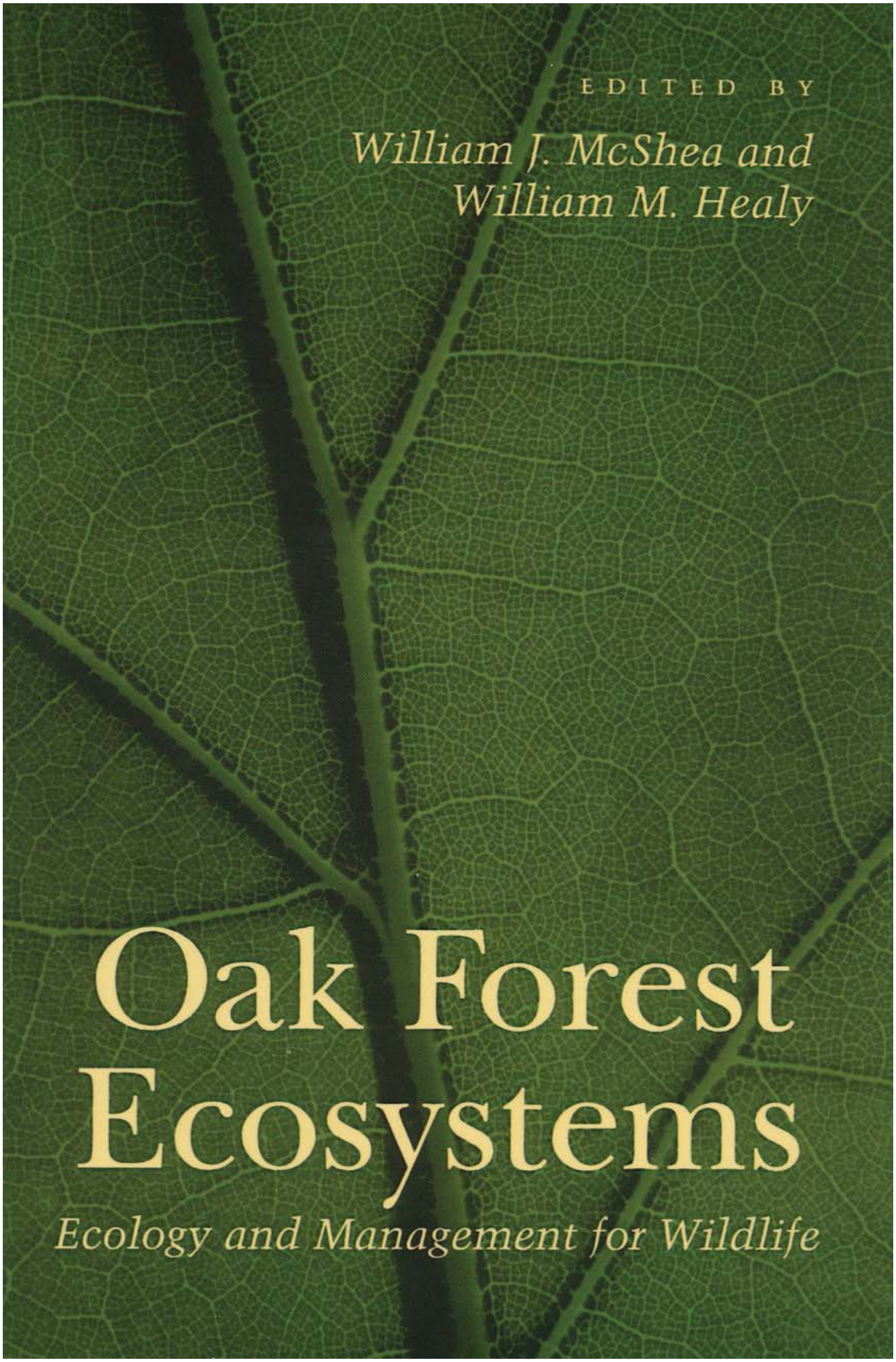

EDITED BY

William J. McShea and
William M. Healy

Oak Forest Ecosystems

Ecology and Management for Wildlife

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Chapter 4

Fire History and Postsettlement Disturbance

DANIEL DEY

Over the past 300 years, forests have undergone dramatic changes, in response to major shifts in disturbance regimes in eastern North America (Orwig and Abrams 1994). Past disturbances were important in the expansion of oaks throughout this region (Nowacki and Abrams 1992). Oak dominance across such a diversity of site types is a legacy of this disturbance history and oak's ability to prosper during periods of disturbance and environmental stress (Hicks 1998). Today's oak forests originated at a time when logging, fuelwood cutting, charcoal production, woods burning, grazing, agriculture, and other anthropogenic disturbances occurred extensively and frequently across the landscape (Nowacki et al. 1990, Abrams 1992, Abrams and McCay 1996). The forest landscape was indelibly altered by a human population that grew exponentially, as did its voracious appetite for food, shelter, and the other amenities of life.

Fire is one of the oldest tools humans have used to manipulate vegetation for the production of food and other plant materials, provision of browse and forage, and to prepare fields for agriculture. Although few fire histories have been documented for eastern oak forests, what we do know is derived from dendrochronological studies of fire scars, pollen and charcoal sediment studies, analyses of early surveyor notes, and reviews of early explorers' and settlers' journals. Disturbance histories are better documented after European settlement.

This chapter highlights what is known about fire history from the late Native American period (circa early 1600s) through European settlement and into the twentieth century. Also covered is the change in human disturbances that occurred when Europeans settled in eastern North America. The nature of human disturbances changed dramatically during the mid-1800s and continues to do so today. The role of fire abruptly diminishes from the 1930s to the 1950s, and fire is replaced by a disturbance regime that is causing the successional replacement of oak-dominated forests in many eastern ecoregions.

USE OF FIRE BY NATIVE AMERICANS

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, Cronon 1983, M. Williams 1989, Delcourt et al. 1993). Indian fires created a mosaic of plant communities quite different from today's landscape. Early explorers and settlers observed a complex, quilt-like pattern of old-growth, open oak, and pine woodlands, oak and pine savannas, prairies, barrens, bald ridges, oak openings, meadows, grasslands, and scrub oak forests throughout eastern North America.

Indian uses of fire favored the widespread dominance of oaks and pines. Repeated burning gave rise to the longleaf pine and mixed southern pine forests; the oak-hardwood forests; the eastern prairies, glades, and barrens; the oak and pine savannas; and the northern pineries. Many forests had an open, parklike appearance because of their long history of fires (Bartram [1791] 1955, Lorimer 1993). In the Cross Timbers region and throughout the Midwest, the cycle of fire determined the balance between tallgrass prairie, oak savanna, oak woodlands, and pine forests (Gleason 1913, Curtis 1959, Grimm 1984, Engle et al. 1996). However, in some regions fire was less common, due to low human population or cultural characteristics of the resident population (e.g., hunter-gatherer versus agrarian societies); and this lower incidence of fire affected forest type by permitting succession to more shade-tolerant and fire-sensitive species. Elements of a fire regime that influence succession include frequency, intensity, seasonality, spatial extent, and type of fire.

During the Native American period, annual fires were common in regions of prairies and oak-pine savannas (M. Williams 1989, Whitney 1994). Fires burned extensively, favoring the eastern extension of grass-dominated ecosystems. Elsewhere, Indians burned berry- and nut-producing areas on a 3-to-5-year basis and woodlands every 10 to 15 years, although there was variation across regions (Table 4.1). In the

Table 4.1
Fire frequency before 1850 for oak-pine-dominated forests in eastern North America

Region	*Mean fire interval (years)*	*Reference*
Missouri Ozarks	2–6	Cutter and Guyette 1994, Guyette and Dey 1997
New Jersey Piedmont	14	Buell et al. 1954
Southeastern United States	2–10	Wright and Bailey 1982
Northeastern United States	1–15	Little 1974
Southern New England	1–10	Niering et al. 1970
Central Ontario	10–17	Dey and Guyette 2000

southeastern Coastal Plain, fires every 2 to 3 years favored longleaf pine forests, but less frequent burning (e.g., every 10 years) led to loblolly pine dominance (Garren 1943).

Frequent fires reduced the density and size of woody species in the understories of oak-dominated and pine-dominated forests, increased the diversity in ground flora, and favored the growth of grasses, legumes, and other herbaceous plants (Garren 1943, Wright and Bailey 1982, Reich et al. 1990, Kruger and Reich 1997a,b). 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, and in prairies, glades, and barrens.

The length of fire-free intervals varied substantially, ranging from 1 to 70 years throughout eastern North America (Harmon 1982, Abrams 1985, Cutter and Guyette 1994, Dey and Guyette 2000). This variability in fire frequency played a critical role in the regeneration and recruitment of species into the overstory, because pines and oaks require a fire-free period to develop sufficient bark thickness to minimize burning injury during the next fire. Species such as oaks that can persist as grubs or stool sprouts during periods of frequent fire are able to produce rapid shoot growth during fire-free periods and thus increase their fire resistance and probability of surviving subsequent fires. Pines can grow rapidly, produce thick bark early, and develop fire resistance quickly during fire-free periods when they grow in low to moderate competition conditions.

Before fire suppression became prevalent, low-intensity fires were common in eastern hardwood forests, occurring every 5 to 15 years (Heinselman 1973, Little 1974, Whitney 1994, Sutherland 1997). Fires of moderate and greater intensity happened less frequently (e.g., every 40–50 years) and coincided with regional or subcontinental drought (Heinselman 1973, Cwynar 1977, Guyette et al. 1995, 1999). Catastrophic fires, intense enough to induce stand replacement, were least common in eastern hardwood forests. The periodicity of such fires is not well documented. Frequent low-intensity fires decreased the probability of stand replacement by fragmenting fuels and limiting fuel loads.

