INFLUENCE OF DISTURBANCE ON STAND DEVELOPMENT DURING FOREST SUCCESSION

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Abstract.—Eighty years of data on stand development on 39 strip transects were used to elucidate the influence of disturbance on forest composition. Transects were measured at 10-year intervals between 1927 and 2007, except for 1947, and the resulting data include records of 35,953 stems. Disturbances included a wildfire in 1932, single-year defoliations (1964, 1972, 1981), and multi-year defoliations (1961-1963, 1971-1972, 1981). Wildfire reduced basal area by 46 percent. During the first defoliation period, oak basal area mortality averaged 36 (multi-year) and 12 percent (single-year). In 2007, oak density (stems per acre) on burned transects in 2007 was twice that observed on unburned transects, 90 and 42; while maple density was higher on transects that had had only single-year defoliations (190) compared with multi-year defoliation (119). In contrast, birch density was lower on transects with single-year defoliations (97) compared to multi-year defoliation (198). Oak ingrowth was highest following wildfire, 244 stems per acre per decade (SA^{10}) and was negligible during subsequent decades, 6 SA^{10}. Transects with multi-year defoliations averaged 80 birch SA^{10} compared with 44 maple SA^{10} between 1967 and 1997. During that same period, maple ingrowth averaged 35 SA^{10} and birch ingrowth averaged 14 SA^{10} following single-year defoliations. Disturbance type has a long-term impact on forest composition.

INTRODUCTION

Disturbances to different canopy strata can have both short-term (<20 years) and long- term (>20 years) effects on stand composition and structure. Most research has focused on short-term responses to disturbances, including forest management; few published studies span more than a decade on the hardwood forest dynamics. Studying the trajectory of species composition and stand structure for longer than a decade is important because predictions based on short-term observations may, or may not, be accurate (Brose 2010).

Although there is a paucity of information on the long-term effects (> 20 years) of fire in eastern hardwoods, short-term effects have been well documented (Brose et al. 2006). Eleven years after prescribed burning, oak dominance increased with fire intensity in Virginia (Brose 2010). In Rhode Island, 5 to 51 years after high-intensity fires, relative density of oak was twice as high on burned compared to unburned sites (Brown 1960). High-intensity fires did not change the average frequency of black oak (*Quercus velutina*), but did reduce the average frequency of red maple (*Acer rubrum*) and white oak (*Quercus alba*) in New York (Swan 1970).

The short-term impacts of gypsy moth (*Lymantria dispa*r L.) defoliation have been thoroughly studied. Oak diameter growth decreases by 30 to 60 percent during outbreaks (Baker 1941, Brown et al. 1979, Campbell and Garlo 1982, Muzika and Liebhold 1999), and mortality is concentrated in the lower canopy oaks (Brown et al. 1979, Campbell and Sloan 1977, Kegg 1971). In general, these studies reported that diameter growth and tree health recovered 2 to 10 years after heavy defoliation.

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Surprisingly, reports on the effects of gypsy moth defoliations on regeneration are limited to the several years after the defoliation. Studies 4 to 7 years after defoliation found increases of red maple and birch in Pennsylvania and Maryland (Allen and Bowersox 1989, Fajvan and Wood 1996, Hix et al. 1991). Two years after defoliation, red maple and black cherry were the predominant seedling species in West Virginia (Muzika and Twery 1995).

The objective of this research was to compare the effects of three distinct disturbance regimes (wildfire, repeated multi-year defoliations, and single-year defoliations) on forest composition and regeneration over an 80-year period. This information will be useful for forest managers wanting to predict the long-term composition of forests impacted by a variety of disturbance regimes, especially in unmanaged natural preserves.

STUDY AREAS

The first Old-Series study area was established on the Turkey Hill Tract (80 acres), Cockaponset State Forest, Haddam, CT, in 1926. In 1927 three additional Old-Series study areas were established in Meshomasic State Forest, Portland, CT: Cabin (40 acres), Cox (50 acres), and Reeves Tracts (40 acres). These four tracts form a study unique because of its length (80 years), depth (43,560 stems distributed to more than 50 species), breadth of information (species, diameter, crown class, spatial location, etc.), continuity (eight inventories), and replication on four sites.

