

---

# Prescribing Fire in Eastern Oak Forests: Is Time Running Out?

Marc D. Abrams, *School of Forest Resources, Pennsylvania State University, University Park, PA 16802.*

**ABSTRACT:** *Before European settlement, vast areas of the eastern US deciduous forest were dominated by oak species. Evidence indicates that periodic understory fire was an important ecological factor in the historical development of oak forests. During European settlement of the late 19th and early 20th century, much of the eastern United States was impacted by land-clearing, extensive timber harvesting, severe fires, the chestnut blight, and then fire suppression and intensive deer browsing. These activities had the greatest negative impact on the once-dominant white oak, while temporarily promoting the expansion of other oaks such as red oak and chestnut oak. More recently, however, recruitment of all the dominant upland oaks waned on all but the most xeric sites. Mixed-mesophytic and later successional hardwood species, such as red maple, sugar maple, black birch, beech, black gum and black cherry, are aggressively replacing oak. The leaf litter of these replacement species is less flammable and more rapidly mineralized than that of the upland oaks, reinforcing the lack of fire. The trend toward increases in nonoak tree species will continue in fire-suppressed forests, rendering them less combustible for forest managers who wish to restore natural fires regimes. This situation greatly differs from the western United States, where fire suppression during the 20th century has made a variety of conifer-dominated forests more prone to stand-replacing fire. North. J. Appl. For. 22(3):190–196.*

**Key Words:** Historical ecology, disturbance, succession, fire suppression, oak replacement.

The increased importance of oak (*Quercus*) during the Holocene epoch was associated with warmer and drier climate and elevated fire frequency after glacial retreat (reviewed in Abrams 2002). Significant levels of charcoal influx occurred almost routinely with oak pollen in lake and bog sediments throughout the Holocene (Delcourt and Delcourt 1997). As American Indian populations increased throughout the eastern United States, so did their use of fire, land clearing, and other agricultural activities (Whitney 1994). Thus, low to moderate levels of biotic and abiotic disturbance and climate change were an intrinsic part of the Holocene ecology, resulting in a dynamic equilibrium in regional forests.

The magnitude of anthropogenic disturbances in North American forests changed dramatically after European settlement. These included extensive logging, land clearing, and catastrophic fire, followed by fire suppression and the introduction of exotic insects and diseases (Brose et al. 2001). All of these have led to unprecedented and rapid changes in forest composition and structure. This is partic-

ularly true for the eastern United States, which has seen the extirpation of the once dominant chestnut (*Castanea dentata*) overstory from blight, loss of vast white pine (*Pinus strobus*) forests from logging followed by intense fires, a virtual cessation of oak regeneration from fire suppression and intensive deer browsing, and a rapid increase in native and exotic invasives (Keever 1953, Abrams 1992, 1998, Whitney 1994). Some authors have characterized the landscape as undergoing a near complete transformation over the last 350 years (Whitney 1994, Foster et al. 1998).

Oak was the dominant genus in the pre-European settlement forests throughout much of the eastern United States (Abrams 1992, Whitney 1994). However, very little recruitment of oak has occurred during the 20th century (Cho and Boerner 1991, Abrams et al. 1995), with the possible exception of the southwest portion of the eastern deciduous forest (parts of Missouri, Oklahoma, and Arkansas) that lacks many of the later successional, oak-replacement species (Abrams 1992). There is evidence of a dramatic decline in oak forests from presettlement to present day for much of the eastern United States (Glitzenstein et al. 1990, Fralish et al. 1991, Whitney 1994, Abrams and Ruffner 1995). Anthropogenic impacts during the late 19th and early 20th centuries included both the height and the tail end of the clearcutting era, catastrophic wildfires, the start of the fire

---

NOTE: Marc D. Abrams can be reached at (814) 865-4901; Fax: (814) 865-3725; agl@psu.edu. The author thanks Bryan Black, Greg Nowacki, and Robert Peet for critically reviewing portions of the article. Copyright © 2005 by the Society of American Foresters.

suppression era, and the chestnut blight. This article will synthesize studies of land-use history, witness trees (from early land surveys), dendroecology (tree-ring studies), and fire history to investigate the major ecological and environmental changes that have occurred in the eastern deciduous forest after European settlement. Due to the large increase in nonpyrogenic, mixed-mesophytic tree species, the window of opportunity to restore natural fire regimes in eastern oak forests may be closing in the foreseeable future.

### Oak Abundance in the Presettlement Forest

Oak distribution in the pre-European settlement forests of New England differed dramatically from north to south.

Little or no oak exists in northern New England, except along the Connecticut River Valley (Table 1; Burns and Honkala 1990, Cogbill et al. 2002). However, in southern New England and eastern New York, white oak was typically the first-rank species, with composition percentages ranging from about 17 to 36% (Table 1). Other dominant tree species in these forests included white pine, hickory (*Carya*), chestnut, and hemlock (*Tsuga canadensis*).

