THE PALEOECOLOGY OF FIRE AND OAKS IN EASTERN FORESTS

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Abstract.—Oaks (*Quercus* spp.) currently dominate eastern deciduous forests, but are widely perceived as declining, with regeneration inadequate to perpetuate many stands. Most stands regenerated following fire in the 19th and early 20th centuries, and a lack of recent fire is viewed as contributing to the shortage of sapling and pole-size stands. But paleoecological studies provide conflicting evidence for the role of fire in the long-term maintenance of oak forests. Here I describe the methods used in reconstructing past vegetation and fire regimes, review the results of previous studies, and present new results for sites from Virginia to Maine. Oaks have dominated mixed mesophytic forests in western Virginia for more than 6,000 years, with sedimentary charcoal levels suggesting a fire regime dominated by infrequent, light surface fires. The arrival of European settlers and a presumed increase in fire activity had little effect on oak abundance. At a higher elevation on more xeric soils, increased fire with settlement caused a shift from oak to pine dominance. On Long Island, NY, oaks have dominated xeric soils for thousands of years, but with more fire than in western Virginia. However, a dramatic increase in fire activity with settlement increased the importance of pines relative to oaks in southeastern Massachusetts' outwash plains. On the Maine coast, where oaks have been minor component of the vegetation for thousands of years, fires appear to have caused slight increases in oak importance both before and especially since European settlement. These results suggest that, depending on the landscape context, fire can favor or select against oaks, and that managers should carefully consider how fires will interact with climate, topography, and other factors before prescribing fire as a solution to the current lack of oak regeneration. It is likely that burn severity and fire return intervals, as they impact both oaks and their potential competitors, will determine whether or not individual oak stands will benefit from the reintroduction of fire.

INTRODUCTION

With at least 36 species, one or more of which occur in every state east of the Great Plains (Samuelson and Hogan 2006), oaks (genus *Quercus*) are the preeminent trees of the eastern forest. Twenty-one species are at least locally important as timber species (Burns and Honkala 1990). All, and especially those of the white oak (Leucobalanus) group, provide mast for game and nongame species of wildlife. Species not important for timber (e.g., the scrub oaks as a group) provide essential food and cover for several species of Lepidoptera (moth) larvae that are rare in at least portions of their ranges (Wagner et al. 2003). Oaks dominate in a variety of habitats, from rich cove forests of the southern Appalachians to dry ridgetops and sand plains of New England and the Atlantic Coastal Plain.

Throughout the range of oaks there is a widely held belief that regeneration is inadequate to perpetuate existing stands. Abundant deer, especially in urban interface areas, browse and kill seedlings and saplings. Late 20th-century fire suppression is blamed for the lack of regeneration in many stands. Tirmenstein (1991) citing several studies, observed:

> Fire has played an important role in deciduous forests of the eastern United States. Evidence suggests that most oaks are favored by a regime of relatively frequent fire. Many present-day oak forests may have developed in response to recurrent fire. Declines of oak forests have been noted throughout much of the East and are often attributed to reduced fire frequency.

Detailed information on the effects of fire on many oak species is available through the Fire Effects Information System. Most are viewed as being favored, at least in the regeneration stage, by fire. Tirmenstein (1991) noted, in discussing the fire ecology of white oak: "it is unable to regenerate beneath the shade of parent trees and relies on periodic fires for its perpetuation. The exclusion of fire has inhibited white oak regeneration through much of its range." Crow (1988) argued that frequent fires are required to maintain northern red oak (*Quercus rubra*),

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and that increased fire frequency has caused, in some cases, the replacement of mesic hardwoods (e.g. sugar maple, *Acer saccharum*) by red oak. Conversely, reduced fire frequency is resulting in the replacement of northern red oak by mesic hardwoods in many areas of the Lake States and Northeast (Crow 1988).

The important role of fire in the development of oak stands during the historic period, i.e., roughly since the arrival of European settlers on the North American continent, is well documented (see Abrams et al. and Ruffner, this volume). Although this period spans many human generations, it represents no more than several for most oak species, which typically live 150 to 250 years with some (e.g., white oak) living more than 600 years (Tirmenstine 1991). Given the longevity of oaks and the time that it takes forest stands to develop, mature, and be replaced by new growth, managers should consider long-term interactions between oaks and environmental factors, including fire. The goal of this paper is to examine the paleoecology of oak as a genus, and to examine the interaction between oaks and fire over hundreds and even thousands of years. I start from the premise that it is through understanding the long-term history of the interaction of fire and oaks that we will gain the wisdom required to manage modern oak ecosystems and to perpetuate them far into the future.

PALEOECOLOGICAL METHODS

It is widely accepted that Native Americans more than lightning were the primary source of ignitions that burned through eastern forests prior to the arrival of Europeans (Bromley 1935; Day 1953; Cronon 1983). Although opinions differ on the extent of Native American burning (Russell 1983), there can be little argument that human-caused fires affected vegetation development, at least near Native American population centers (Patterson and Sassaman 1988). The first successful European settlements were in the early 17th century in Virginia and Massachusetts, but Mann (2002) argued that Europeans influenced Native populations, and by inference their effects on vegetation through burning, long before that. As early as the late 15th century with Spanish exploration in the South, and perhaps earlier (by Vikings to the north), Europeans brought diseases that decimated Native American populations throughout the East. To the extent that human populations were reduced, the influence of fire on vegetation probably was similarly reduced.

There are several methods for exploring fire and vegetation history: written accounts by explorers and naturalists, dendroecology and fire scar analysis, evaluation of 19th century photos in comparison with modern photographs (repeat photography), and, in the 20th century in particular, fire records and quantitative descriptions of fire effects. All of these methods have been applied effectively to describe vegetation and fire interactions before or at the time that Europeans settled the West. But few are useful in the East, where an understanding of fire regimes and fire-vegetation interactions unaffected by Europeans depends on a knowledge of how fire, vegetation, and humans interacted 500 or more years ago. Trees older than about 400 years are rare in the East, especially outside of swamps. Historical accounts described the land only at the time of observation, and extrapolation to before 1600 AD is tenuous (Mann 2002). Photographs, written records and ecological data from the 19th and 20th centuries tell us little about what might have occurred 300 to 400 years earlier.

Thus, paleoecologists have only fossil pollen and charcoal analyses of lake and bog sediments with which to investigate fire-vegetation interactions for the prehistoric period. Fossil pollen analysis, first developed by von Post (1916, cited in Davis 1963) in Scandinavia, has been used in North America since the 1930's to reconstruct vegetation-climate interactions. Iversen (1941) first used charcoal analysis to investigate the effects of Stone Age people on vegetation of Denmark. But the technique has only recently (since about 1950 initially, and, widely, since the 1970's) been employed in North America (Patterson et al. 1987). Both pollen and charcoal analyses involve examination of indirect evidence of vegetation and fire and are fraught with a series of assumptions and constraints. But the data they provide about periods in the past for which no other information is available is of great value.