The history of these study areas was typical of most second-growth forests in southern New England. They are a mixture of abandoned agricultural lands, grazed woodlots, and areas repeatedly cut for fuelwood, charcoal, and lumber (Stephens and Waggoner 1980). The median age of upper canopy oaks was 80 years in 1983, indicating that anthropogenic disturbance ended around 1900. Although there are many American chestnut (*Castanea dentata)* sprouts on all study areas, no large chestnuts were found when the tracts were first inventoried in 1926-27 (Hicock et al. 1931). Upland oaks have dominated both dominant and codominant crown classes since the study began in 1926.

The acidic soils (pH 4.5-6.0) are very stony to extremely stony, fine sandy loams derived from gneiss and schist glacial tills. Mean oak site index was 67 feet (reference age 50 years) on moderately well drained soil. Topography is gently rolling with elevations ranging from 90 to 170 m.s.l. Climatic data are from Hartford, CT, approximately 16 km northwest of the Meshomasic tracts (National Oceanic and Atmospheric Administration 1991). The area is in the northern temperate climate zone. There is an average of 176 frost free days per year. Mean monthly temperature ranges from 25 °F in January to 73°F in July. Average annual precipitation is 44 inches per year evenly divided over all months.

The four Old-Series tracts have had three distinct disturbance regimes since the first inventories. <u>MULTI</u>-Three tracts in Portland had multi-year episodes of moderate to severe defoliation (>35 percent) in 1961-63 and 1971-1972, and a single year of defoliation in 1981 due to gypsy moth, canker worm (*Paleacrita vernata*), and elm spanworm (*Ennomos subsignarius*). These defoliations and subsequent infestations by secondary agents, such as the two-lined chestnut borer (*Agrilus bilineatus*) and shoestring root rot (*Armillaria mellea*), resulted in the loss of more than 90 percent oaks in the intermediate and suppressed crown classes along with half of codominant red oaks (Ward 2007). <u>SINGLE</u> - Moderate to severe defoliations at the Turkey Hill tract were limited to single year episodes in 1964, 1972, and 1981. FIRE - A summer wildfire burned approximately 40 percent of the Turkey Hill tract in 1932. The burned area was inventoried in 1934 to note which trees survived the fire. The wildfire provided abundant growing space for new trees by killing 92 percent of saplings, 58 percent of poles, and 24 percent of sawtimber (Ward and Stephens 1989).

METHODS

Field Measurements

Trees were measured in transect segments 16.5 feet wide and 66 feet long. Transect lines had from 10 to 20 segments and were spaced 264 feet apart on all tracts except Turkey Hill where transects were spaced 330 feet apart. Transect sections adjacent to roads, trails, and other human disturbance were excluded from this analysis, as were sections in poorly drained muck soils. Trees were mapped to the nearest 4 inches. These maps were used to relocate trees in the subsequent inventories of 1937, 1957, 1967, 1977, 1987, 1997, and 2007. The species, diameter, and crown class of each tree were also recorded. Minimum diameter (at 4.5 feet aboveground) was 0.6 inch in 1927 and 1937; since 1957, the minimum diameter has been 1.5 inches. A total of 35,953 individual tree records were used in this analysis. More details on study protocols can be found in Ward et al. (1999).

A special concern of long-term studies is maintenance of data quality, i.e., consistency of data measurements and methods. Transects locations were permanently established with rock cairns and wooden stakes at 132-foot intervals in 1926. The wooden stakes were replaced by metal bars in 1976. The centerline of each transect segment was located by stretching a tape between stakes. Individual trees were then identified by matching their location, species, and diameter with previous records using detailed maps from the previous inventory.

Data Analysis

To allow estimation of stand-level changes of density and basal area, individual transects of each tract were considered as a sample unit. Because transects were at least 264 feet apart within a tract, at least three tree heights apart, pseudo-replication was not considered a factor. Thirty-nine transects that were at least 200 feet long and without anthropogenic disturbance, primarily cutting, were included in the study: MULTI (n=26), SINGLE (n=7), FIRE (n=6). Density and basal area estimates for each transect were transformed to per acre values before analysis because lengths varied by both the number of initial segments per transect and the number of segments that were excluded because of anthropogenic disturbance.

To simplify analysis of changes over the past 80 years, this report examined three species groups in detail: maple (*Acer saccharum*, *A. rubrum*), oak (*Quercus rubra*, *Q. velutina*, *Q. coccinea*, *Q. alba*, *Q. prinus*), birch (*Betula alleghaniensis*, *B. lenta*). These nine species accounted for 74 percent of observed stems of species that had the potential of forming part of the upper canopy in a mature forest. Ingrowth was defined at those trees that grew large enough between surveys to be measured for the first time, i.e., new trees.

