ECOLOGICAL AND ECOPHYSIOLOGICAL ATTRIBUTES AND RESPONSES TO FIRE IN EASTERN OAK FORESTS

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Abstract.—Prior to European settlement vast areas of the eastern U. S. 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, 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. At Fort Indiantown Gap in southeast Pennsylvania, periodic burning over the last 50 years resulted in sites with lower tree density and a higher proportion of overstory oak species than unburned stands. Oak saplings averaged 875 per ha in burned forests and 31 per ha in unburned forests. Red maple had overstory importance of 7 percent and 24 percent in burned and unburned stands, respectively. The leaf litter of many oak replacement species (e.g., red maple, sugar maple, black birch, beech, black gum and black cherry) is less flammable and more rapidly mineralized than that of the upland oaks, reinforcing the lack of fire. The trend toward increases in non-oak tree species will continue in fire-suppressed forests, rendering them less combustible for forest managers who wish to restore natural fires regimes. Moreover, many of the oak replacement species are now growing too large, both above and below ground, to readily kill with understory fire. 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. Thus, forest supervisors in the East who wish to use fire as a management tool in oak forests need to act sooner rather than later.

KEY WORDS: historical ecology, disturbance, succession, fire suppression, oak replacement

INTRODUCTION

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 following 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 particularly 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,

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there has been little recruitment of oak 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 the present 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 end of the clearcutting era, catastrophic wildfires, the beginning of the fire suppression era, and chestnut blight. In this paper I 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 following European settlement. Due to the large increase in non-pyrogenic, 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. There is little or no oak 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 percent (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 percent of certain presettlement forests in southern and central Michigan and Wisconsin, in some 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 clearly was 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 the dominant species, with a frequency of 21 to 49 percent. White oak was second to black oak (*Q. velutina*; 33 percent) with a frequency of 17 to 30 percent 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 on valley floors, but was a codominant 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 northeastern Ohio and western New York were dominated by sugar maple and beech (*Fagus grandifolia*), with lesser amounts (5 to 14 percent) 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.

There is much less information on pre-European forest composition for the South and Southeast (Table 1). The few existing studies suggest that oak species were not typically dominant but did achieve frequencies of 5 to 18 percent 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 in the original forest (Braun 1950, Peet and Christensen 1980, Monk et al. 1990; Barnes 1991).

OAK DECLINE FOLLOWING EUROPEAN SETTLEMENT

Significant changes in the composition of oak forests occurred in most regions from presettlement the to present. In 18 of 26 examples reviewed here, white oak experienced a decline in frequency of 10 percent or more (Table 2). Six examples reported no significant change,

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

Region and location	Presettlement forest composition	Reference
Northeast		
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
Lake States		
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
Mid-Atlantic		
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
eastern WV		
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
southern WV	white oak (24), chestnut (12), hickory (9), chestnut oak (6)	Abrams et al. 1995
northern 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
Mid-west and central region		
central MO	white oak (32), black oak (11), sugar maple (9), elm (8),	Wuenscher and Valiunas 1967
eastern IL	white oak (27), black oak (18), hickory (6), elm (10)	Rodgers and Anderson 1979
southern IL		
south slopes	white oak (81)	Fralish et al. 1991
ridge tops	white oak (45), black oak (33),	Fralish et al. 1991
northeast OH		
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
South and southeast		
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

Table 2.—Percent frequency of present-day forest composition in the Eastern United States (examples chosen based on availability of corresponding pre-European settlement witness tree data)

Region and location	Present day	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
Midwest 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	sugar maple (28), elm (14), basswood (11), white ask (10), white oak (5)	Whitney 1994
southern WI	(savanna)white oak (34), hickory (30), black oak (24), black cherry (12)	Whitney 1994
southern WI	(savanna)white oak (54), black oak (25), black cherry (17)	Cottam 1949
central Wisconsin	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

whereas two cases actually showed an increase or more than 10 percent 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 more than 20 percent in the Connecticut Valley and Eastern Lowlands (Table 2; Foster et al. 1998). In the Hudson Valley of eastern New York, white oak declined mroe than 30 percent (Glitzenstein et al. 1990). Similar declines were noted for white oak in northwest and southeastern 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 percent to 30 percent) was reported on south slopes in southern Illinois (Fralish et al. 1991).