Fossil Pollen Analysis

Paleoecologists obtain sediments from small ponds, lakes, and bogs using coring devices that preserve the stratigraphy of the core, with the youngest sediments at the top and older ones below. Cores are extracted in 0.5- to 1-m lengths and samples are withdrawn at intervals that depend on the rate at which sediments are estimated to have accumulated and the objectives of the particular study. A study of vegetation-climate interactions over thousands of years might involve sampling a core at intervals of 10 or more cm (100- to 200-year precision). Fire-vegetation interactions, are best described by data from cores sampled at one to several centimeters (with perhaps 5- to 20-year precision).

The theory of pollen analysis is well established. Von Post (1916), and, more recently, several North American studies observed that pollen is generally well preserved in cold, anaerobic, acidic, lake and bog sediments; that pollen of different species or genera can be distinguished one from another; and that for most species the proportion of pollen grains of different types in sediment samples approximates the proportion of plants of those types on the landscape. Sediments from cores drawn from small ponds or wetlands are more likely to reflect local conditions (Jacobson and Bradshaw 1981), with cores from bogs often containing information about vegetation of both the wetland and the surrounding upland.

Not all species can be distinguished based on their pollen; this is a particular problem for oaks. None of the 36 species native to eastern North America can be distinguished one from another based on pollen characteristics. Oaks as a group can be distinguished from other members of the Fagaceae family, e.g. beech and chestnut, and they can be distinguished from the hickories, birches, hemlock and pines, so it is largely at the level of genera that we can make inferences about fire and oak interactions. As with the other wind-pollinated species mentioned, oaks produce abundant pollen compared to maples and other largely insect-pollinated species.

Pollen data usually are expressed as a percentage, with the amount of oak pollen, as an example, a percentage of all fossil pollen identified on microscope slides after sediments are processed to remove inorganic and nonpollen organic constituents (Faegri and Iversen 1989). Percentage data suffer from the inherent limitation that if the absolute abundance of one constituent (e.g., oak pollen) increases (or decreases) dramatically, then the other constituents (e.g., pine, hemlock, hickory, birch and whatever other pollen types are identified as being present in the sample) must decline (or increase), on a precentage basis, even when the absolute number of pollen grains remains constant. The problem is illustrated with hypothetical data (Table 1A), where an absolute decline in hemlock pollen is reflected in an apparent increase in pine, oak, and other types even though they have the same absolute amounts in all samples. This problem can be circumvented if a known quantity (say 40,000 grains per cubic centimeter of sediment being processed) of a marker grain (pollen of a type not present in the local flora, e.g., *Eucalyptus* pollen for the Eastern United States) is added during processing of the sediment and counted along with the fossil grains. Where the amount of fossil pollen is compared with that of the marker grains, fossil pollen can be expressed as an absolute amount of pollen (number of grains per unit volume of sediment, see Table 1B).

If sediment accumulates at the same rate in a basin over time, the absolute pollen frequency (APF) allows species/genera represented in the data set to be evaluated independently of other types (Davis 1965). However, sediment accumulation rates are not always the same, so APF (number of grains/cm^3) is divided by sediment accumulation rate (cm/year) to yield a pollen influx rate (in number of grains/cm^2/year) (Davis and Deevey 1964). This measure of pollen abundance represents an ideal that is not always attainable because sediment accumulation rates cannot always be estimated accurately.

Cores are dated and sedimentation rates established by a variety of methods. Carbon-14 dating can establish absolute dates to 30,000 or more years before the present. But the accuracy of C-14 dates is on the order of decades to 100 years or more (Bradley 1999) and declines rapidly in sediments less than about 500 years

Table 1.—Hypothetical pollen data showing the effects a large change in the absolute amount of one pollen type (hemlock) on the percentages of other types. The number of hemlock grains (A) decreases from 150 to 5 from the deepest to the shallowest sample, whereas the number of all other types does not change. The decrease in hemlock grains is properly reflected in a sharp decline in hemlock pollen as a percentage of the total even though the total number of grains identified declines. But the percentages of the total represented by the other three types—pine, oak and all other types combined (other)—increase by more than 50 percent. Expressing the pollen as number of grains per cubic centimeter (absolute pollen frequency) yields a more appropriate interpretation (B). The addition of 40,000 grains of an exotic pollen grain per cc of sediment sample processed, and counting these grains along with the fossil grains, is assumed. Expressing data as APF still assumes that each sample represents the same number of years of accumulated sediment, an assumption that must be verified by careful dating of many sediment samples and the calculation of sediment accumulation rates for different portions of the core being analyzed.

A

depth	Pine #	Pine %	Oak #	Oak %	Hemlock #	Hemlock %	Other #	Other %	Total #	EXOTIC #
500	100	39.2	25	9.8	5	2.0	125	49.0	255	400
503	100	39.2	25	9.8	5	2.0	125	49.0	255	375
506	100	39.2	25	9.8	5	2.0	125	49.0	255	350
509	100	38.5	25	9.6	10	3.8	125	48.1	260	400
512	100	33.3	25	8.3	50	16.7	125	41.7	300	375
515	100	25.0	25	6.3	150	37.5	125	31.3	400	425

B

	#/cc	#/cc	#/cc	#/cc	#/cc
500	10000	2500	500	12500	25500
503	10667	2667	533	13333	27200
506	11429	2857	571	14286	29143
509	10000	2500	1000	12500	26000
512	10667	2667	5333	13333	32000
515	9412	2353	14118	11765	37647

old. Other isotopes, including Lead-210 (Pb-210), are useful for dating younger sediments. Lead-210 is a decay product of radon gas, which occurs naturally in soils. Concentrations of Lead-210 in sediments are used to establish sediment accumulation rates and to date sediments that generally are less than 150 to 200 years old. Cesium-137, a product of atomic bomb testing in the 1940's, allows dating of younger sediments.

Regionwide changes in the abundance of several pollen types have been dated independently. Examples include the decline in hemlock (*Tsuga canadensis*) in eastern North America approximately 5,000 years ago (Webb 1982) and the recent (1900-1920 AD) decline in chestnut (*Castanea dentata*) due to the chestnut blight (Anderson 1974). Increases in the abundance of pollen of ragweed (*Ambrosia* spp.) and plantain (*Plantago* spp.) mark the local advent of European agriculture from 300 to 350 years ago on the East Coast to 100 to 150 years ago in Minnesota.

The most precise estimates of sediment accumulation rates can be obtained from varved lake sediments, i.e. those that have alternating layers of light and dark sediment that correspond to changes in seasons within a year. A pair of one light and one dark layer forms a couplet that indicates a full year of sediment accumulation (Fig. 1). Several processes can form banded (or laminated) sediments (O'Sullivan 1983), and precise chronologies can be established from them. However, they are rare, having been identified in no more than a dozen or so lakes in Eastern North America.