For combined species, repeated measures ANOVA for density and basal area using SYSTAT 13 was used with survey year as the within subjects factor and disturbance type as the between subjects factor. Differences were judged significant at $p < 0.05$ using the conservative Greenhouse-Geisser

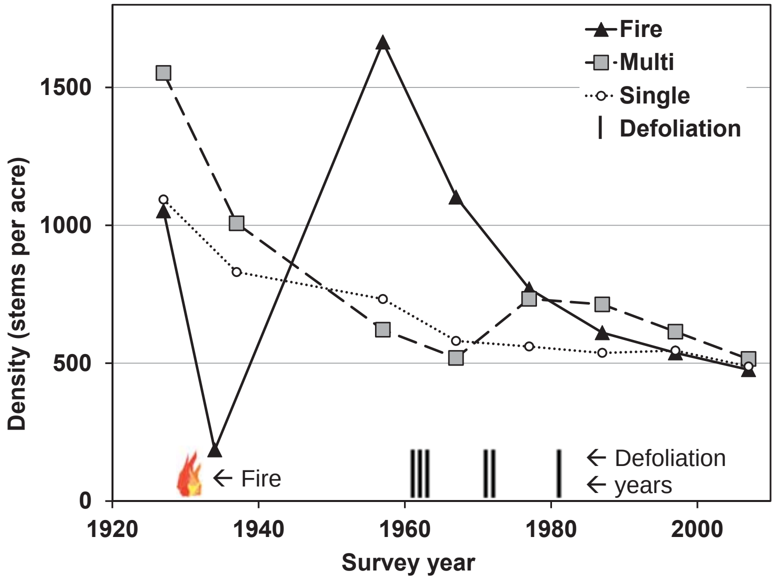


Figure 1.—Stand density (stems/acre) by disturbance type and survey year for Old-Series tracts in central Connecticut. Disturbance types: FIRE-wildfire in 1932, MULTI-repeated multi-year defoliations, and SINGLE-single-year defoliations.

correction for deviation from compound symmetry. For each species group and for combined species, a one-factor (disturbance type) ANOVA weighted by transect length was used to compare the influence of disturbance type on density and basal area in 2007. Tukey's HSD test was used to test for significant differences $P < 0.05$.

RESULTS

Density

Repeated measures ANOVA indicated stand density was not independent of the interaction of survey year and disturbance type ($F=15.05$, $df=14$, $P<0.001$). Stand density (stems/acre) steadily declined since 1927 on transects that experienced single-year defoliation episodes (Fig. 1). Transects burned by the 1932 wildfire had a sharp drop and then rapid increase of stem density through 1957, followed by a steady decline through 2007. A third pattern was observed on transects that had multi-year defoliations; density declined through 1967 and then increased for 20 years before beginning to decline again. Remarkably, by 1997, density did not differ among transects that had experienced the distinct disturbance regimes ($F=1.463$, $df=2$, $P=0.245$) and was nearly identical in 2007, 476 to 515 stems/acre.

The decline on transects with single-year defoliations was not uniformly distributed among species groups; oak declined by 82 percent and birch by 60 percent, while maple actually increased by 27 percent (Table 1). The more rapid decline of oak relative to other species is not unique to this study and has been observed in other unmanaged forests from North Carolina (Christensen 1977), north to Massachusetts (Foster et al. 1998), and west to Missouri (Nigh et al. 1985).

Recent research has highlighted the importance of understory disturbance, e.g., prescribed burning, if oak is to be maintained as a component of the eastern deciduous forest (Brose et al. 2006). Oak density dramatically increased in the decades following the 1932 wildfire and was more abundant than on the unburned transects 65 years after the burn ($F=4.886$, $df=2$, $P=0.013$). Shorter term (20- to 30-year) increases of maple and birch density were also associated with the wildfire (Table 1).

Table 1.—Changes in stand density (stems/acre) over time by species group and disturbance type for Old-Series tracts in central Connecticut; for a given species group, values followed by a letter within a column were not significantly different at P < 0.05

		1927	1937	1957	1967	1977	1987	1997	2007
Oak	Fire	270	46	515	293	170	146	124	90 a‡
	Multiple	346	237	109	50	50	57	48	42 b
	Single	236	177	135	79	52	53	51	43 ab
Maple	Fire	179	67	340	310	253	213	185	159 ab
	Multiple	345	248	176	175	232	217	166	119 a
	Single	151	146	189	195	220	236	225	192 b
Birch	Fire	134	37	249	183	133	119	104	99 a
	Multi	307	203	135	142	236	277	246	198 b
	Single	241	211	171	134	125	118	108	97 a

‡Column values followed by the same letter were not significantly different at P < 0.05.