Currently, 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 - 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). Apart from 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).

Large increases in red oak and chestnut oak also occurred from presettlement to the present (Tables 1 - 2). Red oak increased from 7 to 19 percent in central Massachusetts and from 2 to 22 percent on north-facing slopes in southern Illinois (Fralish et al. 1991; Whitney and Davis 1986). Red oak has importance values of 37 to 51 percent in present forests of north-central Wisconsin, where it formerly represented less than 1 percent of the original northern hardwood-conifer forest (Nowacki et al. 1990). Increases in red oak ranging from 9 to 19 percent and in chestnut oak from 7 to 25 percent 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 percent (from 1932 to 1982), while red maple increased from 1 to 11 percent (Stephenson et al. 1992). Chestnut oak increased in frequency from less than 1 percent to 26 percent 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 intensive logging and burning of both high- and low-elevation 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 had a frequency exceeding 5 percent. It is likely that there were small populations of red oak 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 probably was facilitated by its increase in surrounding forests that were more highly disturbed (Abrams et al. 1995; Abrams and Copenheaver 1999).

The post-settlement 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 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 codominated in the original forest, chestnut oak was the apparent victor following the catastrophic disturbances. However, many chestnut oak forests now are being invaded by red maple (Table 2).

RISE IN RED MAPLE IN EASTERN OAK FORESTS

By far, the largest increases in species frequency on present-day upland oaks sites are from red maple (Tables

1 - 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 region. This is even more impressive when you consider that little red maple was 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. 2001; 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 now is the dominant later successional, oak replacement species on mesic, nutrient-rich sites (Pallardy et al. 1988; Fralish et al. 1991).

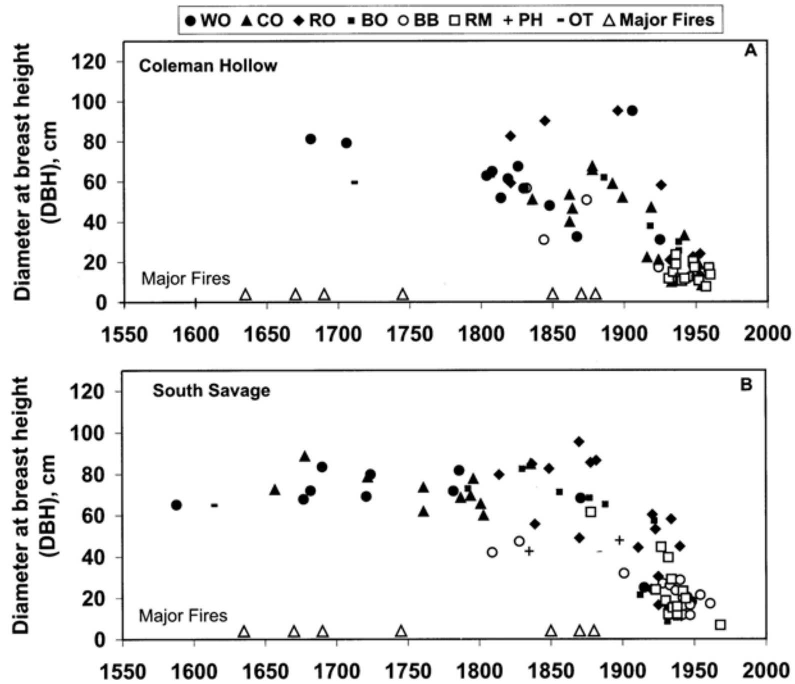

Figure 1.—Age-diameter relationships for all cored trees and the major fire years (> 25% of sampled trees scarred; indicated by triangles along x-axis) in two old-growth forests on Savage Mountain in western Maryland (adapted from Shumway et al. 2001). WO = white oak; CO = chestnut oak, BO = black oak, BB = black birch, RM = red maple, PH = pignut hickory, OT = other tree species.