Oak species occurred in the southern and central regions of the Lake States (Burns and Honkala 1990). White oak represented 19 to 26% of certain presettlement forests in southern and central Michigan and Wisconsin, in some

**Table 1. Percent composition of witness tree species in pre-European settlement forests in the eastern United States.**

Region, location	Presettlement forest composition (%)	Reference
<b>Northeast</b>		
Northern VT, NH	Beech (32), spruce (14), maple (12), hemlock (12), oak (5)	Cogbill et al. 2002
Western NY	Beech (32), sugar maple (18), basswood (12), white oak (11)	Seischab 1990
Eastern NY	White oak (36), black oak (15), hickory (10), elm (6)	Glitzenstein et al. 1990
Central MA	White oak (27), black oak (26), pine (18), hickory (9)	Whitney and Davis 1986
Central MA	White oak (20), pine (20), hemlock (10), chestnut (8)	Foster et al. 1998
CT and RI	White oak (33), hickory (10), chestnut (9)	Cogbill et al. 2002
MA	White oak (25), pine (16), maple (6), hemlock (6)	Cogbill et al. 2002
Eastern NY	White oak (17), beech (16), hemlock (10), pine (9)	Cogbill et al. 2002
<b>Lake States</b>		
Central MI	Jack pine (20), red pine (19), white pine (11), white oak (2)	Whitney 1994
Central MI	Red pine (40), white oak (19), white pine (15), aspen (12)	Kilburn 1960
Southern WI	Bur oak (60%), white oak (26), black oak (13)	Cottam 1949
Central WI	Sugar maple (37), white oak (25), red oak (16), elm (12)	Curtis 1959
Central WI	Pine (28), aspen (17), larch (12), white oak (10)	Nowacki et al. 1990
<b>Mid-Atlantic</b>		
Northern NJ	White oak (34), black oak (18), hickory (15), red oak (9)	Russell 1981
Northern NJ	White oak (31), hickory (25), black oak (19), chestnut (12)	Ehrenfeld 1982
Northwest PA	White oak (21), beech (13), maple (17), black oak (6)	Whitney and Decant 2001
Southeast PA	Black oak (33), white oak (17), chestnut (15), hickory (15)	Mikan et al. 1994
Southeast PA	Black oak (33), white oak (30), hickory (28)	Black and Abrams 2001
Southwest PA	White oak (40), black oak (9), hickory (9), dogwood (8)	Abrams and Downs 1990
Central PA		
Allegheny Mts.		
Plateaus	White oak (26), chestnut (19), pine (19), maple (10)	Abrams and Ruffner 1995
Stream valleys	Hemlock (24), maple (21), white pine (15), birch (15)	Abrams and Ruffner 1995
Ridge and Valley		
Ridges	Chestnut oak (14), white oak (12), pine (19), chestnut (11)	Abrams and Ruffner 1995
Valleys	White oak (30), pine (25), hickory (17), black oak (10)	Abrams and Ruffner 1995
Ridges	Pine (27), chestnut oak (18), white oak (11), chestnut (13)	Nowacki and Abrams 1992
Valley	White oak (41), white pine (12), hickory (12), black oak (9)	Nowacki and Abrams 1992
<b>Eastern WV</b>		
Ridges	White oak (35), chestnut (15), chestnut oak (13), black oak (12)	Abrams and McCay 1996
Valleys	White oak (23), maple (22), pine (15), basswood (10)	Abrams and McCay 1996
<b>Southern WV</b>		
Northern VA	White oak (24), chestnut (12), hickory (9), chestnut oak (6)	Abrams et al. 1995
Southeast VA	White oak (49), red oak (26), hickory (7)	Orwig and Abrams 1994
Southwest VA	Red oak (25), white oak (18), chestnut (9)	McCormick and Platt 1980
Western Virginia	White oak (26), pine (13), chestnut oak (9), hickory (9)	Stephenson et al. 1992
<b>Midwest and Central Region</b>		
Central MO	White oak (32), black oak (11), sugar maple (9), elm (8)	Wuenscher et al. 1967
Eastern IL	White oak (27), black oak (18), hickory (6), elm (10)	Rogers and Anderson 1979
<b>Southern IL</b>		
South slopes	White oak (81)	Fralish et al. 1991
Ridge tops	White oak (45), black oak (33)	Fralish et al. 1991
<b>Northeast OH</b>		
Fine till	Beech (36), sugar maple (17), white oak (14)	Whitney 1994
Coarse till	White oak (37), hickory (13), black oak (6)	Whitney 1994
North-central OH	Hickory (34), white oak (30), bur oak (11), black oak (11)	Whitney 1994
Southeast OH	White oak (40), hickory (14), black oak (12), beech (8)	Dyer 2001
<b>South and Southeast</b>		
North FL	Magnolia (21), beech (14), maple (7), white oak (5)	Delcourt and Delcourt 1977
Central GA	Pine (27), black and red oak (21), post oak (18), white oak (7)	Cowell 1995
Southeast TX	Pine (25), white oak (18), pin oak (10), red oak (9)	Schafale and Harcombe 1983
Eastern AL	White oak (13), beech (9), pine (9), maple (5)	Black et al. 2002