Native Americans often set brush-clearing fires in the spring and fall seasons when dry weather and fine fuels such as grasses, leaf litter, and other herbaceous plant litter made burning easy (Little 1974, Pyne 1982, Cronon 1983). Many of these fires burned at a time of year when plants were dormant. An abundance of fine fuels such as the warm-season grasses, which responded well to frequent burning, made it easier for fires to ignite, and increased the length of fire seasons. In southern regions, where snow cover is intermittent or absent during the winter, burning was done whenever weather and fuel conditions permitted, which might be in any month. In years of normal or above average precipitation, fires were less common during the growing season. In dense forests, summer fires were rare except in years of severe drought, because fires do not spread well in the understory of closed-canopy forests after leaf-out. The chance of growing-season fires increased, however, in drought years and in areas that had extensive stands of warm-season grasses and other herbaceous plants that created a continuous matrix of fine, flashy fuels.

Once ignited, fires usually burned extensively, because there was little to no effort by man to extinguish them. They burned out when they ran into natural fire breaks, the weather changed to rain or snow, or they encountered a less combustible fuel type. Periodically, during subcontinental droughts, fires would burn simultaneously throughout eastern North America. Such a year was 1780, when fires burned large tracts of oak, pine, and mixed hardwoods in Algonquin Park, Ontario, and in the Missouri Ozarks (Guyette and Dey 1995, Guyette et al. 1999).

Fires were common in bottomland areas, and even wetlands burned during drought periods (Whitney 1994, DeBano et al. 1998). Europeans found large prairies and openings along the valleys of rivers such as the Potomac, Rappahannock, Shenandoah, Missouri, and Mississippi, which were the result of Indian fires (M. Williams 1989). George Catlin (1844), who left St. Louis in 1832, recorded extensive fires and expansive prairies and savannas in the bottomlands and surrounding countryside as he traveled the Missouri River to Fort Union.

During the Native American period, most fires in eastern hardwood forests were surface fires (Whitney 1994). In the northeastern northern hardwoods, surface fires were common and caused injury rather than death to mature trees (Stickel 1935). Surface fires also were common in Ontario oak-pine forests (Dey and Guyette 2000) and in the Great Lakes region (Heinselman 1973), where they led to the development of multiaged overstories. Before European settlement, the disturbance regime in oak forests included surface fires that caused noncatastrophic, small-scale mortality of mature trees (Abrams et al. 1995). More severe and even catastrophic fires did occur, however, though less frequently. Fires were more likely to induce stand replacement when they occurred in drought years, or, later in North American history, when they burned after logging on the site.

Fire history in eastern North America has been linked to human history (Pyne 1982, Cronon 1983, M. Williams 1989). Diseases introduced by Europeans decimated Indian populations, often killing upwards of 80% of the people (Delcourt et al. 1993). The frequency of fire was greatly reduced during this period, which may have lasted from 100 to 200 years (Dey and Guyette 2000). Migrating Indian tribes, displaced from their ancestral lands in the East, carried fire into areas of low population as did the vanguards of European settlement. Thereafter, fire's presence and role would be ever changing in eastern North America.

FIRE AND EUROPEAN SETTLEMENT

European settlers continued Indian burning practices but often increased fire frequency and carried fire into more remote areas (Pyne 1982, Cronon 1983, Batek et al. 1999). In general, during the period 1850 to 1930 (somewhat earlier in New England and Atlantic coastal areas), when Europeans were busy converting a North American wilderness into farms and villages, fires were the most frequent in the region's history. At the beginning of the twentieth century, fires burned on average every 5 to 6 years in Ontario oak-pine forests (Howe and White 1913, Dey and Guyette 2000), every 3 to 4 years in southeastern Ohio oak forests (Sutherland 1997), every 10 years in northeast Kansas oak gallery forests (Abrams 1985) and in southern New England (Niering et al.

1970), and every 13 years in oak-pine forests of the Great Smoky Mountains (Harmon 1982). Similar fire frequencies and trends in fire history have been reported for oak woodlands and glades in the Missouri Ozarks (Guyette and McGinnes 1982, Guyette and Cutter 1991, Cutter and Guyette 1994). These estimates of fire frequency are conservative, because not all fires resulted in fire scars on surviving trees.

Fires, and now other forest disturbances such as grazing, logging, and fuelwood cutting, maintained the open, parklike character of eastern forests, with understories dominated by grasses and herbaceous plants (Komarek 1974, Wright and Bailey 1982). Frequent burning, grazing, and logging created forests of sprout origin dominated by oaks. In fact, when much of the area of southern New England, New York, and New Jersey was mapped by Hawley and Hawes (1912), they named it the "Sprout Hardwoods Region."

Fires burned extensively following wholesale logging of the Great Pineries of eastern North America (Howe and White 1913, Kittredge and Chittenden 1929). In the early 1900s, 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 logging and burning also greatly reduced the extent of pine forests in eastern North America. After the mature, seed-bearing pines were harvested, intense slash fires and repeated burnings eliminated or greatly reduced the abundance of pine reproduction. In addition, frequent burning (e.g., every 3 years on average) for up to 100 years before the pine logging era may have eliminated much of the pine advance reproduction (Record 1910, Guyette and Dey 1997). Aspen, white birch, and jack pine replaced the white and red pine forests in the Great Lakes Region (Heinselman 1973). Elsewhere, oaks succeeded the pines and shade-tolerant mesophytic hardwoods (Abrams 1992). Oaks expanded their dominance on mesic, highly productive sites through frequent and widespread burning. The stage was set for a great expansion of oak throughout eastern North America.

The widespread suppression of wildland fires began in the 1930s and 1940s in most regions of eastern North America; however, in the Ozark Highlands and in the South, wildland fires were common until the 1950s (Pyne 1982, Pyne et al. 1996). The occurrence of wildland fires has dropped drastically over the past 100 years. At the beginning of the twentieth century, the fire rotation period was 90 years in Michigan and 50 years in Pennsylvania (Whitney 1994). Before European settlement in the Missouri Ozarks, mean fire intervals averaged about 3 years (Guyette and Cutter 1991, Cutter and Guyette 1994), and the fire rotation period

Table 4.2
Estimated fire rotation periods for the modern period for oak-pine-dominated forests in eastern North America

Region	*Fire rotation period (years)*	*Reference*
Missouri Ozarks	715	Westin 1992
Pennsylvania	910	Whitney 1994
Lower Michigan	1,400 to 2,000	Whitney 1986, 1994
Upper Michigan	1,273[a]; 4,545[b]	Frelich and Lorimer 1991
Smokey Mountains	> 2,000	Harmon 1982
Southern Illinois	900	Haines et al. 1975
Monongahela National Forest, West Virginia	6,000	Haines et al. 1975

[a] For surface fires.
[b] For stand replacement fires.

in the Smoky Mountains before 1940 was less than 10 years (Harmon 1982). Now, the fire rotation period is estimated to be significantly longer (Table 4.2).

At the outset of the fire suppression period, modern oak forests developed rapidly across eastern North America, expanding their range by replacing savannas, barrens, and prairies and dominating old fields and cutover lands. Oak advance reproduction in these systems grew quickly into closed-canopy forests once fires were suppressed (Cottam 1949, Curtis 1959, Grimm 1984).

As fires continue to be suppressed throughout eastern North America, oak forests are being replaced by more shade-tolerant, mesophytic species, such as the maples (Lorimer 1984, Pallardy et al. 1988, Hix and Lorimer 1991, Abrams 1992, 1998). Where fires have been absent, oak forests have increased in structural complexity, and this has been accompanied by the growth of a midstory of shade-tolerant trees and an understory dominated by shade-tolerant shrubs and advance reproduction. In the heavy shade, large oak advance reproduction is unable to develop, and other species dominate following overstory disturbances. However, on xeric pine sites in the southeastern Coastal Plain succession in the absence of fire is to oaks and other southern hardwoods (Garren 1943, Wright and Bailey 1982).

Although wildland fires are less extensive and less frequent than they were just 60 years ago, humans continue to be the most significant source of wildland fires in eastern North America (Guyette et al. 1999). For example, arsonists ignited 47% of all wildland fires that occurred in

Arkansas from 1991 to 1996 (Garner 1999). These fires accounted for 64% of the total acreage of burned wildland. Another 27% of Arkansas's wildland fires were started by humans burning debris. Nationally, arson and debris burning accounted for 74% of wildland fires from 1983 to 1987 (Garner 1999). On the other hand, lightning caused less than 2% of all fires in Arkansas (1991–96) (Westin 1992, Garner 1999). In the East, most lightning occurs during thunderstorms and is accompanied by rain, which reduces the likelihood of fire ignition or spread. Outside the southeasternmost portion of the United States, lighting causes fewer than 5 fires per million acres in eastern North America. Throughout the Mid-Atlantic and Midwest less than 1 fire per million acres results from lightning.

AGRICULTURAL AND INDUSTRIAL TRANSFORMATION PERIOD

Forest clearing for agriculture was the primary cause of deforestation in eastern North America (Whitney 1994). Only 10%–30% of the forest remained in southern New England by the mid-1800s; coastal forests had been cleared much earlier (Niering et al. 1970). As settlers moved into the Ohio Valley, they established farms until, by 1900, most (85%) of the land had been cleared (Sutherland 1997). Similar events played out in the Lake States (Pyne et al. 1996) and the Southeast (Martin and Boyce 1993). From 1860 to 1910, the rate of conversion to agriculture accelerated such that more forests (190 million acres) were converted during this period than in all previous time since European arrival in North America (M. Williams 1989, Powell et al. 1993). Since the 1850s, forest clearing and drainage of wetlands for agriculture have caused the loss of 70%–98% of bottomland forests in the United States (Sharitz and Mitsch 1993).