The situation for red maple is somewhat analogous to the rise in red oak 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 red oak, and would have been less common on uplands. After 1900, red maple quickly expanded out of the protected areas and began 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, e.g., red oak, red maple, black birch, and black cherry (Whitney 1994; Whitney and Decant 2001).

A CASE STUDY OF FIRE HISTORY AND OAK RECRUITMENT IN AN OLD-GROWTH OAK FOREST

Fire history and dendroecology (based on tree ring analysis) 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 percent), chestnut oak (23 percent), white oak (20 percent), red oak (14 percent), and black oak (9 percent), whereas the South Savage stand is dominated by chestnut oak (20 percent), black birch (*Betula lenta*; 18 percent), red oak (17 percent), red maple (17 percent), black oak (11 percent), and white oak (6 percent). 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 percent), hickory (18 percent), black oak (12 percent), chestnut oak (11 percent), chestnut (10 percent), and red oak (5 percent).

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 to 1780) and early post-settlement (1780 to 1900). These included seven major fires year in which at least 25 percent of the sample trees were scarred in a given year (Fig. 1). 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, it is difficult to explain the large reduction in white oak and chestnut oak recruitment after 1800, though they might have been outcompeted by the other oaks. After 1900, red oak was the only oak species to recruit in significant numbers. This was associated with the loss of overstory chestnut from the blight.

Coleman Hollow differed from South Savage in species composition and the fact that it contained only two very old oaks—white oaks 290 and 320 years old (Fig. 1). 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. There was little recruitment of white oak 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 to 20 years in other oak forests in the Eastern and Central United States (Guyette and Dey 1995; Sutherland 1997; Schuler and McClain 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 and red oak recruitment study in West Virginia (Schuler and McClain 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, red maple and black birch were absent from the witness tree record and among the older trees in the forests, even though they can live for more than 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.

IMPACTS OF RECENT, RECURRING FIRE ON OAK FOREST COMPOSITION AND RECRUITMENT

The National Guard Training Center at Fort Indiantown Gap near Harrisburg, Pennsylvania, has experienced frequent fires since the 1950's on the ridges and since the 1980's in the valleys as a result of military training exercises. This represented an unique opportunity to investigate the role of recent and repeated fire in oak forests in the Eastern United States. We investigated four frequently burned and two unburned sites replicated in Ridge and Valley ecosystems (Signell et al. 2006).

The cross sections collected from stand VB1 indicate that it initiated following a fire in 1941; a second fire occurred in 1953 (Fig. 2). Most cross sections had pith dates of 1953 but several individuals initiated in 1942 and one of these had a 1953 fire scar. VB1 has also experienced major fires in 1984, 1986, 1990 and 1992, with mean fire return interval (FRI) of 2.7 years for the period. The diameter distribution of VB1 is bell shaped rather than positively skewed as in VU (Fig. 3). Oak dominated every size class and shade-tolerant/fire sensitive species were uncommon. Total oak importance value exceeded 94 percent in this stand. Cross sections from stand VB2 showed recruitment dates from the early 1940s. Like VB1, this stand experienced a fire-free period following stand initiation. No fire scars were found until the early 1980s, after which at least three fires occurred, in 1982, 1985 and 1990, resulting in a mean FRI of 4 years. VB2 has a bell-shaped diameter distribution similar to that for VB1, and oak dominated all size classes (Fig. 3). However, VB2 has more shade tolerant-species present in the smaller diameter classes, including red maple and blackgum, than were observed in stand VB1. Total oak importance value in stand VB2 was 81.1 percent.