regions occurring with red pine (*P. resinosa*) and white pine, as part of bur oak (*Q. macrocarpa*) savannas, or with sugar maple (*Acer saccharum*) and red oak (*Q. rubra*) (Cottam 1949, Kilburn 1960, Nowacki et al. 1990).

The peak distribution for oak species in the presettlement forest was clearly in the oak-hickory, oak-pine, and former oak-chestnut regions of the Mid-Atlantic, central Appalachians and Piedmont, Midwest, and Central States (Table 1). In the Mid-Atlantic region, oak was the first- or second-rank species in 16 of 18 studies reviewed here. In 12 of these examples, white oak was dominant species, representing 21 to 49% frequency. White oak was second to black oak (*Q. velutina*; 33%) with a frequency of 17 to 30% in the Piedmont of southeastern Pennsylvania (Mikan et al. 1994, Black and Abrams 2001). In the Ridge and Valley of Pennsylvania, white oak was the first-rank dominant species on valley floors, but was a co-dominant species behind pine species and chestnut oak on ridges (Nowacki and Abrams 1992, Abrams and Ruffner 1995).

In the Midwest and central regions, white oak followed by black oak were the dominant species in six of eight examples (Table 1). However, fine till soils in northeast Ohio and western New York were dominated by sugar maple and beech (*Fagus grandifolia*), with lesser amounts (5–14%) of white oak (Seischab 1990, Whitney 1994). White oak and black oak typically grew with hickory on drier and less fertile sites throughout the region.

Much less information on pre-European forest composition exists for the South and Southeast (Table 1). The few existing studies suggest that oak species were not typically dominant, but they did achieve frequencies of 5–18% in forests with *Magnolia*, beech, maple, pine, and other oak species (Table 1). However, more numerous studies of 20th century forests and old-growth remnants farther north in the Piedmont and central and southern Appalachians suggest that oaks were a dominant species in the original forest (Braun 1950, Peet and Christensen 1980, Monk et al. 1990, Barnes 1991).

### Oak Decline After European Settlement

Significant changes in the composition of oak forests occurred in most regions from presettlement to present day. In 18 of 26 examples reviewed here, white oak experienced a decline in frequency of 10% or more (Table 2). Six examples reported no significant change, whereas two cases actually showed a greater than 10% increase for the species. The latter examples are rather special cases that involved the conversion of bur oak savannas to closed oak forests in southern Wisconsin following Euro-American settlement and fire suppression (Cottam 1949, Whitney 1994).

The magnitude of decline in the once-dominant white oak has been dramatic. For example, in central Massachusetts, oak (mainly white oak) decreased in frequency by over 20% in the Connecticut Valley and Eastern Lowlands

**Table 2. Percent frequency of present-day forest composition in the eastern United States. Examples were chosen based on the availability of corresponding pre-European settlement witness tree data (cf. Table 1).**