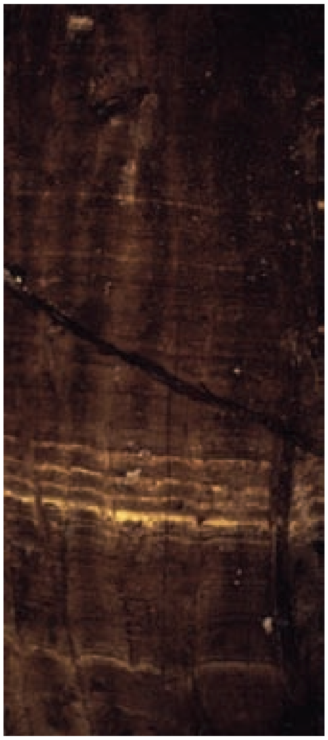

Figure 1.—Photomicrograph of varved sediments from a lake in northwestern Minnesota. Thin, horizontal bands of light and dark sediments throughout the core are thought to represent changes in the chemical composition of sediments related to seasonal variations in oxygen content of the bottom waters, with each pair of bands representing one year (Foster 1976). Broad bands in the middle of the section may have been formed by erosion events, and pairs may or may not represent one year's sediment accumulation (Patterson 1978). The core section is approximately 10 cm wide by 25 cm long, with the youngest sediments at the top of the section.

In summary, although imprecise by the standards applied to modern ecological studies, fossil pollen analysis techniques are largely standardized among research labs and limitations are well understood. Pollen analysis provides information about time periods for which no other information is available and is a useful tool for exploring hypotheses about past vegetation development and vegetation-environment interactions.

Sedimentary Charcoal Analysis

Sedimentary charcoal analysis is less widely used than pollen analysis, and there are a variety of competing techniques for quantifying past charcoal production i.e., fire activity. The half dozen or so U.S. labs routinely performing charcoal analysis tend to use a variety of methods that may or may not yield comparable results when applied to the same sediments (Patterson et al. 1987). Recent advances in the theory and methods of sedimentary charcoal analysis (Clark 1988a, b) are most useful when accurate and precise information on sediment accumulation rates is available.

Unlike pollen, which is produced annually in roughly the same amounts from similar vegetation types, charcoal is produced intermittently from fires that occur at different return intervals and that burn with different intensities in different fuels across varying potions of a landscape. Abundant charcoal is carried long distances in towering convection columns from large, intense crown fires burning in conifer forests. Conversely, charcoal produced by lower intensity surface fires burning in deciduous forest (e.g., oak and other hardwoods in the Eastern United States) is less likely to be transported long distances by air, even when large areas burn in a single fire. Short-distance transport by air and hydrologic transport in runoff probably characterizes these fires. Analysis of pollen data tends to focus on running averages that emphasize the year-to-year continuity in pollen production and gradual changes in vegetation, whereas fires can elicit dramatic changes in charcoal influx from one year to the next, and can dramatically affect pollen production within the area contributing pollen to a basin.

Patterson et al. (1987) discussed how charcoal is produced, transported to deposition sites, and eventually preserved in sediments. Larger charcoal particles signal locally occurring fires (Clark and Patterson 1997; Clark and Royall 1995a), so quantifying charcoal by particle size rather than by number of fragments has been emphasized. Charcoal often is quantified on microscope slides prepared for pollen analysis, but Clark (1988b) argued that it is the abundance of macroscopic charcoal (i.e., fragments longer than 150 to 200 microns) that provides the most information about local fire history. This is likely true for intense fires burning in heavy fuels in dry conifer forests. It is less clear if the generalization applies to fires burning through predominantly leaf (nonwoody) litter in deciduous forests.

Charcoal area (the sum of the sizes of all fragments in a sample) often is represented relative to fossil pollen content (i.e., square microns of charcoal:number of fossil pollen grains, or μ^2Ch:P) based on the idea that local fires produce large charcoal particles while at the same time reducing pollen production by killing plants. Because fires, and thus charcoal production, are transient on the landscape, reconstructing fire histories requires sampling sediments at close intervals and the analysis of contiguous (or nearly so) analysis of samples—what Green and Dolman (1988) refered to as fine resolution analyses. It is for this type of analysis that varved sediments can be most useful (Swain 1973; Clark 1988a). However, they are not required, as shown by Motzkin et al.'s (1993) detailed reconstruction of the fire and vegetation history of a Cape Cod cedar swamp. It is perhaps most important to sample small basins with well-defined watersheds relative to the area burned if one hopes to identify the response of vegetation to individual fires (Patterson and Backman 1988).

THE PALEOECOLOGY OF OAKS

Hundreds of sites have been cored and evaluated for fossil pollen content in North America. The National Oceanographic and Atmospheric Administration's (NOAA) Fossil and Surface Pollen Data website provides access to data for many of these. A map of the distribution of sites for which data are archived can be viewed at: http://www.ncdc.noaa.gov/paleo/pollen.html by clicking on the North American portion of the Web Mapper box. The cursor can be used to outline the eastern portion of the resulting view of North America to locate individual sites. Clicking on individual red stars allows the viewer to see a pollen diagram for that site, or access the original data used to generate the diagram. As an example, clicking on the one star in the state of Kentucky and then clicking on Diagram (rather than Data) provides view of the pollen diagram for Jackson Pond (Wilkins et al. 1991). The site has sediments that date to at least 20,000 years ago, and the pollen data show that oaks have dominated on the surrounding upland for approximately 10,000 years.

There are more than 100 sites for Eastern North America in the North American Pollen Data Base, and diagrams and data are available for each. Data from these sites have been merged to provide maps of North America which show the abundance of individual pollen types at discrete times (generally in increments of 500 or 1,000 years) in the past. By clicking on the Pollen Viewer box, you can access animated reconstructions of the spatial and temporal variation in the abundance of individual types. Using the scroll box to locate Quercus (5,20 and 40%) brings up color-coded range and abundance maps for oak for the past 21,000 years. Comparisons across many sites of oak pollen abundance in modern sediments with the occurrence of oak species on the surrounding landscape (as from forest inventory data) allow us to make inferences about the importance of oak as a component of past vegetation. When oak pollen exceeds approximately 5 percent, oak generally is at least present within the area contributing pollen to the basin. At 20 percent, oak is abundant; at 40 percent it dominates the overstory in the surrounding forests (Webb 1978; Webb et al. 1978). By clicking on the Play button, you can see changes in oak pollen percentages over the past 21,000 years and interpret the extent of oak trees on the landscape.

Animating the pollen viewer shows that oaks reached their current range limit by approximately 10,000 years ago and were most important during the Holocene, from 9,000 to 10,000 BP. They were the first hardwoods to establish and dominate following the retreat of boreal spruce-fir forests to the north, and their lower pollen percentages after about 9,000 BP is partly a reflection of the arrival and establishment of other species of the eastern deciduous forest (e.g., beech, the hickories and maples and, finally, chestnut). The pollen viewer shows a contraction of the area dominated by oaks (> 40 percent) during the past 500 years, especially in the Central States west of the Appalachians. This probably reflects the loss of forest land to agriculture in the Midwest. Similar declines (but more recent recoveries) in the Northeastern States have been attributed to overcutting of oaks for fuelwood in the 18^{th} and early 19^{th} centuries (Brugam 1978; Backman 1984). Cordwood shortages during this period are documented in the historic records for south-coastal New England (Stevens 1996).