Stands RU and RB1 were part of an uninterrupted forest stand in 1952. Tree-ring data show that the

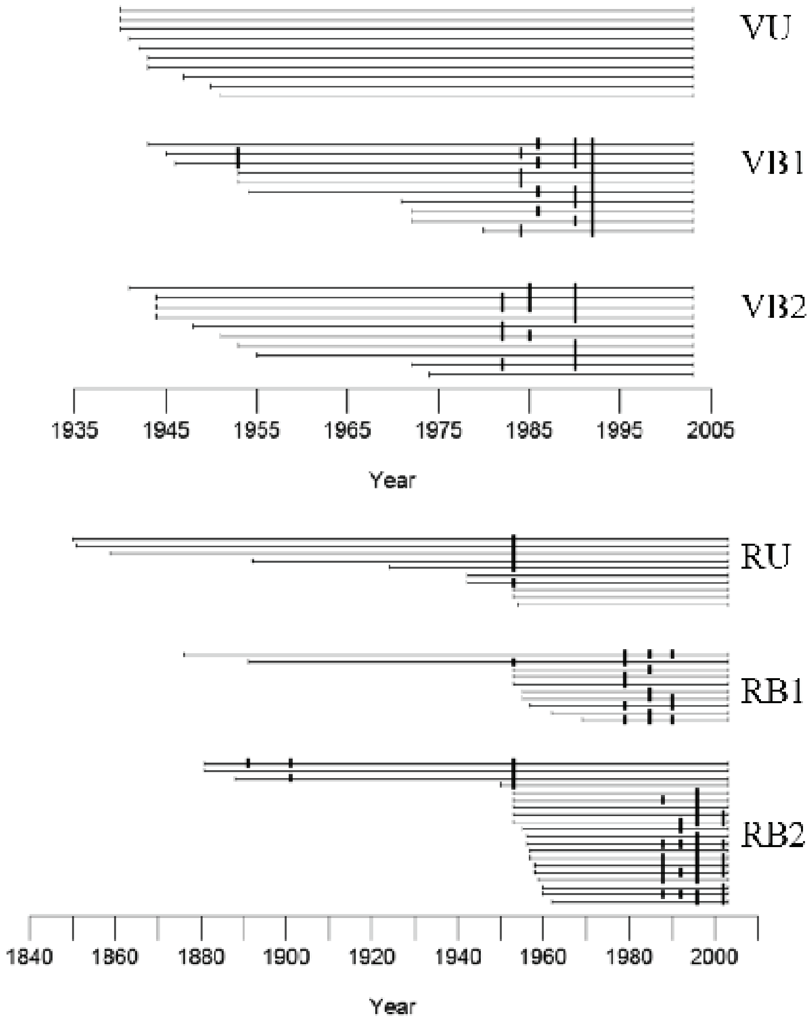

Figure 2.—Fire scar records obtained from tree basal cross sections at Fort Indiantown Gap, Pennsylvania. Horizontal lines represent the visible growth rings for each tree, and vertical bars represent fire scars (adapted from Signell et al. 2005).

oldest trees in both stands originated around 1845 (Fig. 2). No fire scars were found in any of the cross sections obtained from these stands until 1952, when both stands experienced a fire severe enough to scar many of the approximately 100-year-old chestnut oaks present at the time. Between 1952 and 1956, a road was constructed between the two stands. Following the road construction, RB1 experienced fires in 1979, 1983 and 1991, while RU has been free of fire (Fig.2).