Region, location	Present-day dominants (%)	Reference
Northeast		
MA		
Connecticut Valley	Maple (30), oak (22), hemlock (15), pine (11), birch (11)	Foster et al. 1998
Pellham Hills	Maple (27), oak (21), hemlock (15), birch (15), pine (11)	Foster et al. 1998
Central uplands	Maple (24), oak (23), pine (16), birch (12), hemlock (12)	Foster et al. 1998
Eastern lowlands	Oak (35), maple (23), pine (21), birch (8)	Foster et al. 1998
Central MA	White pine (23), black oak (21), red oak (19), white oak (9)	Whitney and Davis 1986
Eastern NY	Maple (30), chestnut oak (14), red oak (10), pine (9), white oak (4)	Glitzenstein et al. 1990
Mid-Atlantic		
Northwest PA	Red maple (22), black cherry (14), hemlock (7), white oak (3)	Whitney and Decant 2001
Southeast PA	Chestnut oak (26), red maple (18), black oak (15), white oak (4)	Black and Abrams 2001
Southeast PA	Box elder (23), red maple (19), ash (8), elm (7), white oak (1)	Kuhn (unpublished data)
Central PA		
Allegheny Mts.	Red maple (35), white oak (19), red oak (11), chestnut oak (9)	Abrams and Ruffner 1995
Ridge and Valley	Chestnut oak (28), red maple (14), red oak (14), white oak (13)	Abrams and Ruffner 1995
Valleys	White oak (43), red maple (15), black cherry (10), pine (7)	Nowacki and Abrams 1992
Ridges	Chestnut oak (43), red oak (19), red maple (14), white oak (1)	Nowacki and Abrams 1992
Southwest PA	Red maple (30), beech (23), tulip poplar (17), white oak (5)	Abrams and Downs 1990
Eastern WV	Chestnut oak (15), red oak (14), red maple (12), white oak (9)	Abrams and McCay 1996
Northern VA	White oak (30), hickory (13), poplar (13), dogwood (11)	Orwig and Abrams 1994
Southwest VA	Hickory (14), red oak (12), chestnut oak (8), white oak (5)	McCormick and Platt 1980
Mid-west and Lake States		
Southeast OH	White oak (15), black oak (14), tulip poplar (11), hickory (8)	Dyer 2001
Northeast OH	Beech (11), white oak (11), hickory (9), black cherry (8), red maple (6)	Whitney 1994
Southern WI		
Southern WI (savanna)	Sugar maple (28), elm (14), basswood (11), white ash (10), white oak (5)	Whitney 1994
Southern WI (savanna)	White oak (34), hickory (30), black oak (24), black cherry (12)	Whitney 1994
Central Wisconsin	White oak (54), black oak (25), black cherry (17)	Cottam 1949
Southern IL	Red oak (46), white oak (19), red maple (16)	Nowacki et al. 1990
Southern IL		
South slope	White oak (30), black oak (22), post oak (18), hickory (13)	Fralish et al. 1991
Ridge top	White oak (53), black oak (17), hickory (14), post oak (7)	Fralish et al. 1991
North slope	White oak (21), red oak (22), sugar maple (13), black oak (13)	Fralish et al. 1991

(Table 2; Foster et al. 1998). In the Hudson Valley of eastern New York, white oak declined over 30% (Glitzenstein et al. 1990). Similar declines were noted for white oak in northwest and southeast Pennsylvania, eastern West Virginia, and northern Virginia (Orwig and Abrams 1994, Abrams and McCay 1996, Black and Abrams 2001, Whitney and Decant 2001). However, the largest decline in white oak (from 81 to 30%) was reported on South slopes in southern Illinois (Fralish et al. 1991).

Presently, oak is the first-rank tree species in only 14 of the 26 examples reviewed here, compared to 24 of these examples at the time of European settlement (Tables 1 and 2). There is a greater tendency for present-day oak dominance in the Midwest and Lake States, where they increased in former bur oak savannas and logged and burned-over pine forests (Cottam 1949, Whitney 1994, Nowacki et al. 1990), or in the former prairie peninsula outside the range of red maple (Fralish et al. 1991). Outside of these exceptions, white oak generally experienced a significant decline in frequency even when it maintained the dominant ranking in modern forests (Fralish et al. 1991, Orwig and Abrams 1994, Foster et al. 1998, Dyer 2001).

By far, the largest increases in species frequency on present-day upland oak sites are from red maple (Tables 1 and 2). Red maple now represents the first or second rank dominant in 12 of the 17 examples from southern New England, eastern New York, and the Mid-Atlantic regions. This is even more impressive when you consider that there was very little red maple recorded in the presettlement forests of these areas (Table 1). Moreover, many old-growth oak forests now have abundant young red maple as a dominant tree (Abrams and Downs 1990, Mikan et al. 1994, Shumway et al. 2002, Abrams et al. 1995). The dramatic rise in red maple in oak forests during the 20th century has been attributed to the extensive logging of oak in the late 19th and early 20th century, the chestnut blight, and the suppression of understory burning (Abrams 1992, 1998, Nowacki and Abrams 1992, Stephenson et al. 1992, Mikan et al. 1994). In the prairie regions of Illinois, Iowa, and Missouri, outside the range of red maple, sugar maple is now the dominant later successional, oak replacement species on mesic, nutrient-rich sites (Pallardy et al. 1988, Fralish et al. 1991).

Large increases in red oak and chestnut oak also occurred from presettlement to present day (Tables 1 and 2). Red oak increased from 7 to 19% in central Massachusetts and from 2 to 22% on north-facing slopes in southern Illinois (Fralish et al. 1991, Whitney and Davis 1986). Red oak has obtained importance values of 37–51% in present-day forests in north-central Wisconsin, where it formerly represented <1% of the original northern hardwood-conifer forest (Nowacki et al. 1990). Increases in red oak ranging from 9 to 19% and in chestnut oak from 7 to 25% occurred in the Allegheny Mountains and Ridge and Valley of Pennsylvania and West Virginia (Nowacki and Abrams 1992, Abrams and Ruffner 1995, Abrams and McCay 1996). In western Virginia, red oak increased from 11 to 57% (from 1932 to 1982), while red maple increased from 1 to 11%

(Stephenson et al. 1992). Chestnut oak increased from <1 to 26% frequency in the Piedmont lowlands of southeastern Pennsylvania (Black and Abrams 2001). Red oak and chestnut oak apparently benefited from the death of overstory chestnut (on ridges), selective logging of white oak, and the more intensive logging and burning of both high- and low-elevation forests.