THE PALEOECOLOGY OF FIRE

The NOAA web site referenced for pollen also provides access to fire history data: http://www.ncdc.noaa.gov/paleo/impd/paleofire.html. This site also links to a Web Mapper for North American sites, but the map shows only one "charcoal sediment" site east of the Mississippi River (at Indiana Dunes National Lakeshore). Pollen diagrams with accompanying charcoal data have been produced for dozens of sites in the Eastern United States by researchers from, among others, the Universities of Minnesota, Maine, and Massachusetts; Rutgers, Brown and Duke Universities; and the Harvard Forest (Harvard University). Several of these sites are included in the North American Pollen Data Base, but with no charcoal data.

The reasons for the paucity of data for charcoal for the NOAA sites are many, but perhaps the most important is the lack of a standardized way of reporting charcoal results. Summaries of data for some sites have been published (Patterson and Backman 1988; Patterson and Sassaman 1988; Clark and Royall 1996; Parshall and Foster 2002); From these summaries we can generalize that just before European settlement, the amount of charcoal in sediments decreased from west to east, with the lowest values in the mountainous regions of New England (Patterson and Backman 1988). For the most part, sedimentary charcoal content decreased with the arrival of European settlement west of the Appalachians, but increased in New England. This pattern generally is consistent with perceptions of the role of fire in eastern North America before and after European settlement (Pyne 1982).

THE PALEOECOLOGY OF OAK AND FIRE

Access to charcoal data in the same NOAA formats available for pollen would greatly facilitate an evaluation of the prehistoric role of fire in maintaining oak forests. For now, researchers are left with the evaluation of fire-oak interactions on a site-by-site basis. Reviews are available but the results are ambiguous. Clark and Royal (1995) documented a shift from northern hardwoods to white pine/oak forests with the establishment of a local Indian settlement about 1450 AD in southern Ontario, at Crawford Lake, and attribute the shift to Indian-ignited fires. In support of the role of Native American burning in the maintenance of oak forests, Delcourt and Delcourt (1997) used pollen, charcoal, and archeological data to conclude that "Native Americans played an important role in determining the composition of southern Appalachian vegetation through use of fire." They argued that fires would have stimulated sprouting "thereby increasing the abundance of chestnut and oaks growing in open groves."

Campbell and McAndrews (1995) disagreed with Clark and Royall's (1995b) Crawford Lake interpretation despite an apparent sharp increase in sedimentary charcoal at about the time that oak and pine percentages increased at the expense of elm, sugar maple, and beech. They attributed the change in forest composition to climate anomalies associated with the Little Ice Age. Clark (1995) defended the fire hypothesis but careful examination of the pollen and charcoal data (Figure 3 in Clark and Royall 1995b) apparently shows that oak pollen percentages began to increase just before (ca. 1400 AD) a major fire, as indicated by the highest charcoal influx values (centered on ca. 1450) in the core. Oaks producing pollen that contributed to the increase in percentages ca. 1400 AD probably established as early as 1350, given the several decades that it takes oaks to produce pollen after establishing from seed. Peak pollen values for oak (30 to 40 percent) are in sediments that postdate the ca. 1450 fire (approximately from 1500 to 1800). Clark (1995) notes that the Crawford lake site appears to show a different set of transitions (with a different cause—Native American burning vs. climate change?) compared to other sites in the region. At Devel's Bathtub in west-central New York, Clark and Royal (1996) found abundant oak pollen throughout the Holocene, but surprisingly little charcoal in the sediments. On the basis of data from this site, they questioned the dependence of oak on fire "at Devil's Bathtub and other sites in the northeast" (Abrams 2002).

Following the publication of their discussion with Campbell and McAndrews regarding the interpretation of the Crawford Lake site, Clark and Royall (1996) reviewed local and regional sediment charcoal for evidence of fire in presettelment northeastern North America. Thye reported that "We did not find evidence for fire in mixed oak forests, where it has been speculated that fire might be necessary for oak recruitment." Abrams (2002), reviewed several published pollen and charcoal diagrams, including those for Crawford Lake and Devil's Bathtub. Despite acknowledging the reservations of Clark and Royall (1996), he concluded that "many paleoecological papers show an intrasite increase in regional or local charcoal with increases in oak abundance."

My own review of published and unpublished work for this paper supports the somewhat ambiguous interpretation suggested by Clark and Royall. It is clear that at many sites charcoal is abundant when oak is dominant, or that across sites, samples from sites with more oak tend to have more charcoal than those from sites surrounded by more mesic, less fire-prone forest types. Crawford Lake notwithstanding, what appears to be lacking is evidence that an increase in fire has caused oak to become more abundant where it was less so. Most fire managers would acknowledge that litter fuels in oak forests are more prone to burn than those in mesic forests. Indeed, the northern hardwood forests of western New England are widely referred to by foresters as "asbestos forests" (Borman and Likens 1979), an acknowledgement of the low flammability of beech, maple, and birch litter. But questions remain: Is there more oak pollen in sediment samples with abundant charcoal because fire favors oak-dominated vegetation? Is there more charcoal in sediments with abundant charcoal because oak fuels are more likely to burn?

I believe that insights can be gained by examining individual sites. I next use data from sites in Virginia, southern New England/Long Island, and on the coast of Maine to illustrate some of what we have learned about the interaction between fire and oaks along the Atlantic Seaboard. Following the example of Jacobson (1979), I have chosen pairs of sites in each of the three regions to illustrate how oaks growing on different sites respond differently to fire.

Western Virginia

We reconstructed fire and vegetation histories for two different sites near Staunton in western Virginia (Patterson and Stevens 1995). Brown's Pond, at an elevation of 2,000 feet in Bath County (38°08′50″ N, 79°36′23″ W), lies in a protected cove and is surrounded by mixed mesophytic forests dominated by red and white oaks and a variety of associated hardwood species. Pines occur only occasionally on the surrounding uplands. Soils are deep (greater than 60 inches to bedrock) loams. Pollen (but not charcoal) data for sediments dating to 17,350 BP are available in the North American Pollen Data Base (Kneller and Peteet 1993). We obtained a 90-cm-long core from the site in 1994 and analyzed the sediments for pollen and charcoal content (Fig. 2). Increases in pollen of agricultural indicators (chiefly ragweed) mark the advent of cultivation by Europeans 300 years ago. Oaks have been the dominant species in the Brown's Pond watershed, with pollen ranging from 40 to 60 percent (of all pollen grains identified) in all samples. Charcoal to pollen ratios (Ch:P) range from 0 to more than 400. Our work on Mount Desert Island, Maine suggests that Ch:P values in excess of 150 to 200 indicate fires occurring in the watershed of small ponds, whereas lower values probably represent charcoal blown in from afar (Patterson and Backman 1988; Clark and Patterson 1997). Although individual peaks in charcoal abundance are evident, the sampling interval was broad and identifying individual fires and estimating the interval between them are not possible. Still, we concluded that fires have been part of the local landscape throughout the 6,000-year period represented by the core. Charcoal values were somewhat higher before Europeans arrived, but the overall abundance of fire on the landscape did not change with their arrival.