RU had high stem density, mostly from chestnut oak, red maple, and black birch (Fig. 4), but few individuals more than 30 cm in diameter at breast height, and they were mostly chestnut oak. Nonetheless, these large trees contributed greatly to the high basal area in this stand. Red maple and black birch dominated the smaller size classes (Fig. 4). RB1 had lower stem density than stand RU. Of the major species, only scarlet oak had more stems in stand RB1 versus RU. Most black birch and red maple were concentrated in rocky patches. Chestnut oak had the highest importance in this stand; overall oak importance was 63.7 percent. Stand RB2 had several large chestnut oaks and red oaks that were clustered on a rocky boulder field. Fire occurred in 1890 and 1900, soon after stand establishment (Fig. 2). No fire scars were recorded between 1900 and 1952. Many of the smaller trees recruited following a fire in 1953. RB2 had additional fires in 1986, 1991, 1996, and 2000 (Fig. 2).

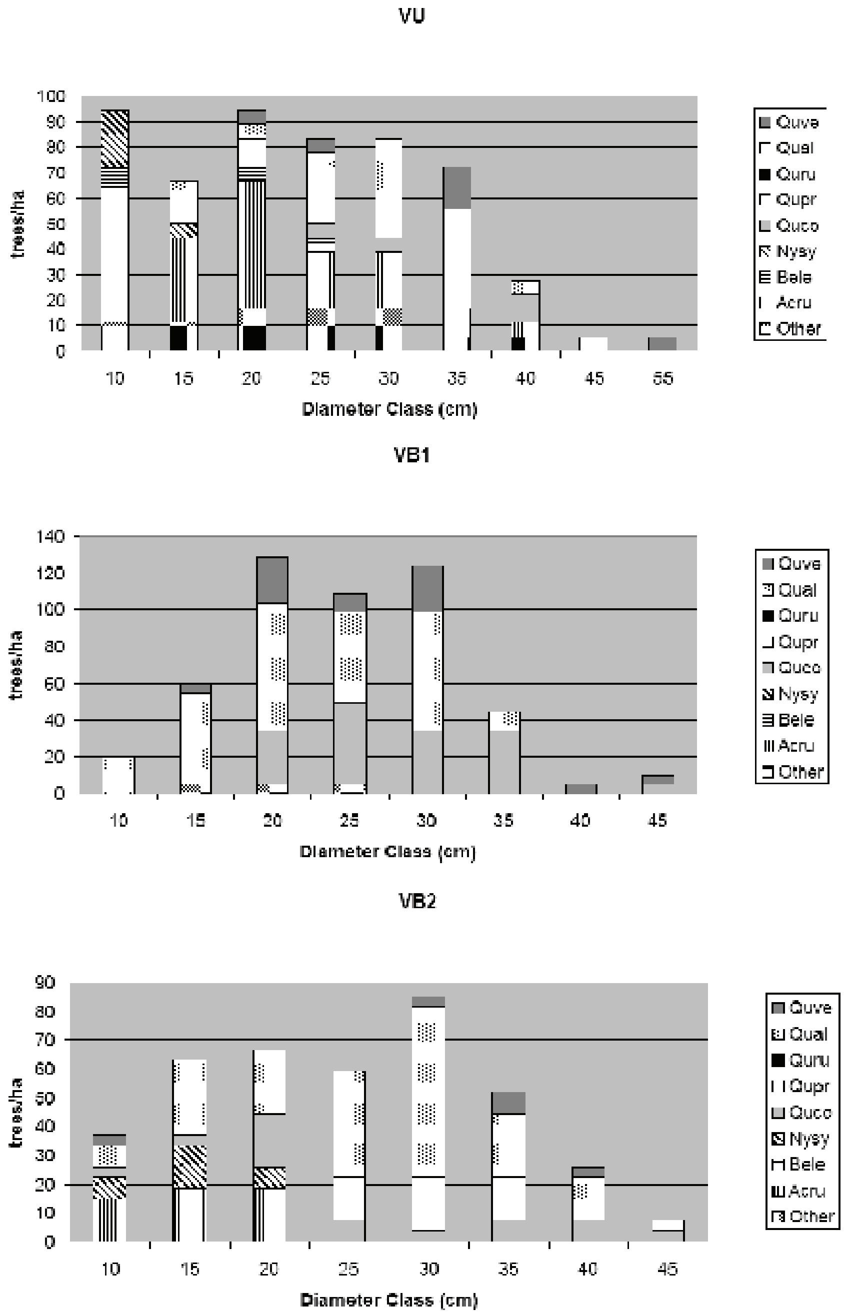

Figure 3.—Diameter distributions for unburned (VU) and burned valley stands (VB1, VB2) at Fort Indiantown Gap, Pennsylvania. Quve = *Quercus velutina*, Qual = *Quercus alba*, Quru = *Quercus rubra*, Qupr = *Quercus prinus*, Quco = *Quercus coccinnea*, Nysy = *Nyssa sylvatica*, Bele = *Betula lenta*, Acru = *Acer rubrum* (adapted from Signell et al. 2005).

RB2 has high tree density, with oak species dominating all diameter classes (Fig. 4). There were substantial numbers of red maple and black birch, primarily on rocky patches. Oak importance was 69.2 percent in this stand.

Burned sites generally had lower tree density and a higher proportion of overstory oak species (64 to 92 percent relative importance value) than unburned stands (47 to 49 percent importance). Oak saplings averaged 875 per ha in burned forests and 31 per ha in unburned forests. Red maple, the most aggressive oak replacement species in the Eastern United States, had overstory importance of 7 percent and 24 percent in burned and unburned stands, respectively. Oak saplings ranged from 824 to 1,545 per ha in three of the four burned