### **A Case Study of Fire History and Tree Recruitment in an Old-Growth Oak Forest**

Fire history and dendroecology (tree ring) were investigated for two stands in an old-growth, mixed-oak stands in western Maryland (Shumway et al. 2001). I believe the ecological history and dynamics of these stands are representative of oak forests throughout much of the eastern forest. One stand (Coleman Hollow) is dominated by red maple (24%), chestnut oak (23%), white oak (20%), red oak (14%), and black oak (9%), whereas the South Savage stand is dominated by chestnut oak (20%), black birch (*Betula lenta*; 18%), red oak (17%), red maple (17%), black oak (11%), and white oak (6%). A greater abundance of rock outcroppings at South Savage may have allowed for more black birch and less white oak in the stand. The presettlement forest on Savage Mountain contained white oak (27%), hickory (18%), black oak (12%), chestnut oak (11%), chestnut (10%), and red oak (5%).

Basal cross-sections were obtained from a partial timber cut in 1986, which provided evidence of 42 fires from 1615 to 1958. Fires occurred on average every 8 years during the presettlement (1600–1780) and early postsettlement (1780–1900) periods. These included seven major fires year in which  $\geq 25\%$  of the sample trees were scarred in a given year. No major fire years occurred after 1900, and no fires were recorded after 1960. The South Savage stand had a larger component of older trees, including a 409-year-old white oak, and exhibited continuous recruitment of oaks from the late 1500s until 1900. Interestingly, white oak and chestnut oak dominated recruitment from 1650 to 1800, whereas red oak and black oak dominated recruitment from 1800 to 1900. The lack of red oak and black oak recruitment prior to 1800 may be due to their relatively short longevity at the site. However, the large reduction in white oak and chestnut oak recruitment after 1800 is difficult to explain, although they might have been out-competed by the other oaks. After 1900, the only oak species to recruit in significant numbers was red oak, and this was associated with the loss of overstory chestnut from the blight.

Coleman Hollow differed from South Savage in terms of species composition and the fact that it contained only two very old oaks, white oaks 290 and 320 years old. Moreover, the abundant oak recruitment during the 19th century included large amounts of chestnut oak and white oak, not seen on Savage South. From 1900 to 1950, recruitment of chestnut oak and red oak was joined by large numbers of red maple and black birch. Very little recruitment of white oak occurred in either stand after 1900.

The results of this study indicate that periodic fires burned through the forest understories between 1600 and

1900 and that some degree of burning continued until 1960 because of its remote location. The fire rotation at Savage Mountain is consistent with mean fire intervals of 4–20 years in other oak forests in the eastern and central United States (Guyette and Dey 1995, Sutherland 1997, Schuler and McCain 2003). The long history of periodic burning at the study site was associated with continuous oak recruitment. A similar result was reported for a fire history, red oak recruitment study in West Virginia (Schuler and McCain 2003). Fires at Savage Mountain likely played an important role in oak ecology, such as preparing a thin litter seedbed, increasing sunlight to the forest floor, and suppressing red maple and black birch. Indeed, these species were absent from the witness tree record and among the older trees in the forests, despite the fact that they can live over 200 years. Large amounts of red oak, chestnut oak, red maple, and birch recruitment were associated with the chestnut blight period from 1910 to 1950. A reduction and eventual cessation of fire further facilitated red maple and black birch invasion in the forest while retarding the recruitment of all oak species.

### History Ecology of Eastern Oak Forests

The witness tree studies reviewed here indicate that the once-dominant white oak grew on a wider range of sites and in greater numbers than any other eastern oak species (Braun 1950, Peet and Christensen 1980, Monk et al. 1990, Barnes 1991). Red oak appears frequently in the witness tree record but only occasionally obtained frequency over 5%. It seems likely that small populations of red oak existed across the eastern forest on most landforms that provided adequate nutrients and some protection from fire and drought.

After the clearcut era of the late 1800s and the chestnut blight of the early 1900s, the fast-growing and opportunistic red oak expanded dramatically from its sheltered areas and grew over vast areas of the eastern forest previously dominated by chestnut, pine, and white oak (Keever 1953, Crow 1988, Nowacki et al. 1990, Barnes 1991, Stephenson et al. 1992). It appears that red oak flourished in response to large-scale anthropogenic disturbances that were much less common in the pre-European settlement forest. Moreover, the invasion of red oak into relatively undisturbed old-growth white oak forests was probably facilitated by its increase in surrounding and more highly disturbed forests (Abrams et al. 1995, Abrams and Copenheaver 1999).