Green Pond is approximately 30 miles southeast of Brown's Pond at an elevation of 3,200 feet in Augusta County (37°56′23″ N, 79°02′51″ W). It lies on an exposed ridge known locally as Big Levels and is surrounded by chestnut (*Quercus prinus*) and black (*Q. velutina*) oaks, and pitch pine (*Pinus rigida*) over dense thickets of ericaceous shrubs. Soils are very stony loamy sands with depths to bedrock of 40 to 48 inches. A

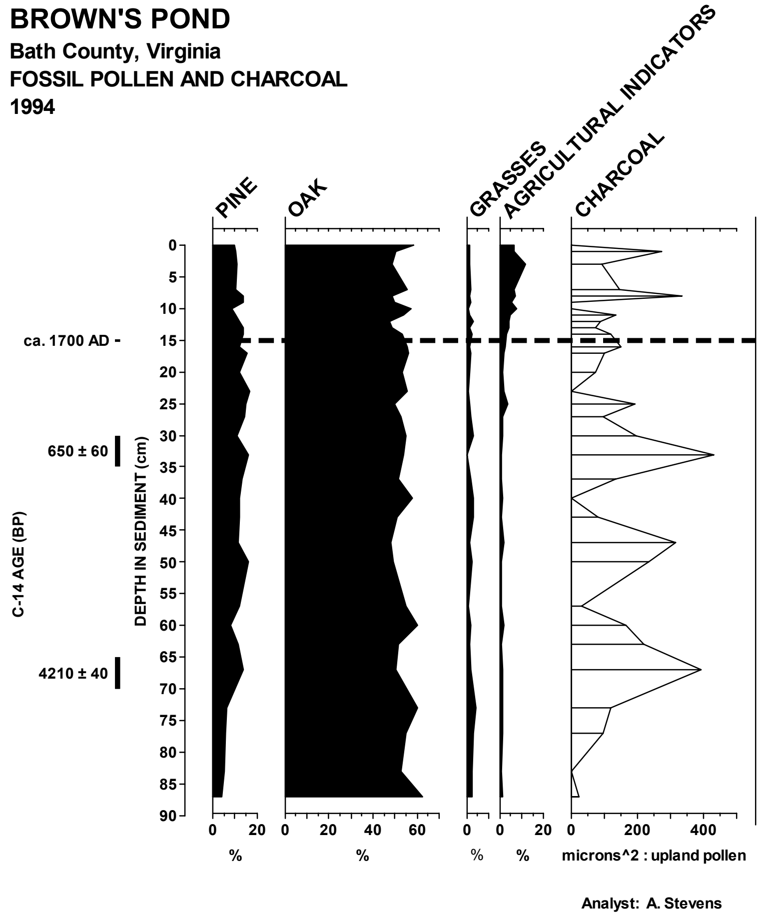

Figure 2.—Pollen and charcoal profiles for Brown's Pond, Bath County western Virginia. The date of local settlement by Europeans (dashed line) is from historical accounts.

35-cm-long sediment core obtained in 1994 represents approximately the last 900 years. Oaks (40 percent of total pollen) dominated the uplands prior to European settlement about 250 years ago. Pines, which like oaks, produce abundant pollen, were less important, and charcoal values were somewhat lower (Ch:P = 0-300) than observed at Brown's Pond. One or more major fires apparently burned near the pond about 150 to 250 years ago, with charcoal abundance increasing to 400 to 600 before declining in recent sediments (Fig. 3). The increase in fire activity was followed by an increase in pine and a decline in oak. Although oaks remain an important component of the modern vegetation, recent pine pollen percentages are more than double those prior to settlement.

Results from Brown's and Green ponds suggest that on mesic soils in protected locations of the southern Appalachians, light surface fires may contribute to maintaining oaks as a dominant component of mixed mesophytic forests—perhaps by selecting against more shade tolerant but less fire tolerant mesophytic hardwood species. On exposed sites with poorer soils where shade-tolerant (mesic-site) species compete less well (e.g., at Green Pond), oaks may persist with less fire. More frequent fires, at least some of which are likely to be more severe on shallow soils, may favor the establishment of pines and increase their importance on the landscape. However, longer lived oaks still persist, even in the face of competition from dense shrub understories, which may prevent pines from regenerating without fire (Patterson and Stevens 1995).

South Coastal New England and Long Island

Deep Pond lies at an elevation of 28 feet on the Ronkonkama Moraine in northeastern Suffolk County, Long Island, New York (40° 56′ 11″N, 72° 49′ 52″W). The uplands surrounding the pond are dominated by black and white oak and pitch pine. Soils are deep, loamy sands. A sediment core spanning the past 2,200

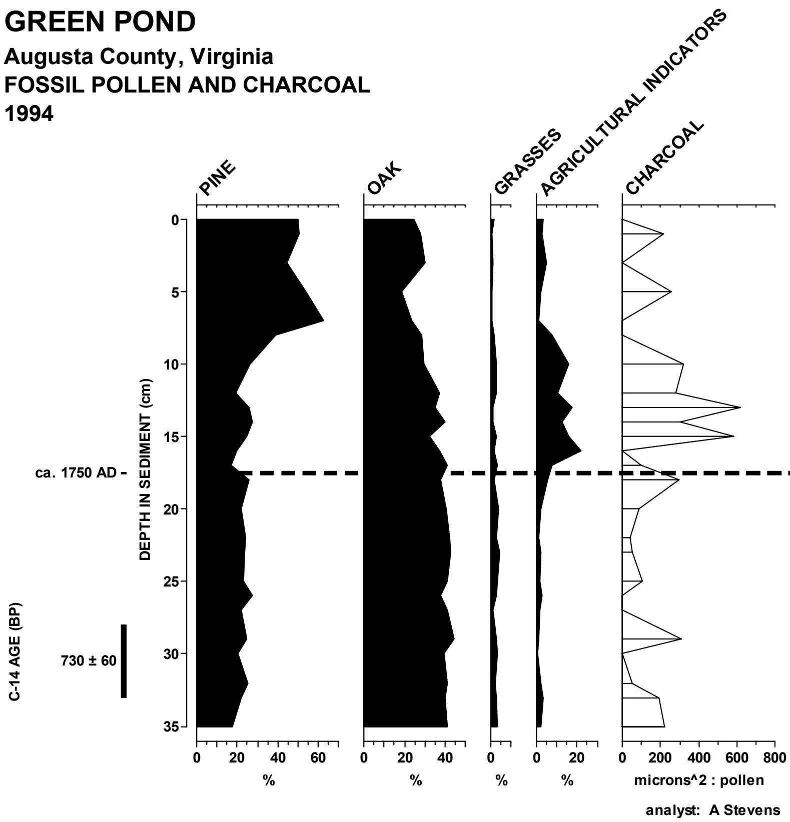

Figure 3.—Pollen and charcoal profiles for Green Pond, Augusta County, western Virginia. The date of local settlement by Europeans (dashed line) is from historical accounts.

years was recovered in 1981 (Backman 1984). Oaks dominated throughout the sample period, though percentages have declined somewhat, with pitch pine increasing in importance since European settlement about 300 years ago (Fig. 4). Charcoal values are high, averaging 400 to 600 before settlement and increasing to 500 to more than 1,000 in recent centuries. As at Green Pond in Virginia, recent increases in fire activity appear to favor pitch pine.