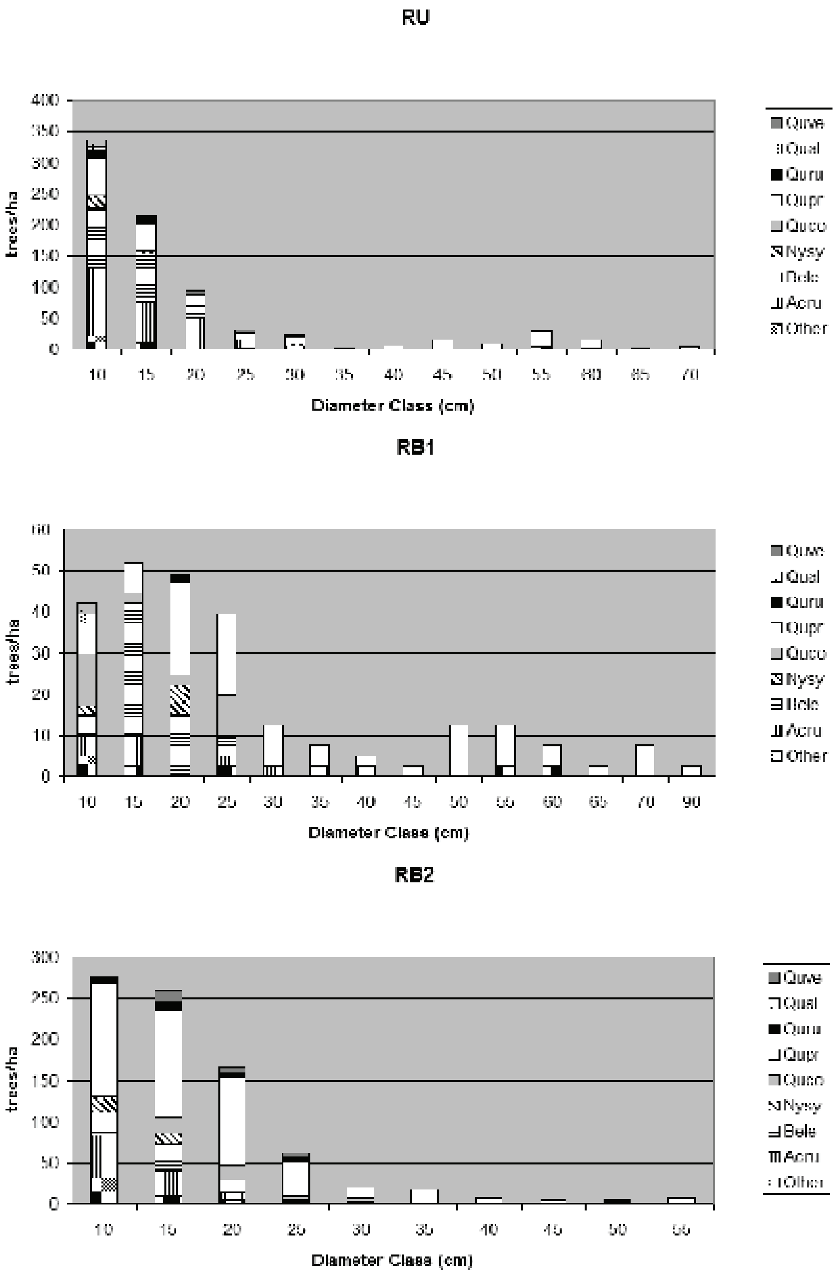

Figure 4.—Diameter distributions for unburned (RU) and burned ridge stands (RB1, RB2) at Fort Indiantown Gap, Pennsylvania. Quve = *Quercus velutina*, Qual = *Quercus alba*, Quru = *Quercus rubra*, Qupr = *Quercus prinus*, Quco = *Quercus coccinnea*, Nysy = *Nyssa sylvatica*, Bele = *Betula lenta*, Acru = *Acer rubrum* (adapted from Signell et al. 2005).

stands and 0 to 62 per ha in the unburned stands. Oak sapling density was only 62 per ha in one recently (2002) burned ridge stand that had the highest tree density. There were no red maple saplings in three of the four burned stands. Oak saplings were most abundant when overstory density was less than 400 trees per ha and understory tree density was less than 200 trees per ha. When overstory or understory tree density exceeded 400 and 200 trees/ha respectively, oak regeneration was virtually absent. The results of this study suggest that periodic fire often reduces overstory and understory stand density and promotes successful regeneration of relatively shade intolerant oak species in the Eastern United States. However, high tree density in forests will retard the development of oak understories and subsequent recruitment even if periodic burning occurs.

Table 3.—Adaptations to fire, drought and understory conditions in upland oaks relative to non-oak hardwood species (adapted from Abrams 1996)

Fire	Drought	Understory
Thick bark	Deep rooting	Low-moderate shade tolerance
Rotting resistance after scarring; tyloses in white oaks	High predawn leaf water potential	Large seed and cotyledons