During this agricultural revolution in North America, fire was used by settlers to clear forests, maintain farm and pasture, and improve the woods for grazing, as the Indians had done but on a much grander scale. Forests were further disturbed by cattle and hogs, who grazed freely everywhere Europeans settled (Cronon 1983, M. Williams 1989, Whitney 1994). Grazing on open range was practiced in many regions (e.g., Ozark highlands) as late as the 1950s and 1960s. Livestock grazing affected forest regeneration, often eliminating it in the understory of woodlands and savannas.

Locally throughout the range of the oak, the production of charcoal for the iron industry affected the surrounding forests. Forest harvesting for charcoal peaked in the late eighteenth century in the Piedmont and Coastal Plain regions (Orwig and Abrams 1994) and later in the nineteenth century in the Midwest and Northeast (Sutherland 1997). Forests were harvested on short rotations (e.g., 20–30 years) and fires fueled by logging slash burned with greater intensity (Cronon 1983, M. Williams 1989, Whitney 1994). These practices created coppice forests dominated by oaks (Clatterbuck 1991, Orwig and Abrams 1994).

Industrial logging transformed the forests of eastern North America during the period from 1850 to 1930. Forest harvesting had previously been a local activity to supply the timber and fuelwood needs of nearby villages and specialty products sought by foreign sovereigns (e.g., masts for British sailing ships). Small populations and primitive transportation systems limited the need and the ability, respectively, to lumber extensively. Timber was transported by log drives down rivers that had connections to ocean ports. Not until railroads were built into the more remote forested regions were many forests linked to population centers. This set the stage for the wholesale logging and "destruction" of eastern North America forests documented in Ontario (Howe and White 1913), the South (Martin and Boyce 1993), the Lake States and Northeast (Cronon 1983, M. Williams 1989), the Ozarks (Cunningham and Hauser 1989), and the central hardwood region (Hicks 1998). Beginning in 1850, the annual production of forest products increased markedly; in 1910 an estimated 13 billion cubic feet of timber were harvested (Powell et al. 1993). Repeated and often catastrophic fires burned the cutover forests. The forests had never before experienced disturbances of such extent or severity. Far from being destroyed, the forests renewed themselves, although they changed in character. This logging and fire history favored the oaks, which rose like the phoenix out of the ashes to assume widespread dominance throughout eastern North America.

Much of the eastern forests have developed on agricultural land abandoned during the late 1700s in the Northeast, Mid-Atlantic, Piedmont, and Coastal Plain, and later in the Midwest, Lake States, and other interior regions. The regrowth of forest on agricultural lands accelerated during the Great Depression. Often, these forests were dominated by pine and oak (Orwig and Abrams 1994). Oak seedlings and grubs sprouted in pastures and, in the absence of mowing or grazing, grew to maturity. Elsewhere, stands dominated by pine provided ideal conditions for oaks to establish and grow in the understory, setting the stage for oak dominance after the pine was harvested. As agricultural land was abandoned throughout the Midwest, Lake States, and Southeast, the amount of forest land increased.

In some places, forest cover has increased to levels approaching that seen by the first European settlers. Current forest acreage in eastern North America equals about two-thirds of the forest area estimated to have existed in the 1600s. In the unglaciated plateau in Ohio, forest cover has increased from 15% to 65% over the past 100 years (Sutherland 1997), and Vermont has gone from being 65% cropland in 1850 to 77% forested today (Powell et al. 1993). Since 1907, the extent of forest land in the United States has stabilized at 730–760 million acres. The change in proportions is due largely to a cessation of forest clearing for agriculture (Powell et al. 1993). Deforestation in the lower Mississippi River bottomlands continues today, however (Sharitz and Mitsch 1993).

Europeans brought to the New World insects and diseases that have affected forest composition and succession over large areas. One of the most notable examples was the introduction of the chestnut blight (*Endothia parasitica* [Murrill] P. J. Anderson and H. W. Anderson), which eliminated chestnut as a major overstory species in eastern North America by the early 1900s. Oak dominance increased after the loss of chestnut in the Appalachian and mid-Atlantic regions (Hinkle et al. 1993, Abrams and McCay 1996, Hicks 1998). Chestnut oak, red oak, and scarlet oak replaced chestnut. The introduction of exotic species and the spread of invasive species will continue to modify natural forest succession and alter native forest character (see Chapters 6 and 7).

Forest product manufacturing in the United States declined from 1910 until after World War II, when a boom in the housing market sparked an increase in harvesting (Powell et al. 1993). Since then, production has increased (see Figure 4.1), resulting in historic levels of harvesting, but annual growth of hardwoods in the East still exceeds timber removals (e.g., by 80% in 1991). In the eastern United States, most (94%) of the 380 million acres of forest land is timberland; this proportion has been relatively constant since the early 1950s (Powell et al. 1993). About half of the eastern forest land is classified as oak-pine (32.2 mill. a.), oak-hickory (129.7 mill. a.), or oak-gum-cypress (29.2 mill. a.) forest type, and the largest areas of highly productive (> 120 cu. ft. per acre per year) forest lands occur in the oak-hickory and loblolly-shortleaf pine types. Most of the timberlands in the East are owned by private

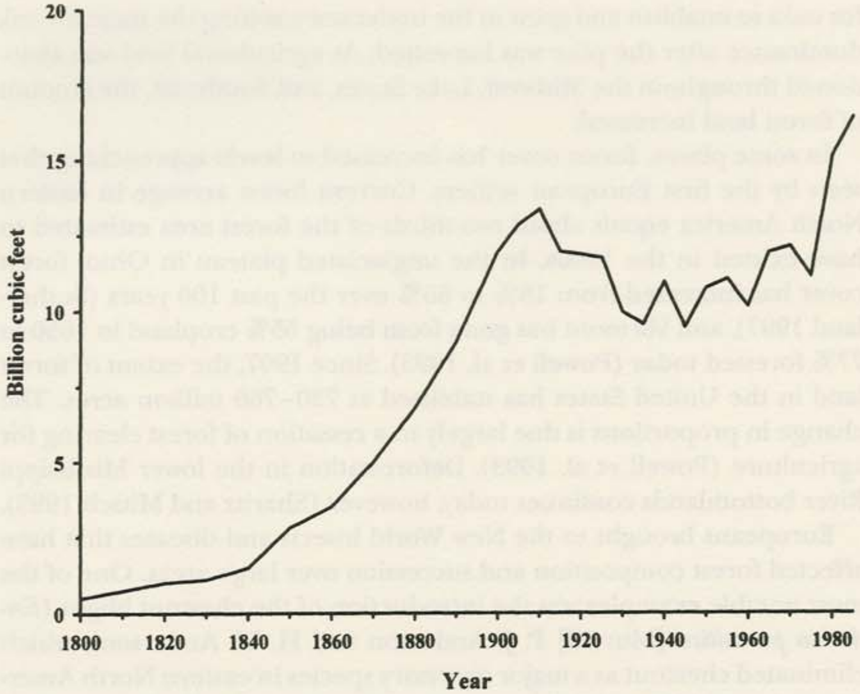

FIGURE 4.1. Domestic production of forest products from 1800 to 1985 in the United States. (Adapted from Powell et al. 1993.)

industry (16%) and nonindustrial private individuals (70%), and they are primarily responsible for the hardwood harvest (e.g., 90% of the hardwood production in 1991).

Unfortunately, written management plans have been used by only an estimated 5% of private forest land owners, who control 39% of the private forest lands (Birch 1996). More than half of all private forest lands have no management plans. Although it is difficult to quantify the amount of timber harvested by regeneration method, common harvesting techniques on unmanaged private land include selective cutting or high grading and diameter limit cutting. These rogue harvesting practices create small gaps in the overstory canopy, which usually do not favor oak development, especially on the more productive sites. Harvesting by these methods often results in understocked stands of reduced quality and value.

WIND DISTURBANCES

Wind has contributed to the overall level of damage to forests, acting in concert with fire, logging, grazing, and other disturbance factors. Since the suppression of wildland fires, wind is the most common natural force capable of altering forest character on a landscape basis (Greenberg and McNab 1998). Humans have had little direct effect on the extent and intensity of wind storms. They have, however, substantially affected the importance of wind disturbances, by altering the type and distribution of forests. For example, much of the original old-growth forest lands that stood at the time of European settlement have been converted to agricultural uses or been harvested to produce younger forests, which are more resistant to damage by wind (Oliver and Larson 1990, Kozlowski et al. 1991). In contrast, high-grade logging and reckless woods burning have increased the amount of decay in hardwood forests (e.g., 37% of the live volume in Missouri is cull) rendering trees more susceptible to windthrow (Powell et al. 1993). Wind storms have been and continue to be an important forest disturbance, altering forest dynamics by creating small gaps in the canopy by the windthrow of a single or several overstory trees or by causing catastrophic extensive loss of the overstory (Lorimer 1980, Myers and Van Lear 1998).

Storms that cause large-scale windthrows generally are rare (Table 4.3). Because large-scale catastrophic wind disturbances are less frequent than those that cause small canopy gaps, much emphasis has been placed on the importance of small-scale disturbances in determining forest succession, structure, and diversity in mesophytic forests of the East. Large infrequent disturbances such as catastrophic wind storms and fires, however, are receiving more recognition for their role in shaping the regional landscape and their ability to influence ecosystem processes for centuries (Lorimer and Frelich 1994, Foster, Knight, and Franklin 1998).