The situation for red oak is somewhat analogous to the rise in red maple that also occurred during the 20th century in the eastern United States (Abrams 1998). Before European settlement, red maple generally was limited to swamps and other areas sheltered from fire. Red maple is much more sensitive to fire than is red oak and would have been less common on uplands. After 1900, red maple quickly expanded out of the protected areas and started to dominate most forest understories throughout its range. The selective logging of the highly prized white oak gave a clear opportunity to less common and/or less desirable species, such as

red oak, red maple, black birch, and black cherry (Whitney 1994, Whitney and Decant 2001).

The postsettlement expansion of chestnut oak can be best explained by the loss of overstory chestnut, pitch pine (*Pinus rigida*), and white oak, and it being tolerant of severe fires that occurred during and after the major clearcut era in the late 1800s (Keever 1953, McCormick and Platt 1980, Abrams and Ruffner 1995, Abrams and McCay 1996). Despite often growing on inaccessible ridge sites and being a low-quality timber species, chestnut oak did not escape extensive cutting during the 19th century. It was an important fuelwood for domestic uses and the charcoal iron industry and a source of tannin for the tanbark industry (Stephenson et al. 1992, Whitney 1994). On sites in which chestnut oak and white oak co-dominated in the original forest, chestnut oak was the apparent victor after the catastrophic disturbances. However, many chestnut oak forests now are being invaded by red maple (Table 2).

### Conclusion

Paleoecological and dendroecological evidence suggest that the process of fire and oak recruitment in upland forests went on for many hundreds and thousands of years. This cycle, however, was broken during the 19th and early 20th century and led to a dramatic decline in the once super-dominant white oak, followed by declines in other oak species. It is doubtful that oaks on mesic sites represent a true self-perpetuating climax in the absence of fire (Lorimer 1985, Abrams 1992, Schuler and McCain 2003). Thus, the broad ecological distribution of oaks in the eastern United States can be directly attributed, probably in large part, to extensive understory burning in the pre-European and early settlement forests. If not for these fires, most oak sites would have been dominated by red maple, sugar maple, birch, beech, and black gum, a trend that is now apparent throughout most of their range.

There has been a nearly complete cessation of oak recruitment over the last 50–100 years in all but the most xeric and nutrient-poor sites. Strong competitive pressure on oak regeneration now exists from a number of later successional and gap-opportunistic trees. The conversion of flammable oak litter, with high lignin content, in forest understories to less combustible and more rapidly decomposed litter of mixed-mesophytic and later successional tree species (Melillo et al. 1982, Lorimer 1985, Washburn and Arthur 2003) is rendering eastern oak forests less prone to burning. In contrast, fire suppression in the western United States and resultant increases in live and dead fuel, stand density, and changes in species composition have made many conifer-dominated forests *more* prone to fire (Biswell 1967, Parson 1976, Brown et al. 2000). The declining combustibility of eastern forests is being further exacerbated by intensive deer browsing, which has reduced the leaf litter from most woody species, especially oaks. Thus, forest managers wishing to restore historical burning regimes to eastern forests in the hope of encouraging more

oak regeneration, while reducing native invasive tree species, should act sooner rather than later, as the window the opportunity may be closing in the foreseeable future.