Deep and extensive rooting	Thick leaves	Large initial seedling and roots
Vigorous sprouting in young trees	High leaf mass per area	Relatively high net photosynthesis
Improved fire-created seedbed	High stomatal density	Relatively low respiration
Increased germination	High leaf nitrogen	Low light compensation point
Increased seedling survival	High net photosynthesis	Medium light saturation values
Lowered seed and seedling predation	High leaf conductance	Slow seedling shoot growth
	High drought threshold for stomatal closure	High c-based phenolics
	High osmotic adjustment	Shoot dieback
	High wilting threshold	Intense seed and seedling predation
	Low nonstomatal inhibition of photosynthesis	Often overtopped by competing species
	Leaves not drought deciduous	Responsive to canopy gaps
		Increase in mixed-mesophytic hardwoods decreasing litter layer flammability

ECOPHYSIOLOGICAL ATTRIBUTES OF UPLAND OAK SPECIES

Upland oaks are prevalent across a broad array of sites, including drought-prone areas, have evolved with periodic understory burning and are transitional to later successional species in the absence of fire on most sites. Thus, upland oaks presumably possess a suite of ecophysiological adaptations for drought and fire but not for competing in a closed forest understory dominated by more shade-tolerant species. In this section I summarize the ecophysiological attributes of upland oaks as they relate to its success in the presettlement forest and subsequent decline following European settlement (Table 3).