CONCLUSION

The abundance, diversity, and extent of eastern forests, savannas, and prairies are intricately linked to human disturbances, demography, and culture. Humans have been one of the most dominant and influential agents of forest disturbance over the past millennium. Fire is one of humankind's oldest and most reliable tools for culturing vegetation. Fre-

Table 4.3
Rotation periods for wind disturbances in common forest types of the eastern United States

Rotation period (years)	*Forest type*	*Disturbance type*[a]	*Region*	*Reference*
110–125	Old-growth mesophytic hardwoods	Small canopy gaps	S.W. Ohio	Runkle 1990
50–200	Old-growth mesophytic hardwoods	Small canopy gaps	Eastern U.S.	Runkle 1985
50–250	Old-growth mesophytic hardwoods	Small canopy gaps	S. Appalachian	Runkle 1982
541	Presettlement; hemlock-northern hardwoods	—	U.P. Michigan	Zhang et al. 1999
1,200	Presettlement; hemlock–white pine–northern hardwoods	Catastrophic wind	Michigan	Whitney 1986
1,300	Presettlement; swamp conifer	—	Michigan	Whitney 1986
1,500	Old-growth hemlock–northern hardwoods	Disturbance that destroys >60% of canopy	U.P. Michigan	Frelich and Lorimer 1991
5,600	Old-growth hemlock–northern hardwoods	Tornadoes >75 mph winds	U.P. Michigan	Frelich and Lorimer 1991
300	Old-growth hemlock–northern hardwoods	Disturbance that destroys 30–50% of canopy	U.P. Michigan	Frelich and Lorimer 1991
6,031	Old-growth hemlock–northern hardwoods	Tornadoes >75 mph winds	N. Wisconsin	Frelich and Lorimer 1991
1,210	Presettlement; hemlock–white pine–northern hardwoods	Catastrophic wind >2.5 acres	N. Wisconsin	Canham and Loucks 1984
1,238	Presettlement; hemlock–white pine–northern hardwoods	Catastrophic wind >25 acres	N. Wisconsin	Canham and Loucks 1984
1,470	Presettlement; hemlock–white pine–northern hardwoods	Catastrophic wind >250 acres	N. Wisconsin	Canham and Loucks 1984
2,903	Presettlement; hemlock–white pine–northern hardwoods	Catastrophic wind >2,500 acres	N. Wisconsin	Canham and Loucks 1984
540	Old-growth hemlock–northern hardwood	—	N.W. Pennsylvania	Whitney 1994
1,000–2,000	Hemlock–white pine–northern hardwoods	—	N.W. Pennsylvania	Whitney 1990
9,000	Northern hardwoods	—	Central New York	Marks et al. 1992
2,000	Hemlock–northern hardwoods	—	W. New York	Seischab 1990
1,150	Northern hardwoods–spruce–fir	—	N. Maine	Lorimer 1977

[a] Unless otherwise noted, disturbance type is catastrophic winds that cause stand regeneration.

quent burning by Indians promoted nut- and berry-producing trees and shrubs and bountiful grasslands. At the landscape level, anthropogenic fire produced a mosaic of fire-dependent ecosystems. European settlers noted extensive eastern prairies, oak openings, meadows, orchards, barrens, and oak and pine forests and savannas.

Europeans imposed a new and unique suite of disturbances that changed the nature and distribution of the ecosystems they encountered in North America. Conversion of forest, prairie, and wetland to agriculture, along with commercial logging, forest grazing, and woods burning, changed the landscape in a way and at a rate unparalleled in recent history. Following the exploitation phase of European settlement, forests reclaimed abandoned farmland, invaded former prairies, and regenerated lands that had been cutover and repeatedly burned. On these lands, as a consequence of fire prevention and suppression programs that abruptly removed fire as a primary forest disturbance, oaks dominated the regeneration. We are just now beginning to witness the long-term effects of these major shifts in disturbance regimes and to recognize the ecological role of fire in the maintenance of many of our forest ecosystems.

Modern oak forests are a product of this disturbance history, because trees are relatively long-lived and processes such as succession are long-term. Previous disturbances set successional pathways that led to oak dominance because oaks are well adapted to high disturbance and stress environments where fire, drought, grazing, and logging occur periodically. In turn, current disturbance regimes are shaping the nature of future forests. Disturbance regimes characterized by less frequent, intense, or extensive burning, and less harvesting and grazing promote competitors of oak, especially on productive sites where environmental conditions are less limiting to tree growth.

In the past, wind and fire acted together to favor oak. Today, wind promotes succession to oak's competitors in the absence of fire. Succession following small gap disturbances favors shade-tolerant species, and catastrophic windthrow promotes fast-growing intolerant species at the expense of oaks.

Knowledge of historical disturbance regimes is important, because modern oak forests originated at a time when fire, logging, and other human disturbances were more common than they are today. A study of the fire ecology and disturbance history of oak and its associates can provide an understanding of the widespread occurrence of oak, and establish a basis for management strategies to restore and sustain oak ecosystems.

Chapter 5

The Ecological Basis for Oak Silviculture in Eastern North America

DANIEL DEY

Quercus is a dominant genus throughout North America and has been for the past 10,000 years or more (see Chapters 2 and 3). Oak distribution has shifted in response to changes in climate, disturbance regime, and human population and culture. Oak dominance has increased throughout the Holocene period. However, a recent successional trend is the replacement of oak-dominated ecosystems throughout the range of oak.

The inability of oak reproduction to compete with either large shade-tolerant advance reproduction or aggressive pioneer species is the fundamental cause of problems in oak regeneration and sustainability (Lorimer 1993). Oak regeneration problems and reductions in oak stocking are most likely on higher-quality mesic sites (site index > 60 feet, base age 50). Oaks appear to be successionally most stable on xeric sites, under current disturbance regimes, which are typified by frequent small-scale disturbances that cause isolated mortality to overstory trees and the absence of fire (Johnson 1993a). However, increased competition from shade-tolerant trees and shrubs threatens oak regeneration potential even on these drier sites.

Oaks are adapted to environments characterized by disturbance and stress. The primary factor leading to the successional displacement of oak in eastern North America 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 the invasion and population of America by Europeans (Abrams 1992). Since the 1930s, fire suppression has nearly eliminated wildfire as a forest disturbance. This drastic reduction in fire frequency is the most often cited cause of the recent oak regeneration problem, especially on high-quality sites (Little 1974, Van Lear 1991, Lorimer 1993).

It appears that, under current disturbance regimes and without human intervention through management, oak dominance will be increasingly confined to the less productive sites. The more productive sites will succeed to other species, with a possible loss of the species diversity and mast production that are important to so many wildlife species (see Chapters 14–17). Sustainable management of oak dominated ecosystems is predicated on an understanding of oak silvics, regeneration ecology, and response to disturbance. This chapter describes some of the more important ecological requirements of oaks, their responses to disturbances, and their competitive relationships with co-occurring tree species.

LIGHT RELATIONS

Inadequate light often limits oak regeneration and recruitment into the overstory (Lorimer 1993). Oak is much less shade tolerant than many of its competitors (see Table 5.1). Acorn germination and initial seedling development are not limited by light levels, because the seed is relatively large and supplies the bulk of the carbohydrates for growth until seed reserves are exhausted.

Growth and survival of oak in shaded microsites depend upon photosynthetic CO_2 fixation exceeding the respiratory requirements of seedlings, that is, net photosynthesis > 0 (Figure 5.1). The minimum light level required by oak seedlings to produce enough carbohydrate to meet their respiration needs (i.e., the light compensation point, where net photosynthesis $= 0$) is low, about 2% to 5% of full sunlight for northern red oak (Gottschalk 1987, Hanson et al. 1987). With higher levels of photosynthetically active radiation, net photosynthesis increases to a saturation point at which it remains relatively stable with further increases in light intensity.

Although survival of oak seedlings at low light levels may be possible, sufficient carbohydrate to support the production of new tissue requires

Table 5.1
Shade tolerance in oak species and common competitors

Oak species	*Shade tolerance*	*Competing species*	*Shade tolerance*
Bear	Very intolerant	American beech	Very tolerant
Black	Intolerant–intermediate	American elm	Intermediate
Blackjack	Intolerant	Black cherry	Intolerant
Bur	Intermediate	Black gum	Tolerant
Cherrybark	Intolerant	Black locust	Intolerant
Chestnut	Intermediate	Box elder	Tolerant
Chinkapin	Intolerant–intermediate	Cucumber tree	Intermediate
Laurel	Tolerant	Eastern cottonwood	Very intolerant
Live	Intermediate	Eastern hop hornbeam	Tolerant
Northern pin	Intolerant	Flowering dogwood	Very tolerant
Northern red	Intermediate	Green ash	Tolerant
Nuttall	Intolerant–intermediate	Hackberry	Intermediate
Overcup	Intolerant–intermediate	Pin cherry	Very intolerant
Pin	Intolerant	Quaking aspen	Very intolerant
Post	Intolerant	Red maple	Tolerant
Scarlet	Very intolerant	Silver maple	Tolerant
Shingle	Intolerant	Sourwood	Tolerant
Shumard	Intolerant	Southern magnolia	Tolerant
Southern red	Intermediate	Striped maple	Very tolerant
Swamp chestnut	Intolerant–intermediate	Sugar maple	Very tolerant
Swamp white	Intermediate	Sweet birch	Intolerant
Turkey	Intolerant	Sweetgum	Intolerant
Water	Intolerant	Water tupelo	Very tolerant
White	Intermediate	White birch	Intolerant
Willow	Intolerant	Yellow-poplar	Intolerant

Sources: Adapted from Burns and Honkala 1990, Smith 1993.

greater light. Light saturation of photosynthesis in oak seedlings (e.g., northern red oak and cherrybark oak) occurs at 30% to 50% of full sunlight (Teskey and Shrestha 1985, McGraw et al. 1990, Ashton and Berlyn 1994). Growth in height and diameter is near maximum at light intensities approaching 50% to 70% of full sunlight (Hodges and Gardiner 1993, Gottschalk 1994). In contrast, shade-tolerant species (e.g., red maple and beech) show maximum net photosynthesis at light intensities as low as 5% to 10% of full sunlight, and they have better whole-plant carbon balances in low light than less tolerant species such as the oaks (Bazzaz 1979, Kozlowski et al. 1991). Shade-intolerant species require full sunlight for light saturation of net photosynthesis, which promotes maximum growth rates that exceed those in oak.