## Literature Cited

- ABRAMS, M.D. 1992. Fire and the development of oak forests. *Bioscience* 42:346–353.
- ABRAMS, M.D. 1998. The red maple paradox. *BioScience* 48:355–364.
- ABRAMS, M.D. 2002. The postglacial history of oak forests in eastern North America. P. 34–45 in *Oaks Forest ecosystems*, McShea, W.J., and W.M. Healy (eds). The Johns Hopkins University Press, Baltimore.
- ABRAMS, M.D., AND C.A. COPENHEAVER. 1999. Temporal variation in species recruitment and dendroecology of an old-growth white oak forest in the Virginia Piedmont, USA. *For. Ecol. Manage.* 124:275–284.
- ABRAMS, M.D., AND J.A. DOWNS. 1990. Successional replacement of old-growth white oak by mixed-mesophytic hardwoods in southwest Pennsylvania. *Can. J. For. Res.* 20:1864–1870.
- ABRAMS, M.D., AND D.M. MCCAY. 1996. Vegetation-site relationships of witness trees (1780–1856) in the presettlement forests of eastern West Virginia. *Can. J. For. Res.* 26:217–224.
- ABRAMS, M.D., AND C.M. RUFFNER. 1995. Physiographic analysis of witness-tree distribution (1765–1798) and present forest cover through northcentral Pennsylvania. *Can. J. For. Res.* 25:659–668.
- ABRAMS, M.D., D.A. ORWIG, AND T.E. DEMEO. 1995. Dendroecological analysis of successional dynamics for a presettlement-origin white pine-mixed oak forest in the southern Appalachians, USA. *J. Ecol.* 83:123–133.
- BARNES, B.V. 1991. Deciduous forests of North America. P. 219–344 in *Ecosystems of the world 7: Temperate deciduous forests*, Rohrig, E., and B. Ulrich (eds.). Elsevier, Amsterdam.
- BISWELL, H.H. 1967. Forest fire in perspective. *Proc. Tall Timbers Fire Ecol. Conf.* 6:43–64.
- BLACK, B.A., AND M.D. ABRAMS. 2001. Influences of Native Americans and surveyor biases on metes and bounds witness tree distribution. *Ecology* 82:2574–2586.
- BLACK, B.A., FOSTER, H.T., AND M.D. ABRAMS. 2002. Combining environmentally dependent and independent analyses of witness tree data in east-central Alabama. *Can. J. For. Res.* 32:2060–2075.
- BRAUN, E.L. 1950. *Deciduous forests of eastern North America*. MacMillan, New York, 596 p.
- BROSE, P., T. SCHULER, D. VAN LEAR, AND J. BERST. 2001. Bringing fire back: The changing regimes of the Appalachian mixed oak forests. *J. For.* 99:30–35.
- BROWN, P.M., M.G. RYAN, AND T.G. ANDREWS. 2000. Historical surface fire frequency in ponderosa pine stands in research natural areas, central Rocky Mountains and Black Hills, USA. *Natural Areas J.* 20:133–139.
- BURNS, R.M., AND B.H. HONKALA. 1990. *Silvics of North America*. Vol. 1: Conifers and Vol. 2: Hardwoods. USDA Agricultural Handbook 654, Washington DC. 877 p.
- CHO, D.S., AND R.E.J. BOERNER. 1991. Canopy disturbance patterns and regeneration of *Quercus* species in two Ohio old-growth forests. *Vegetation* 93:9–18.
- COGBILL, C., J. BURK, AND G. MOTZKIN. 2002. The forests of presettlement New England, USA: Spatial and compositional patterns based on town proprietors surveys. *J. Biogeog.* 29:1–26.
- COTTAM, G. 1949. The phytosociology of an oak woods in southwestern Wisconsin. *Ecology* 30:271–287.
- COWELL, C.M. 1995. Presettlement Piedmont Forests: Patterns of composition and disturbance in central Georgia. *Ann. Assoc. Am. Geographers* 85:65–83.
- CROW, T.R. 1988. Reproductive mode and mechanism for self-replacement of northern red oak (*Quercus rubra*): A review. *For. Sci.* 34:19–40.
- DELCOURT, H.R., AND P.A. DELCOURT. 1977. Presettlement magnolia-beech climax of the gulf coastal plain: Quantitative evidence from the Apalachicola River Bluffs, north central Florida. *Ecology* 58:1085–1093.
- DELCOURT, H.R., AND P.A. DELCOURT. 1997. Pre-Columbian native American use of fire on southern Appalachian landscapes. *Cons. Biol.* 11(4):1010–1014.
- DYER, J.M. 2001. Using witness trees to assess forest change in southeastern Ohio. *Can. J. Bot.* 31:1708–1718.
- EHRENFELD, J.G. 1982. The history of the vegetation and the land of Morristown National Historical Park, New Jersey, since 1700. *Bull. New Jersey Acad. Sci.* 27:1–19.
- FOSTER, D.R., G. MOTZKIN, AND B. SLATER. 1998. Land-use history as long-term broad-scale disturbance: Regional forest dynamics in central New England. *Ecosystems* 1:96–119.
- FRALISH, J.S., F.B. COOKS, J.L. CHAMBERS, AND F.M. HARTY. 1991. Comparison of presettlement, second-growth and old-growth forest on six site types in the Illinois Shawnee Hills. *Am. Midl. Natur.* 125:294–309.
- GLITZENSTEIN, J.C., C.D. CANHAM, M.J. McDONNELL, AND D.R. STRENG. 1990. Effects of environment and land-use history on upland forests of the Cary Arboretum, Hudson Valley, New York. *Bull. Torrey Botanical Club* 117:106–122.