Charge Pond, at an elevation of 66 feet in Plymouth County, Massachusetts (41° 48′ 58″N, 70° 40′ 31″W), occupies a kettle hole in outwash of the Wisconsin glacial stage. Course, sandy soils currently support a mixture of pitch pine and scrub oaks. The area around the pond burned most recently in a catastrophic fire in 1957. Backman (1985) described the fire and vegetation history for the past several hundred years based on his analysis of a core obtained in 1981 (Fig. 5). Fire activity has been high throughout the last several hundred years, as evidenced by charcoal values which rise from 500 to 1,000 before European settlement to 4,000 to 5,000 during the post-settlement period. Oaks and white pine (*Pinus strobus*) were dominant before settlement. Because tree oaks are more likely to occur with white pine, we assume that white and black oak were more important than scrub oaks (Patterson and Backman 1988). Today, the vegetation on the upland is referred to as pitch pine-scrub oak barrens, but our data suggest that these species—especially pitch pine—have been dominant only since fire activity increased following European settlement.

Data from Deep and Charge ponds suggest that on course-textured soils, where pines are better able to compete with oaks, oaks survive at moderately high fire activity, but composition has shifted towards an increasing importance of pitch pine with the high fire activity during the post-settlement period. A more detailed examination of the pollen data suggests that with increasing fire activity, more mesic hardwood species, including hickory (*Carya* spp.), maple and beech, decline in importance.

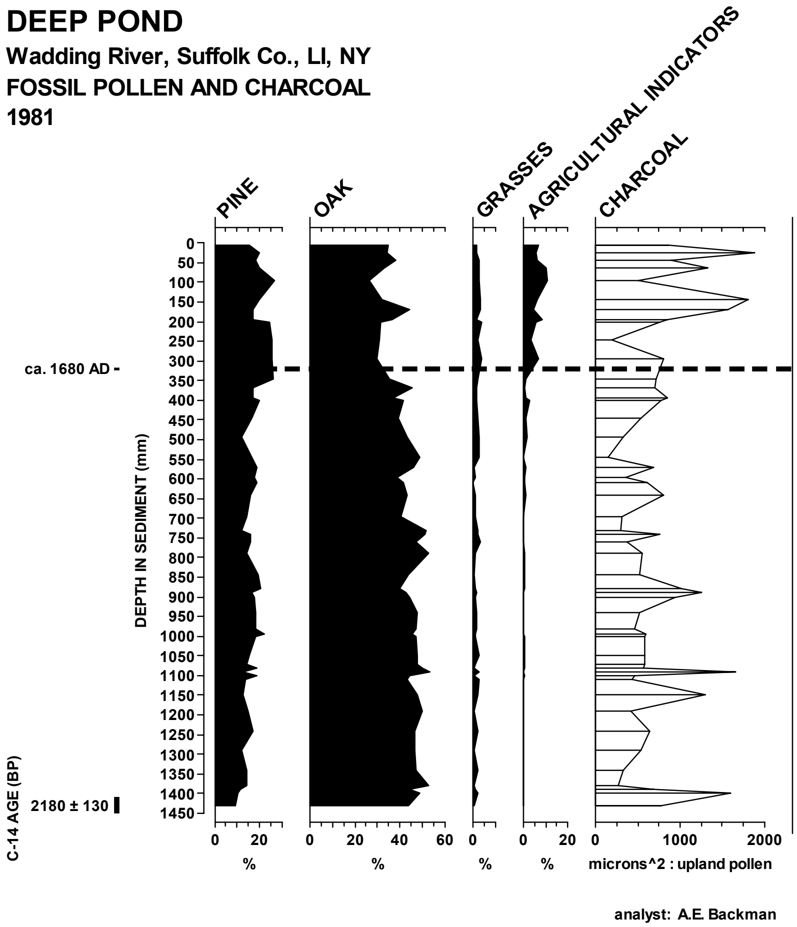

Figure 4.—Pollen and charcoal profiles for Deep Pond, Suffolk County, Long Island, New York. The date of local settlement by Europeans (dashed line) is from historical accounts.

Coastal Maine

Mount Desert Island in Hancock County, Maine, is a 120,000-acre mountainous, ocean island 40 miles south of Bangor. Diagrams for two small ponds provide insights about the interaction between fire and oaks near their northern range limit. Only red and bear oak (*Quercus ilicifolia*) occur naturally on the island today.

Sargent Mountain Pond is at an elevation of 1,145 feet (44° 20′ 04″N, 68° 16′ 10″W). Mature spruce (*Picea* spp.) forests on shallow-to-bedrock, granitic soils surround the small mountain pond, which lies just outside the western boundary of the great Bar Harbor Fire, which burned nearly 20,000 acres on the Island in October 1947. Oaks are not present in the pond's small watershed but there is a stand of red oak regenerated by the 1947 fire about 1 mile to the north. Pollen and charcoal analysis of a 30-cm-long sediment core provides information on the fire and vegetation history of the watershed for the past 400 years (Fig. 6). At least two fires burned the surrounding upland, one about 1700 AD, 60 years before the first permanent settlement on the Island at Somesville 2 miles to the west, and a second in the mid-19th century. The second fire probably occurred in conjunction with the logging of the mountain's virgin stands of spruce. Charcoal at background levels of less than 200 μ^2 for the rest of the core shows that no other fires have burned within the watershed during the period of record. The two discrete fires separated by 150 years allow interpretation of post-fire succession—alder (*Alnus* spp.), followed by birch, and finally spruce—that is consistent with what has been observed following early and mid-20th century fires (Patterson et al. 1983; Patterson and Backman 1988). Oak pollen occurs at generally less than 5 percent and rises only slightly following fires, perhaps reflecting the increased importance of regional pollen following stand-replacement fires on the watershed.