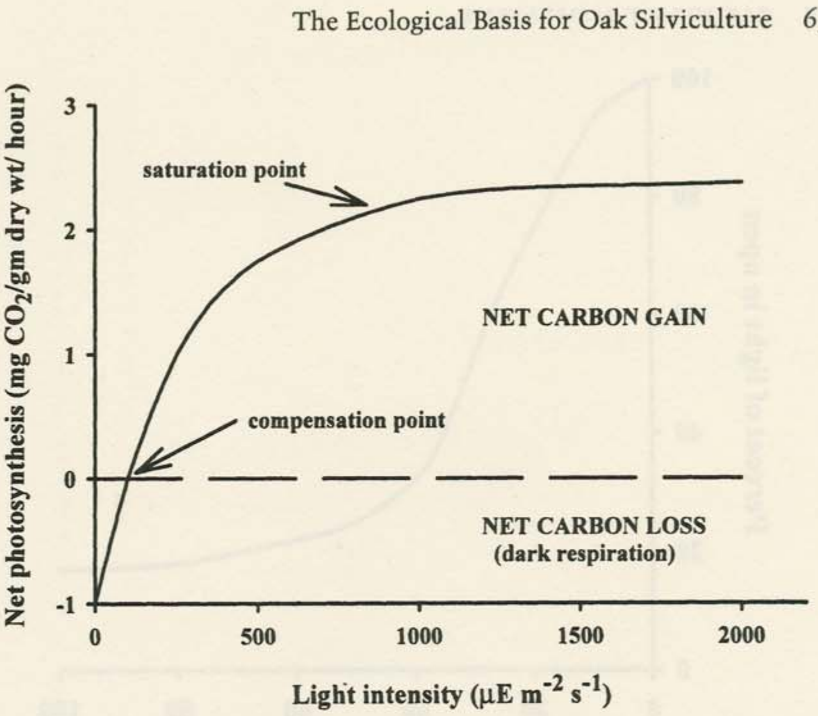

FIGURE 5.1. Relationship between rate of net photosynthesis and light intensity.

Response of Understory Light to Overstory Manipulation

Oak reproduction rarely persists long or grows much in the understory of mature hardwood forests, because the light intensity is usually less than the light compensation point for oaks (Canham et al. 1990). Dense overstory cover and subcanopies of trees and shrubs intercept most of the sunlight.

The amount of light after harvesting does not increase in linear proportion with the amount of canopy removed (Figure 5.2). Shelterwood harvests in northern hardwoods need to remove more than 50% of the basal area to increase light intensities at the forest floor to 35% to 50% of full sunlight (Marquis 1988, Dey and Parker 1996). In group selection harvests, light levels rise at an increasing rate as the size of canopy gap increases until a threshold gap-size is reached. Light increases in the center of gaps as the ratio of gap diameter (d) to the average height of the

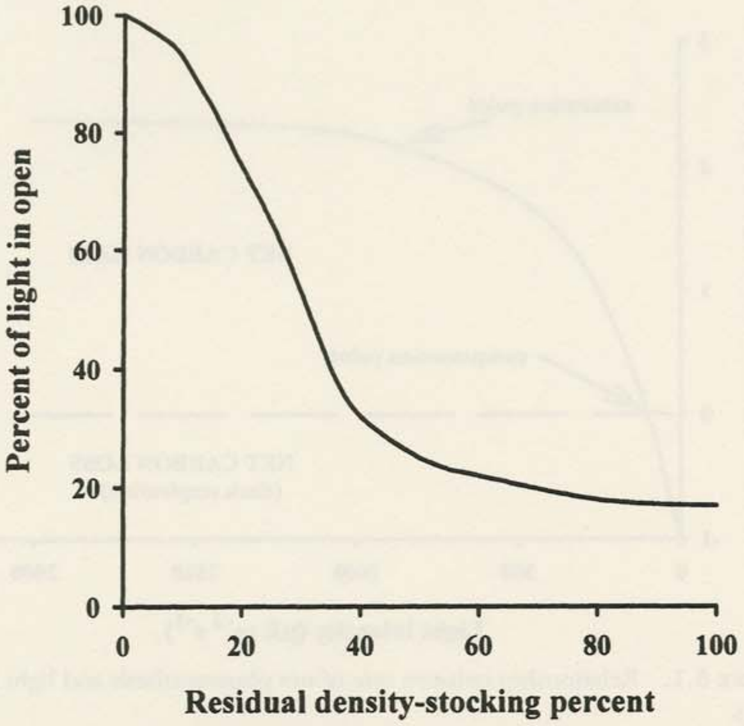

FIGURE 5.2. The effect of residual overstory stocking on light intensity 8 inches above the ground in the central hardwood forests. The absolute values may change for forests at different latitudes, but the general relationships remain the same. (Adapted from Sander 1979.)

adjacent stand (h) increases, leveling off when d/h approaches 2.0 (Minckler et al. 1973). In openings of any size, light increases from the edge of the gap to the center. Whether shelterwood or group selection methods are used to increase light for oak reproduction, understory strata of shade-tolerant species must be controlled for oak reproduction to benefit fully from reductions in overstory density.

Light and Regeneration Methods

Regeneration methods from single-tree selection to clearcutting can be used to create canopy gaps ranging from the smallest of openings (i.e., a single-tree gap) to the largest of disturbances (several acres or more), which have much the same effect as natural disturbances on forest structure. The single-tree selection method produces understory light levels that are similar to unmanaged, mature hardwood stands. Shade-intolerant and intermediate species can germinate under heavy shade, but understory light levels are often insufficient for their long-term survival. Shade-tolerant species such as sugar maple and beech can survive in low light (e.g., < 5% of full sunlight) for decades, and respond to release following reduction in overstory density (Poulson and Platt 1989). In this manner, they can grow into the overstory through repeated cycles of suppression and release (Canham 1985). Therefore, shade-tolerant species have the competitive advantage over oaks in stands managed by the single-tree method or that experience other small-scale canopy gap disturbances (Jenkins and Parker 1998).

Group selection harvesting has been used to increase understory light levels to encourage regeneration of species of intermediate shade tolerance. However, these openings are often dominated by large shade-tolerant advance reproduction (Canham 1988, 1989, H. C. Smith 1981) or by yellow-poplar (Weigel and Parker 1997, Jenkins and Parker 1998), because competing vegetation is not controlled and oak advance reproduction is lacking before harvest. Oak advance reproduction grows well in gaps if it receives 20% to 50% of full sunlight, which occurs in gaps with a d/h ratio equal to 1.0 (Marquis 1965). Large stems of shade-tolerant species may need to be felled during harvest to permit adequate light at the forest floor. Once reproduction is established, larger openings are better for oaks, especially if future harvesting will be delayed. In larger openings, postharvest treatments to control competing vegetation may be necessary to maintain oak dominance, especially when yellow-poplar is present (Brose and Van Lear 1998).

The shelterwood method is often recommended for promoting oak regeneration. Factors common to the successful use of this method for regenerating oak include the presence of oak advance reproduction before harvest, control of competing woody vegetation, and reduction of overstory density to moderate levels. Shelterwoods can be used to produce a wide range of environments for regeneration. The overstory may need to be reduced to 40%–60% stocking and any shade-tolerant midstory canopy removed to provide sufficient light for oak reproduction (Schlesinger et al. 1993, Lorimer et al. 1994). Higher overstory densities can be maintained without adversely affecting the growth of oak seedlings when understory competition is controlled. On higher-quality sites, control of understory competing vegetation is particularly important, as is the maintenance of higher residual shelterwood density to help control oak competitors (Loftis 1990a). However, residual overstory densities with more than 70% of crown cover or > 60 square feet per acre basal area limit oak seedling growth and survival (Larsen et al. 1997).

MOISTURE RELATIONS

The oaks as a group are quite tolerant of drought, primarily because they have large root systems, leaf morphological characteristics that reduce transpiration, and the ability to maintain gas exchange and net photosynthesis to comparatively low levels of leaf water (Abrams 1990, Pallardy and Rhoads 1993). The development of a strong taproot system in oaks provides them access to moisture from deep soil layers, a source less available to their more shallow-rooted competitors. The oaks are better adapted to xeric environments than many of their common mesophytic competitors. Although northern red oak is one of the least drought tolerant of the upland oaks of eastern North America (Seidel 1972, Kleiner et al. 1992), it is still more adapted to drought than many species, such as aspen, white birch, dogwood, black cherry, and maple (Bahari et al. 1985, Martin et al. 1987, Abrams 1990). Among the oaks, those species found on xeric uplands (e.g., post oak and blackjack oak) are more drought tolerant than the more mesic species (e.g., northern red oak) (Reich and Hinckley 1980, 1989).