- GUYETTE, R.P., AND D. DEY. 1995. A history of fire, disturbance, and growth in a red oak stand in the Bancroft District, Ontario. Ontario Forest Research Institute, Forest research Information paper No. 119. 14 p.
- KEEVER, C. 1953. Present composition of some stands of the former oak-chestnut forest in the southern Blue Ridge Mountains. *Ecology* 34:44–54.
- KILBURN, P.D. 1960. Effects of logging and fire on xerophytic forests in northern Michigan. *Bull. Torrey Botanical Club* 87:42–45.
- LORIMER, C.G. 1985. The role of fire in the perpetuation of oak forests. P. 8–25 in *Challenges in oak management and utilization*. Johnson, J.E. (ed.). Cooperative Extension Service, University of Wisconsin, Madison, WI.
- MCCORMICK, J.F., AND R.B. PLATT. 1980. Recovery of an Appalachian forest following the chestnut blight or Catherine Keever—you were right! *The Am. Midl. Natur.* 104:264–273.
- MELILLO, J.M., J.D. ABER, AND J.F. MURATORE. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63:621–626.
- MIKAN, C.J., D.A. ORWIG, AND M.D. ABRAMS. 1994. Age structure and successional dynamics of a presettlement-origin chestnut oak forest in the Pennsylvania Piedmont. *Bull. Torrey Botanical Club* 121:13–23.
- MONK, C.D., D.W. IMM, AND R.L. POTTER. 1990. OAK FORESTS OF EASTERN NORTH AMERICA. *CASTNEA* 55:77–96.
- NOWACKI, G.J., M.D. ABRAMS, AND C.G. LORIMER. 1990. Composition, structure, and historical development of northern red oak stands along an edaphic gradient in northcentral Wisconsin. *For. Sci.* 36:276–292.
- NOWACKI, G.J., AND M.D. ABRAMS. 1992. Community, edaphic and historical analysis of mixed oak forests of the Ridge and Valley Province in central Pennsylvania. *Can. J. For. Res.* 22:790–800.
- ORWIG, D.A., AND M.D. ABRAMS. 1994. Land-use history (1720–1992), composition, and dynamics of oak-pine forests within the Piedmont and Coastal Plain of northern Virginia. *Can. J. For. Res.* 24:1216–1225.
- PALLARDY, S.G., T.A. NIGH, AND H.E. GARRETT. 1988. Changes in forest composition in central Missouri: 1968–1982. *Am. Midl. Natur.* 120:380–390.
- PARSON, D.J. 1976. The role of fire in natural communities: An example from the southern Sierra Nevada, California. *Environmental Conservation*. 3:91–99.
- PEET, R.K., AND N.L. CHRISTENSEN. 1980. Hardwood forest vegetation of the North Carolina Piedmont. *Veroff Geobotanical Institute ETH, Shift, Rubel.* 69:14–39.
- RODGERS, C.S., AND R.C. ANDERSON. 1979. Presettlement vegetation of two prairie counties. *Botanical Gazette* 140:232–240.
- RUSSELL, E.W.B. 1981. Vegetation of northern New Jersey before European settlement. *Am. Midl. Natur.* 105:1–12.
- SCHAPFALE, M.P., AND P.A. HARCUMBE. 1983. Presettlement vegetation of Hardin County, Texas. *Am. Midl. Natur.* 109:355–366.
- SCHULER, T.M., AND W.R. MCCLAIN. 2003. Fire history of a Ridge and Valley oak forest. *USDA For. Serv. Northeastern Res. Sta. Res. Pap. NE-274*. 9 p.
- SEISCHAB, F.K. 1990. Presettlement forests of the Phelps and Gorham purchase in western New York. *Bull. Torrey Botanical Club* 117:27–38.
- SHUMWAY, D.L., M.D. ABRAMS, AND C.M. RUFFNER. 2001. A 400-year history of fire and oak recruitment in an old-growth oak forest in western Maryland, USA. *Can. J. For. Res.* 31:1437–1443.
- STEPHENSON, S.L., H.S. ADAMS, AND M.L. LIPFORD. 1992. The impacts of human activities on the upland forests of western Virginia. *Virginia J. Sci.* 43:121–131.
- SUTHERLAND, E.K. 1997. History of fire in a southern Ohio second-growth mixed-oak forest. P. 172–183 in *Proc. 11th Central Hardwood Forest Conference*, Pallardy, S.G., R.A. Cecich, E.H. Garrett, and P.S. Johnson (eds.). USDA For. Serv. Gen. Tech. Rep. NC-188.

- WASHBURN, C.S.M., AND M.A. ARTHUR. 2003. Spatial variability in soil nutrient availability in an oak-pine forest: Potential effects of tree species. *Can. J. For. Res.* 33:2321–2330.
- WHITNEY, G.G. 1994. *From coastal wilderness to fruited plain*. Cambridge University Press, Cambridge, United Kingdom. 451 p.
- WHITNEY, G.G., AND W.C. DAVIS. 1986. Thoreau and the forest history of Concord, Massachusetts. *J. For. History* 30:70–81.
- WHITNEY, G.G., AND J.P. DECANT. 2001. Government land office surveys and other early land surveys. P. 147–172 *in* *The historical ecology handbook: A restorationist's guide to reference ecosystems*. Island Press, Washington DC.
- WUENSCHER, J.E., AND A.J. VALIUNAS. 1967. Presettlement forest composition of the River Hills region of Missouri. *Am. Midl. Natur.* 78:487–495.
-