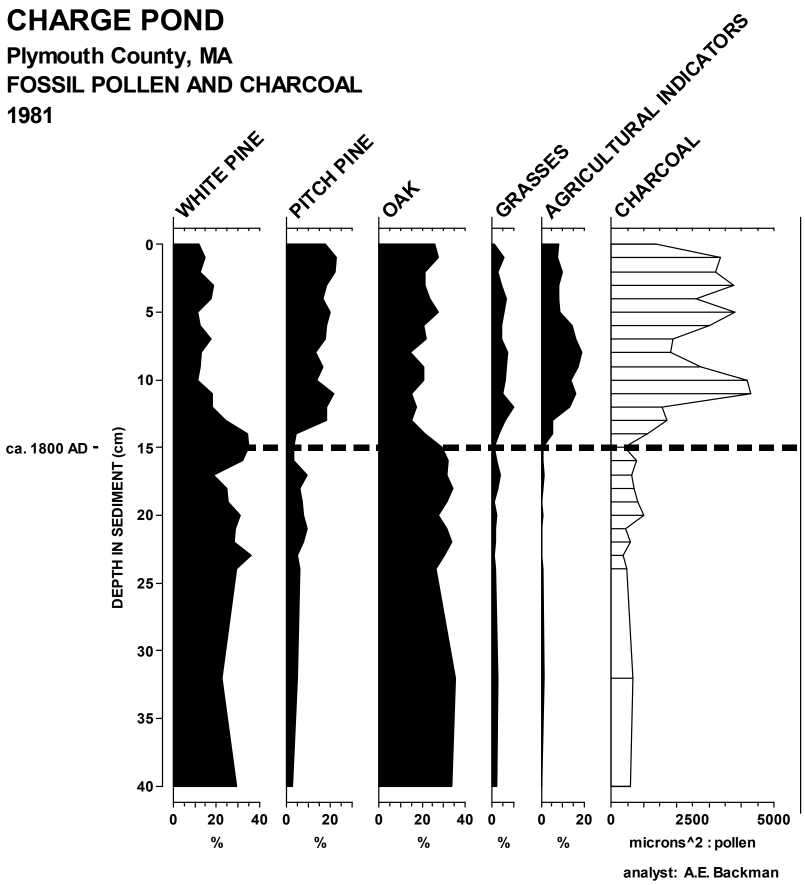

Figure 5.—Pollen and charcoal profiles for Charge Pond, Plymouth County, Massachusetts. The date of local settlement by Europeans (dashed line) is from historical accounts.

Lake Wood, at a lower elevation (35 feet) and 6 miles northeast of Sargent Mountain Pond (44° 24′ 27″N, 68° 16′ 06″W), lies in a glacially scoured valley with soils derived from course glacial debris overlain in places by marine clays. The entire watershed of Lake Wood burned in the 1947 fire. The vegetation today is dominated by paper (*Betula papyrifera*) and gray birch (*B. populifolia*), red (*Pinus resinosa*) and white pine, and occasional red oaks. A small stand of hemlock in the southeastern part of the watershed regenerated following the 1947 fire. Hemlock is uncommon in the forests of Mount Desert Island.

Like Brown's Pond in western Virginia, we have a long record of fire-vegetation interactions from Lake Wood. Unlike the Virginia core, the Lake Wood core was sampled and analyzed with very fine resolution; sample-to-sample precision is on the order of 20 to 40 years. The pollen data suggest oak has been present as at least a minor component of the local vegetation for much of the past 6,000 years despite substantial changes in species dominance. Hemlock, white pine, birch, sugar maple, and beech (not shown in Fig. 7) dominated until about 2,000 years ago when spruce (plus cedar and fir) replaced the hemlock and northern hardwoods. The charcoal record clearly documents the local occurrence of the 1947 Bar Harbor fire at the top of the profile. This fire occurred during the driest month in more than 150 years of recorded weather history in Maine (Baron et al. 1980), and may have been the most severe fire to occur on the watershed during the entire 6,000 year period represented by the core. However, different fire regimes appear to dominate at different times, and the abundance of oak varies with them. Approximately 3,000 to 6,200 BP as many as five or six charcoal peaks occurred, usually in conjunction with changes in the abundance of hemlock. We are investigating whether these fires followed declines in hemlock caused by insects, disease, or blowdown, or themselves were the cause of the declines (unpublished data), but oaks are

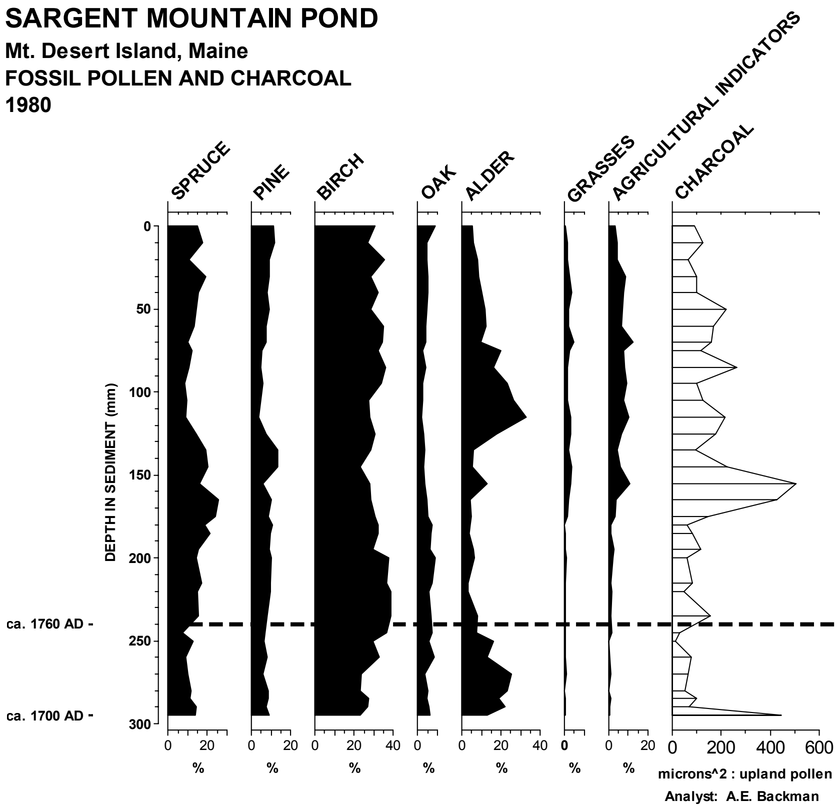

Figure 6.—Pollen and charcoal profiles for Sargent Mountain Pond, Hancock County, Maine. The date of local settlement by Europeans (dashed line) is from historical accounts and Lead-210 analysis.

clearly more abundant during this period than during the subsequent 1,000-year period (2,000 to 3,000 BP) with no fires. The shift from hemlock to spruce in the region at 2,000 BP is accompanied by an overall increase in fire activity, but oak does not increase again until well after this change in vegetation (and fire regime). Oak pollen percentages at the surface of the core are higher (at 11 percent) than at any time since about 3,700 BP.

In conjunction with a companion site (The Bowl) on the Island for which we have comparable detail for an even longer period of time (unpublished data), the detailed sampling of the Lake Wood core over a long period provides us, with the opportunity to seek answers to the questions posed earlier: Do changes in fire regimes cause changes in oak abundance? Do the increased flammability of oak fuels cause more frequent fires on the landscape? Our analyses to answer these questions are incomplete but the evidence for this one site where fire has historically been infrequent on the landscape suggests at least a correlation between fire activity and oak abundance.