Despite their adaptations to drought, oaks are still subject to injury from water stress. Drought can cause declines in leaf gas exchange, dysfunction of their xylem water transport system, decreases in shoot and root growth of seedlings, and increases in the risk of mortality (Kozlowski et al. 1991, Tyree and Cochard 1996). Under water stress, oak seedlings exhibit lower leaf area and new root production, delayed bud break, reduced shoot elongation, and increased shoot dieback, and they produce less xylem tissue and fewer and smaller vessels.

Moisture and Regeneration Methods

Surface soil moisture is important to seed germination and early seedling establishment. Adequate surface moisture is needed until seedling roots can obtain moisture from the lower soil zones. High evaporation rates in recently clearcut and large group selection openings dry the upper few inches of the soil and cause high mortality in young seedlings. A shelterwood overstory produces more favorable surface soil moisture conditions through increased canopy throughfall of precipitation and reduced overstory transpiration (Minckler et al. 1973, Crunkilton et al. 1992, Breda et al. 1995). Advance reproduction and stump sprouts are better able than seedlings to access moisture in the lower soil horizons, because they have well-established root systems. Compared to seedlings, they have better water relations under drought conditions and are better adapted to survive the high summer temperatures and vapor pressure deficits common in clearcut environments. Moisture throughout the soil profile, however, is generally lower for longer periods in fully-stocked, mature forests than in larger clearcut or group selection openings (Bormann and Likens 1979, Kramer and Boyer 1995).

REGENERATION

Potential for Regeneration

Regeneration potential refers to the ability of trees, from seedlings to mature individuals, to contribute to stand regeneration through sexual or vegetative reproduction (Johnson 1993a). Mature trees may produce seed and contribute to the regeneration potential by adding to the population of new seedlings or by increasing the storehouse of seed in the forest floor. Reproduction may also arise from dormant or adventitious buds that sprout after shoot injury or death in overstory and understory trees.

In many hardwood ecosystems, the flora present at the time of disturbance control to a significant extent the future composition and structure of the ecosystem. In other words, the capacity of a species to regenerate and dominate the growing space made available by a stand-initiating disturbance is determined by the characteristics of the parent stand (Loftis 1990a, Dey et al. 1996). For example, the amount of seed produced is strongly influenced by the basal area of the species in the upper-crown classes of the parent stand (Bjorkbom 1979). Similarly, the abundance and size of advance reproduction are related to overstory characteristics, including species composition, density of mature trees, and stand structure (Bjorkbom 1979, Johnson 1992, Larsen et al. 1997). Characteristics of the understory vegetation such as the abundance, size and composition of advance reproduction significantly influence species dominance after stand-initiating disturbances (Sander 1971, Loftis 1990a, Dey et al. 1996).

The regeneration potential of a stand, therefore, is a measurable and predictable attribute (Dey 1993). For oaks and other hardwoods, it can be determined from predisturbance characteristics, including the advance reproduction and the overstory. To quantify the regeneration potential of a stand, the various sources of reproduction must be considered. Oaks and other hardwoods regenerate as new seedlings, seedling-sprouts, and stump or basal sprouts from overstory trees.

Reproduction by Seed

Most oak seedling establishment occurs in years of good acorn production (Lorimer 1993). Seed production is highly variable among oak species, between individual trees, over the years, and from one location to the next. For all oak species, some trees are consistently good producers and others are consistently poor producers. Ability to produce acorns is most often attributed to the genetic capability of the tree. However, other factors, such as weather, insects, soil fertility, stand density, diseases, and wildlife, are also important in determining the size and frequency of acorn crops. In the long term, tree characteristics such as size, crown area, crown class and age, and genetics are probably more important than environmental factors in determining acorn production (Beck 1993). In general, oaks have large seed crops at 2- to 10-year intervals.

Acorns must maintain relatively high seed-moisture content to remain viable. Seed viability drops rapidly when moisture content falls below 30% to 50% for species in the white oak group and 20% to 30% for those in the red oak group (Korstian 1927). On the ground, dessication can cause rapid deterioration of acorns. Much of the seed that escapes predation by insects, birds, and mammals fails to produce seedlings because of low seed-moisture content. Thus, acorns do not remain in the forest floor seedbank for more than a year. Acorns that are buried 2.54 cm to 5.08 cm in the soil and those in contact with mineral soil beneath the leaf litter show the best germination. The presence of a litter layer, provided that it is not too thick (i.e., > 5 cm), protects acorns from desiccation and extreme fluctuations in temperature. Thick litter layers present a physical barrier to the radicle's reaching mineral soil, and acorns mixed with or on top of leaf litter are more likely to suffer desiccation than those in contact with mineral soil.

In areas of persistent snow cover, acorns stand a better chance of surviving the winter, because conditions under the snow cover are ideal for stratification and storage of acorns. In regions lacking snow cover, acorns are exposed to sun, wind, and often to warm temperatures throughout the winter months. White oaks, which germinate in the fall, are less susceptible to desiccation than red oaks, but either seed or germinants can dry out over winter and early spring if they are not protected by a covering of litter and soil.

The use of fire to reduce litter depth usually is not necessary for oak regeneration except on high-quality sites (Stringer and Taylor 1999). Fires that burn after seed dispersal cause high mortality in acorns that are on the forest floor or mixed in the upper litter layers (Auchmoody and Smith 1993). Acorns buried under moist litter layers or in mineral soil are better protected from the heat of surface fires. Oak seedlings germinating from acorns that survive burning may benefit from increased availability of nutrients, reduced competition, and higher light intensity. However, fire can also enhance the germination and establishment of oak competitors, such as sweetgum, pin cherry, yellow-poplar, and *Rubus* (Shearin et al. 1972, Little 1974, Van Lear and Waldrop 1988, Kruger and Reich 1997a,b).

Acorns provide food for hundreds of animal species, and in the process of storing acorns, a few birds and mammals become important in seed dispersal (see Chapter 12). In years of low to moderate acorn production, wildlife and insects can consume or damage the entire seed crop, thus reducing or eliminating seedling establishment for that year (Beck 1993). Periodic surface fires may benefit oak regeneration, because fire temporarily destroys the habitat of small mammals and insects and may reduce populations of acorn insects (Wright 1986, Galford et al. 1988). However, wildlife that store, or "cache," acorns in the soil to provide a winter food source can improve the regeneration of oak by their "planting" of acorns. Burial of acorns in the soil or beneath the litter layer protects the seed from desiccation, from further predation or damage by other animals, and from disturbances such as fire (Barnett 1977, Auchmoody et al. 1994).

Reproduction by Seedlings

Shoot growth of oak seedlings is relatively slow, because oak seedlings possess moderate leaf photosynthetic capacity, relatively thick leaves, and preferential carbon allocation to the roots (Kolb and Steiner 1990, Walters et al. 1993). Suboptimal environmental conditions also slow shoot activity and trigger an allocation of current photosynthate to the roots.

This carbohydrate both supports continued root growth and is stored in the taproot for future use in shoot growth.

For most oak species, slow height growth relative to that of competing vegetation is the most often cited cause of oak regeneration failure, especially on high-quality sites (Lorimer 1993). In the open, young oak seedlings are at a competitive disadvantage when growing with large advance reproduction of shade-tolerant species (e.g., maples) and shade-intolerant reproduction such as yellow-poplar. In mesic and hydric ecosystems, oak species such as northern red oak and water oak can be regenerated successfully from seed if there is an abundant acorn crop and a low to moderate level of competition at the time of overstory removal (Johnson and Jacobs 1981, Loewenstein and Golden 1995). More frequently, intense competition and a lack of acorns or advance reproduction result in oak regeneration failures on these sites.

The preferential maintenance of root growth over shoot growth is an important ecological adaptation that enables oaks to dominate on xeric sites and to persist in high-disturbance environments. A competitive rate of growth for oak reproduction depends on the development of seedlings with a large, physiologically vigorous root system and high root-to-shoot ratio (Johnson 1993a). The number of sprouts, shoot growth, and probability of multiple shoot flushes increase with increasing root mass or its correlate, basal diameter of the stem (Johnson 1979, Dey et al. 1996, Dey and Parker 1997). A large root system provides carbohydrates, water, and nutrients in amounts required to produce new shoots capable of rapid growth after release from overstory cover.

Reproduction by Seedling Sprouts

Seedling sprouts arise from vegetative propagation of seedlings that experience shoot dieback. Shoot dieback releases dormant buds from apical growth hormones, and sprouts begin to grow from buds located under the bark along the stem and clustered near the root collar (Kozlowski et al. 1991). Oaks are better adapted than many of their competitors to disturbances or environmental stresses that cause shoot dieback; they can repeatedly produce new sprouts from their large supply of dormant buds located at the root collar, which is often beneath the soil surface, where buds are protected from fire and herbivores. Oaks that suffer serious injury to their shoots compartmentalize the damaged tissue and do not allocate resources toward the recovery of photosynthesis in that tissue. Instead, they reallocate resources to the production of new sprouts when environmental conditions become more favorable or after the disturbance-induced shoot dieback subsides. Through repeated shoot dieback and sprouting events, oaks can build a large root system, provided there is adequate light.