Fire Adaptations

In an early opinion survey of the fire resistance for 22 northeastern tree species, oaks (chestnut oak, black oak, white oak, and scarlet oak) were rated in four of the top six positions (Starker 1934). A ranking of increasing bark thickness and fire resistance reported that bur oak > black oak > white oak > red oak (Lorimer 1985). White oaks (subgenus *Leucobalanus*), including bur oak, chestnut oak, and white oak, can produce tyloses, eccentric outgrowths of cell walls in response to wounding, which allow for effective compartmentalization of fire scar injuries. In this respect, white oaks should be more resistant to fire than red oaks (Table 3). Fire also may be beneficial to oaks relative to other hardwood species because of their deep and extensive rooting, vigorous sprouting ability, and increased germination and survival on fire-created seedbeds (Table 3).

Drought Adaptations

Oaks are among the most deeply rooted tree species in the Eastern United States, which allows them to maintain relatively high predawn shoot water potential from superior overnight rehydration (Table 3). Oak leaves typically are more xerophytic, having greater thickness, mass per area and stomatal density, and higher nitrogen content than leaves of non-oak species. These factors contribute to the relatively high photosynthesis and transpiration in white oak and other oak species. Oaks need to develop the necessary tissue water relations to support high level of gas exchange, and they often exhibit low osmotic potentials, low relative water content at zero turgor, and low water potential threshold for stomatal closure than non-oak species (reviewed in Abrams 1992).

Adaptations to Forest Understory Conditions

Most upland oaks are considered to have intermediate shade tolerance (Table 3; Burns and Honkala 1990), though Crow (1988) considered red oak to have low shade tolerance. Oaks produce a large acorn that allow for high initial growth, though white oaks typically exhibit low shoot growth after the first year in forest understories (Cho and Boerner 1991). Sapling density is low for most oaks, especially for white oak. This indicates that there is a severe "bottleneck" between the oak seedling and sapling stages (Crow 1988; Nowacki et al. 1990).

The physiological mechanisms for slow growth in oak seedlings are complex. Photosynthetic rates of oak in shaded conditions are often higher than in non-oak species, while oak respiration rates are low to moderate (Table 3). Oak seedlings often produce large root systems but experience recurring partial or complete shoot dieback (Crow 1988; Abrams 1992, 1996). Allocating carbon in this manner has its limitation, particularly for the once dominant white oak. White oak is reported to have slower height growth than chestnut, red oak, and black oak (Whitney 1994). Following a 1985 tornado, white oak seedling/sprouts had among the lowest rates of height growth for seven species (including black oak, red oak, and black cherry; Kauffman 2002).

Upland oaks are well adapted to dealing with a range of moisture conditions, and their moderate shade tolerance is conducive to gap-phase regeneration in fire-maintained forests. However, upland oaks grow slowly in deeply shaded forest understories dominated by later successional species and in heavily disturbed areas, where they are overtopped by competitors. Intensive deer browsing, despite the production of carbon-based defense chemicals, only exacerbates the situation (Table 3). Moreover, the increase in later successional, mixed-mesophytic hardwoods is reducing the flammability of the litter layer, which likely will result in less frequent and intense surface fires in the future. These ecological stressors represent a serious threat to the survival of upland oaks.

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 was broken during the 19th and early 20th century, leading 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 McClain 2003). Thus, the broad ecological distribution of oaks in the Eastern United States can be attributed directly (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 now is apparent throughout most of their range.

There has been a nearly complete cessation of oak recruitment over the last 50 to 100 years in all but the most xeric and nutrient poor sites. There now is strong competitive pressure on oak regeneration 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. By 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 <u>more</u> prone to fire (Biswell 1967; Parsons 1976; Brown et al. 2000). The declining combustibility of eastern forests may be 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 of opportunity may be closing.

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