SUMMARY AND CONCLUSIONS

Paleoecological evidence, such as the fossil pollen and charcoal data presented here, is incomplete, fraught with uncertainties, and dependent on assumptions that often are difficult to evaluate. But they are the only data available that allow us to make inferences about fire and vegetation before the time of recorded history. There is value in considering the long-term interactions between fire and vegetation, especially for long-lived forest trees like the eastern oaks, because processes like fire, which influence stand initiation and development, have secondary effects that are realized over decades or even centuries. Changes in fire return intervals, the interaction between fire occurrence (and effects) and climate (which itself changes), and the rare occurrence (in some systems) of catastrophic fires, must be studied over periods far longer than fire scientists are accustomed to contemplating.

In this paper I have examined the value of using paleoecological data to investigate the response of oaks as a group to fire. Chief among the difficulties is that

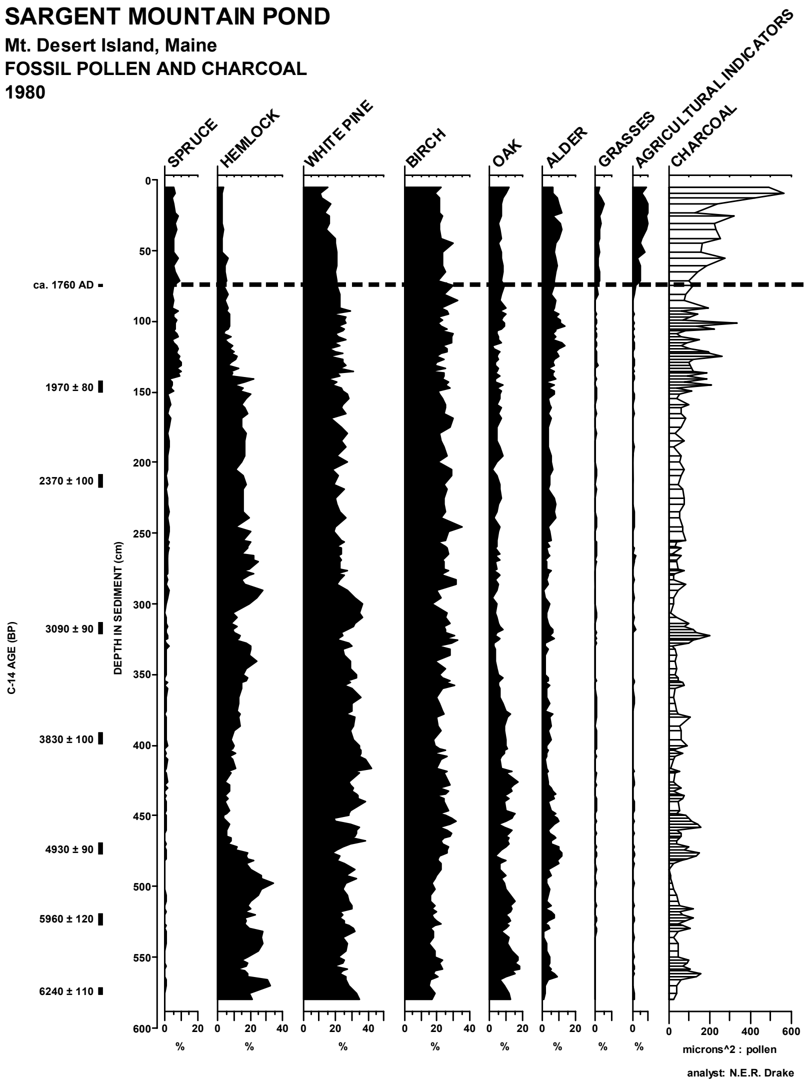

Figure 7.—Pollen and charcoal profiles for Lake Wood, Hancock County, Maine. The date of local settlement by Europeans (dashed line) is from historical accounts.

we cannot distinguish among any of the dozens of oak species based on their pollen morphology. Similarly, we often can only guess at how changes in the abundance of charcoal in sediments relate to the intensity, severity, or extent of individual fires. And it is only under unusual circumstances that we can identify individual fires and their effects on vegetation using fossil data. The detailed analyses for the Sargent Mountain Pond and Lake Wood sediments are unique in this regard.

Yet fossil data do provide information that may be useful in the future management of oak forests. Chief among the lessons we have learned is that it is difficult to generalize about the interaction between fire and oaks on the centuries-long time scales that are relevant to forest stand development and change. Oaks have persisted for thousands of years in a fire regime apparently characterized by relatively infrequent, low-intensity fires at Brown's Pond in western Virginia. But oaks also have persisted for millennia under frequent, probably higher intensity surface fires at Deep Pond on Long Island. At Green Pond, surrounded by more xeric soils and vegetation at higher elevations in Virginia, one or more severe fires at the time that Europeans arrived changed the balance between oaks and pines. The same is true for Charge Pond in southeastern Massachusetts. In neither case were oaks reduced to minor components of the vegetation, but the balance between oak and pine was clearly shifted toward the later. On the Maine coast, near the northern limits of the range of oaks, fire at times has been rare, and oaks have been a minor component of the vegetation as a whole. Yet when fire return intervals are reduced (i.e. fires occur more often), oaks seem to compete better with more shade-tolerant conifers and hardwoods.

In the Upper Midwest, Jacobson (1979) found that white pine migrated into oak forests, perhaps in response to a "slight decrease in fire frequency" at various times during the Holocene. This finding is counter to those for the Green and Charge ponds in the East. Jacobson did not provide charcoal data to support his hypothesis, but it is likely that fires were so frequent in the oak savannah stands he postulates that pines would not have been able to survive. White (1983) found that annual burning maintains oak savannas with grassy understories in prairie-forest transition stands in east-central Minnesota. Jacobson assumed that white pine cannot tolerate return intervals of less than 20 years.

There is little evidence from sites on the East Coast that fires were frequent enough to give rise to savannas like those of the Upper Midwest. At none of the sites I have discussed has an increase in charcoal, either before or after European settlement, coincided with a substantial increase in grass pollen. Stevens (1996) suggested that frequent Native American burning on the island of Martha's Vineyard, Massachusetts, may have been responsible for the coincidence of high charcoal values and high oak and grass pollen percentages. She also found abundant charcoal with abundant oak and grass pollen in post-settlement sediments, but it may have been grazing and cultivation as much as fire that was responsible for this correlation, which was largely restricted to coastal sites regionally (Foster and Motzkin 2003).

Recent work at the Harvard Forest emphasized the variety of opinions on the importance of interactions between fire and oaks in the Northeast. Parshall and Foster (2002) generally discountrd the importance of fire relative to climate and soil factors as influencing regional variation in the vegetation of the oak region of southern New England. But Foster et al. (2002) postulated that fire is important, albeit at lower levels than along the coast, in maintaining oak and chestnut forests in central Massachusetts. Their work shows that detailed reconstructions of fire and vegetation histories at selected sites hold the promise of further advances in our understanding of the long-term relationship between fire and oaks. However, our interpretation of historical data must be informed by a knowledge of fire-vegetation interactions from contemporary studies. Long-term prescribed burning experiments, like those conducted for nearly half a century at the Tall Timbers Research Station in Florida (Stoddard 1962), will increasingly provide information that will allow us to better interpret the paleoecological record.

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