A well-developed root system results in a high shoot-growth potential in oak seedling sprouts, which makes them more competitive than true oak seedlings (i.e., seedlings that have not experienced shoot dieback and sprouting). Greater net photosynthesis in seedling sprouts results from a higher root area–to–leaf area ratio (Kruger and Reich 1993a,b) and, for oak seedling sprouts developing after a fire, improved leaf nitrogen content (Reich et al. 1990). Therefore, successful oak regeneration is dependent upon there being an adequate number of large advance reproduction (primarily seedling sprouts that are present before overstory removal).

Advance Reproduction on Xeric Sites. Oak advance reproduction can accumulate over successive acorn crops on xeric sites throughout eastern North America, even in the absence of disturbances such as fire (Johnson 1993b). Oak accumulator ecosystems are characterized by a relative abundance of large advance reproduction but not necessarily high numbers of seedlings. The probability of having an abundance of large oak advance reproduction increases as overstory density decreases to ≤ 58% stocking (Larsen et al. 1997). Sufficient light reaches the oak advance reproduction when site conditions (e.g., shallow soils, stony soils, fragipans, or hot and dry exposures) limit the structural complexity of the overstory and understory, and thus the intensity of competition (Johnson 1993a,b). Oaks can persist in the open understories on xeric sites despite recurrent shoot dieback. Individual root systems of oak advance reproduction are capable of becoming large and reaching ages of 50 years or more (Merz and Boyce 1956, Tryon and Powell 1984).

Advance Reproduction on Mesic and Hydric Sites. In the absence of fire or similar disturbances, mesic sites (coves, lower slopes, and northeast aspects) and hydric sites (bottomland) do not accumulate oak advance reproduction (Larsen and Johnson 1998). Pulses or waves of oak advance reproduction, as many as 50,000 to 150,000 per acre, may result from a single good acorn crop on mesic and hydric sites, but the large seedlings do not develop, because oak survival is low in heavy shade (Johnson 1975, Loftis 1990b). Hence, there are frequent and prolonged periods with little or no oak advance reproduction. Those seedlings that do persist are small and have low regeneration potential.

Accumulation of oak advance reproduction on mesic and hydric sites requires recurrent disturbances, which historically had been the role of fire before European settlement (see Chapters 3 and 4). Fire increases light at the forest floor by decreasing the density and size of woody species in the understory and by reducing overstory density. In the absence of periodic fires, mesic and hydric sites develop dense overstory canopies and complex vertical structure.

Oak-dominated stands on mesic or hydric sites do not usually regenerate to oak in the absence of disturbances that limit competing vegetation in both the understory and overstory (Johnson 1993b). However, occasionally high densities of small oak advance reproduction or a bumper crop of acorns at the time of overstory removal have led to successful oak regeneration on these sites. Normally, small oak seedlings have little chance to recruit into the overstory, when regenerating in openings in mesic sites, because they cannot compete with species such as cottonwood, green ash, sweetgum, or yellow-poplar. If, however, there are 100,000 or more oak seedlings per acre, then, by stochastic probability, some of them will recruit into the overstory following a regeneration harvest.

Reproduction by Stump Sprouts

Stump sprouts are stems of reproduction that arise from overstory trees (stems ≥ 5.08 cm dbh [diameter at breast height]) cut in a timber harvest or topkilled by fire. The separation between advance reproduction and stump sprouts by stem diameter is arbitrary (Roach and Gingrich 1968). Stump sprouts are physiologically identical to seedling sprouts, and both classes of reproduction have the potential to produce basal sprouts when the parent stem is cut or suffers shoot dieback. Stump sprouts that originate from buds at or near the ground are more likely to survive and produce a quality stem (Kelty 1988, Johnson 1994b).

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. Initially, they are capable of producing four or more flushes of shoot growth per year, even in drought conditions (Johnson 1979, Cobb et al. 1985). This growth advantage is due, in part, to their having a large root system that can deliver sufficient water, nutrients, and other metabolites to the shoot, reducing water stress effects on growth.

The capacity for stump sprouting varies among species (see Figure 5.3) but also depends on a number of environmental and physiological

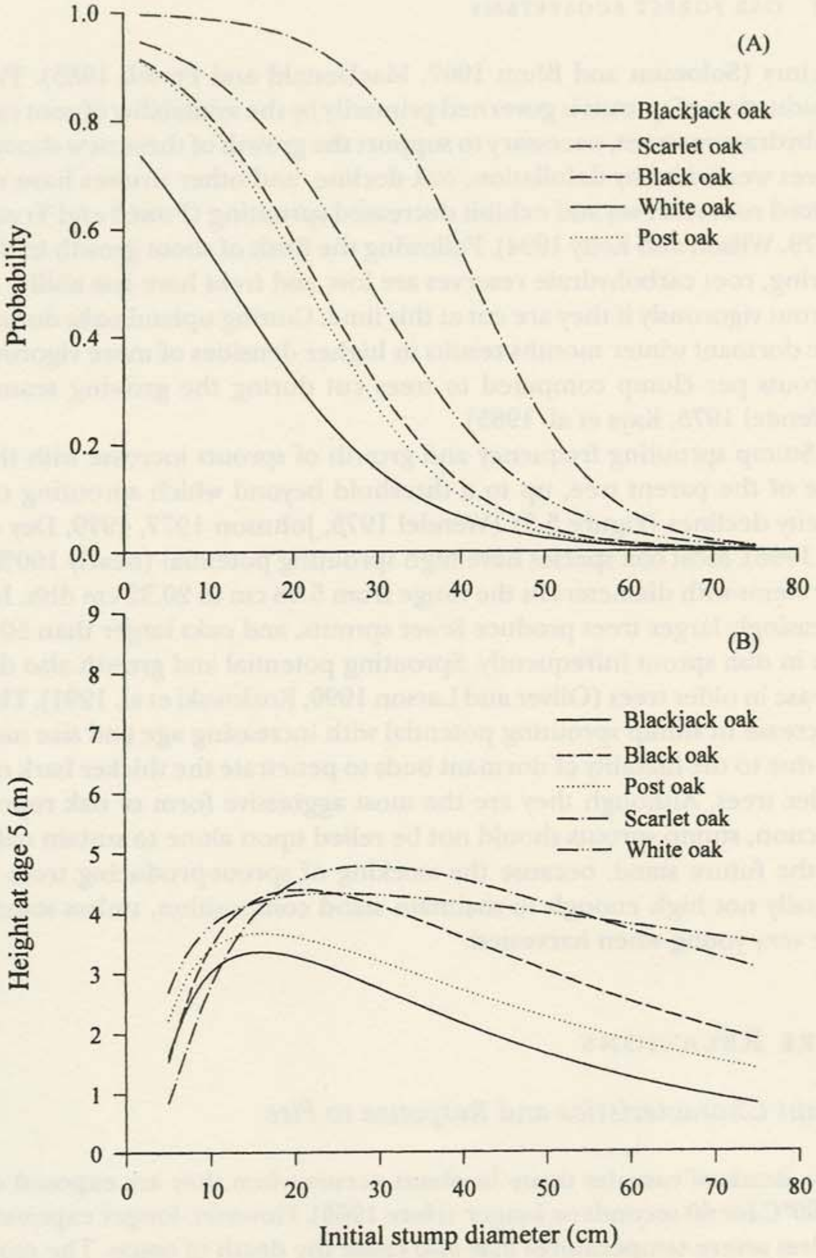

FIGURE 5.3. (*A*) Estimated probabilities that a tree of a given basal diameter will produce a sprout that survives to age 5 after clearcutting. (*B*) Estimated 5th-year heights of oak stump sprouts growing in clearcut openings in relation to basal diameter of the parent stem. (Both adapted from Dey et al. 1996.)

factors (Solomon and Blum 1967, MacDonald and Powell 1985). The production of sprouts is governed primarily by the availability of root carbohydrate reserves, necessary to support the growth of these new shoots. Trees weakened by defoliation, oak decline, and other stresses have reduced root reserves and exhibit decreased sprouting (Powell and Tryon 1979, Wilson and Kelty 1994). Following the flush of shoot growth in the spring, root carbohydrate reserves are low, and trees have less ability to sprout vigorously if they are cut at this time. 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).

Stump sprouting frequency and growth of sprouts increase with the size of the parent tree, up to a threshold beyond which sprouting capacity declines (Figure 5.3) (Wendel 1975, Johnson 1977, 1979, Dey et al. 1996). Most oak species have high sprouting potential (nearly 100%) for stems with diameters in the range from 5.08 cm to 20.32 cm dbh. Increasingly larger trees produce fewer sprouts, and oaks larger than 50.8 cm in dbh sprout infrequently. Sprouting potential and growth also decrease in older trees (Oliver and Larson 1990, Kozlowski et al. 1991). The decrease in stump sprouting potential with increasing age and size may be due to the inability of dormant buds to penetrate the thicker bark on older trees. Although they are the most aggressive 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 stands are very young when harvested.

FIRE RELATIONS

Plant Characteristics and Response to Fire

The death of vascular tissue in plants occurs when they are exposed to ≥ 60°C for 60 seconds or longer (Hare 1965). However, longer exposure to less severe temperatures may also cause the death of tissue. The mortality of trees following fire varies by species, size of tree, bark thickness, physiological activity, stage of plant development, and tree vigor. Mortality is also influenced by fire season, fire intensity and type, and fire frequency.

Bark thickness is a major determinant of fire resistance regardless of tree species (Hengst and Dawson 1994). Thickness is the primary characteristic affecting the bark's ability to insulate cambial tissue and dormant buds from the heat of a fire. Small differences in bark thickness produce large differences in fire resistance, because the duration of heat required to kill tree cambium is proportional to the square of the bark thickness (Hare 1965).

Tree stem diameter has been correlated to survival after burning because it is directly related to bark thickness and tree height, and hence to a tree's ability to resist heat injury to the cambium or to the crown (Loomis 1973, Regelbrugge and Smith 1994). Low to moderately intense surface fires can topkill most hardwood stems that are < 10.16 cm in diameter (Waldrop and Lloyd 1991). Mortality is less for hardwood stems that are ≥ 10.16 cm, although they may suffer topkill or develop advanced decay in the lower bole.

Oaks are generally less susceptible to injury or mortality from repeated burnings than most of their competitors (see Table 5.2), because of relatively thicker bark. Although young and small oak stems (< 10.16 cm dbh) are just as likely as their competitors to suffer shoot topkill from a single fire, they are better adapted to frequent burning because of their ability to repeatedly produce sprouts long after their competitors have perished (Waldrop et al. 1987).

Fire Season

The probability of fire mortality is higher from burns during the growing season than from those during the dormant season. In the summer, lethal temperatures are reached more rapidly because the ambient temperature is higher (Whelan 1995). In addition, summer fires usually burn with greater intensity than winter fires do and therefore can kill larger diameter trees (≥ 12.7 cm dbh), especially in drought years (Waldrop and Lloyd 1991). High physiological activity and cell hydration in the summer predisposes plants to the heat of fire and increases the probability of mortality (DeBano et al. 1998). Growing season fires reduce a tree's ability to sprout following topkill because root carbohydrate reserves are relatively low after leaf expansion and shoot growth. Death of the shoot in the summer lowers root carbohydrate levels due to a loss of leaf area available for photosynthesis, a shortened season of photosynthesis, and reduced translocation of photosynthates from the leaves. Thus, sprouting capacity and sprout vigor are greater after dormant season fires than following growing season burns.

Table 5. 2

Common hardwood and conifer species in eastern North America, by vulnerability to long-term, repeated burning

Very sensitive	*Sensitive*	*Intermediate*	*Resistant*	*Very resistant*
Balsam fir	American holly	Cherrybark oak	Aspen (mature)	Bear oak
Eastern red cedar	Aspen (small)	Nuttall oak	Blackgum	Blackjack oak
Hemlock (young)	Basswood	Overcup oak	Black oak	Bluejack oak
Northern white cedar	Beech	Pin oak	Bur oak	Dwarf chinkapin oak
Red pine (young)	Bigtooth aspen	Scarlet oak	Chestnut oak	Longleaf pine
Virginia pine	Black cherry	Southern red oak	Chinkapin oak	Post oak
White pine (young)	Black walnut	Swamp chestnut oak	Cottonwood (mature)	Slash pine
White spruce	Cottonwood (young)	Swamp white oak	Hickory	Turkey oak
Yellow-poplar (repro)	Dogwood		Northern pin oak	
	Elm		Northern red oak	
	Ironwood		Red pine (mature)	
	Laurel oak		Shortleaf pine	
	Magnolia		White oak	
	Red maple		White pine (mature)	
	Sassafras		Yellow-poplar (mature)	
	Silver maple			
	Striped maple			
	Sugar maple			
	Sweet birch			
	Sweetgum			
	Sycamore			
	Water oak			
	White ash			
	Willow oak			

Sources: Gleason 1913, Nelson et al. 1933, Garren 1943, Beilmann and Brenner 1951, Curtis 1959, Heinselman 1973, Wright and Bailey 1982, Grimm 1984, Harmon 1984, Lorimer 1985, Simard et al. 1986, Burns and Honkala 1990, Reich et al. 1990, Boyer 1990, 1993, Nowacki and Abrams 1992, Abrams 1992, Lorimer 1993, Whitney 1994, Hengst and Dawson 1994, Orwig and Abrams 1994, Huddle and Pallardy 1996, Kruger and Reich 1997a,b, Hicks 1998, Brose and Van Lear 1998.

Fire Intensity

Fire intensity is a primary determining factor in the damage or mortality suffered by trees. The probability of crown scorch and cambial and root injury increases with increasing fire intensity. High-intensity fires can topkill much of the mature overstory trees in hardwood and pine-hardwood stands, but in young to middle-aged stands complete mortality from high-intensity fires is low (e.g., 3% to 8%) (Barden and Woods 1976, Regelbrugge and Smith 1994), because many of the overstory trees have a high sprouting potential. Most overstory hardwoods and conifers are able to tolerate low intensity fires, because of their high crowns and thick bark (Wendel and Smith 1986, Henning and Dickmann 1996).

Dormant or adventitious buds and other reproductive structures buried in mineral soil (below 2.54 cm to 5.08 cm deep) are protected from most surface fires, because soil is a poor conductor of heat, especially when it is dry (DeBano et al. 1998). Oak advance reproduction seedlings, with their root collar buds beneath the soil surface are less likely to suffer fire-induced mortality than species that carry their reproductive structures above ground. Survival after fire of oak advance reproduction is a function of root mass, carbohydrate reserves, and number of adventitious buds that are buried in mineral soil, for given weather conditions and fire behavior

Fire Frequency

Fire usually increases the density of trees in the smaller size classes, by causing shoot dieback and formation of sprout clumps and by promoting the establishment of new seedlings (Waldrop and Lloyd 1991). These stems are more susceptible to mortality or shoot dieback in subsequent fires, because death and injury is size dependent. Thus, frequent fires keep trees in the seedling or stump sprout state, preventing them from increasing their fire resistance by growing larger and developing thicker bark.

Fire frequency affects the accumulation and structure of fuels, which influences fire intensity and tree mortality. Increases in fuel loads during fire-free periods result in higher fire intensities and higher probabilities of tree mortality in future fires. In the absence of fire, growth of understory vegetation increases the vertical structure of fuel in the stand and hence the chance of stand-replacing crown fires, especially in drought years (Heinselman 1973). In contrast, long-term annual burning results in lower fire intensity by reducing the volume of fuel and simplifying the fuel structure.

A single fire set to improve conditions for oak regeneration after an extended fire-free period (e.g., > 20 years) often produces disappointing results, because competing trees have grown large enough to be fairly fire resistant (Johnson 1974, Wendel and Smith 1986, Van Lear and Waldrop 1988). In fact, a single fire frequently increases the density of competing vegetation, by causing stump sprouting and promoting seedling establishment. Repeated fires are necessary to improve oak regeneration in areas where fire has been suppressed for decades, especially on mesic sites.

CONCLUSION

Oak species dominate many of the forest types in eastern North America across a diversity of climate, soil, topography, and hydrology. Oaks are well adapted to persist in stressful and high-disturbance environments where drought, fire, and herbivores are prevalent. Oaks are more tolerant of drought and better adapted to surviving repeated fires than many of their competitors. However, they are only moderately able to unable to prosper in heavy shade. Historically, periodic fire has helped to control oak's competitors, allowing oaks to dominate even on high-quality sites. In the past, frequent fires created a more open stand structure than exists today, which provided adequate light for the development of large oak advance reproduction. Other human disturbances, such as logging, woods grazing, and agriculture, have contributed to oak's dominance across the landscape today. Oak seedling sprouts, with large root systems, were able to grow rapidly once agricultural lands were abandoned, and woods burning and grazing were stopped: within 40 years, in the absence of these disturbances, oak woodlands, barrens, and savannas became closed-canopy forests.

Prevailing disturbance regimes discriminate against recruiting oak on all but the driest site types. Declines in oak dominance are largely the result of man's suppression of fire for the past 50 to 100 years. Without frequent fire, forest stocking has increased, dense understories of shade-tolerant trees and shrubs have invaded oak forests, and oak advance reproduction has failed to develop in the low-light conditions. Overstory mortality due to natural disturbances such as windthrow, insects, and disease usually leads to displacement of oak by its competitors in many forest ecosystems.

Even-aged silvicultural systems (e.g., clearcut and shelterwood) and catastrophic natural disturbances favor shade-intolerant and intermediately tolerant species, while uneven-aged systems (e.g., single-tree and group selection) favor shade-tolerant and intermediately tolerant species. Oak regeneration and recruitment have been most successful where large oak advance reproduction is able to accumulate in the understory and competing vegetation is controlled. On more productive sites it may be necessary to control understory competition and reduce overstory shade to permit growth of oak advance reproduction.

Oak silviculture is inherently complex because successful regeneration is dependent upon having adequate large oak advance reproduction before completion of the regeneration harvest. The process of developing adequate oak advance reproduction normally requires time and a series of planned disturbances to the overstory and understory. Underplanting shelterwoods with oak seedlings can reduce the time required to get adequate advance reproduction established, although this method may be costly. Historically, fire was key to maintaining oak dominance, and realization of this fact has led to increased efforts to develop prescribed burning methods for oak regeneration (see Chapter 18). Successful oak regeneration follows from silvicultural practices that increase light to oak advance reproduction by reducing overstory density while controlling competing vegetation.

Unfortunately, the silvicultural practices that are most useful for perpetuating oak, such as shelterwood harvesting and prescribed burning, can be socially unacceptable or too time-consuming and expensive to interest private landowners. This is particularly significant because most of the oak resource is owned by nonindustrial private landowners. It is a challenge to develop innovative silvicultural systems for oaks that are socially acceptable and affordable. Forest managers need to understand the regeneration and stand replacement process and the critical need to incorporate measures of stand regeneration potential into the management process. Planning for oak regeneration should begin well in advance of the regeneration harvest, and assessments of stand regeneration potential can be used to develop silvicultural prescriptions that are more likely to regenerate oak.