Mortality was much higher during the period of multi-year defoliations, 35-44 percent for codominant red oaks, than for the decades before or after, 5 and 3 percent, respectively (Ward 2007). The mortality pulse increased the amount of light reaching the forest floor, resulting in an increase of density as seedlings responded to the increased light and grew large enough to be measured. Surprisingly, birch density increased more than maple density, and for a longer time. In 2007, 26 years after the last defoliations, birch density was higher on the tracts that had experienced multi-year defoliations than on the tracts with other disturbance histories (F=9.250, df=2, P<0.001).

Basal Area

Stand basal area has continually increased over the past 80 years, except for the 1927-1937 period on wildfire transects and the 1967-1977 period on transects that had multiple years of defoliation (Fig. 2). In 2007, stand basal area did not differ among tracts with difference disturbance histories (F=2.183, df=2, P=0.127).

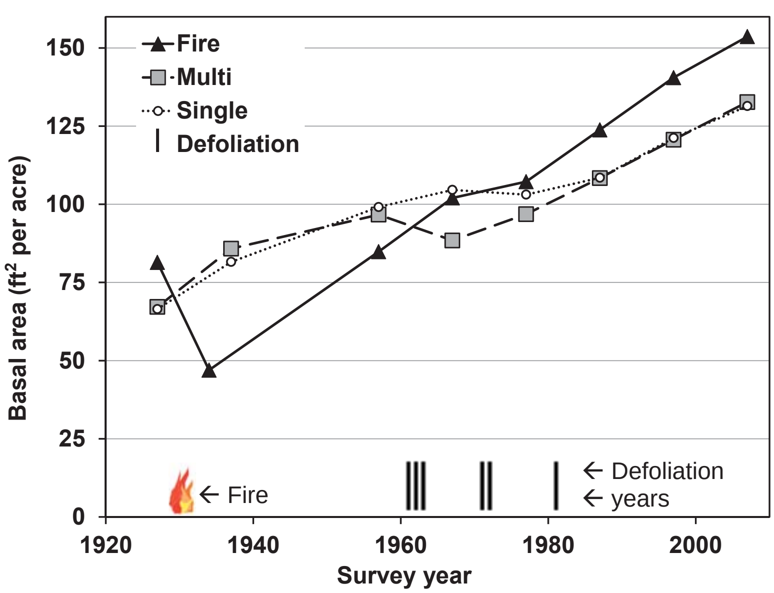


Figure 2.—Stand basal area (ft^2/acre) by disturbance type and survey year for Old-Series tracts in central Connecticut. Disturbance types: FIRE-wildfire in 1932, MULTI-repeated multi-year defoliations, and SINGLE-single-year defoliations.

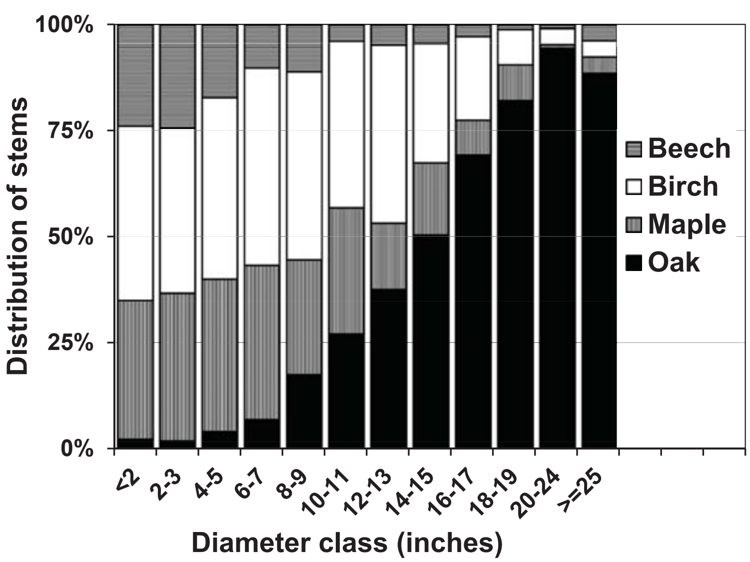
Table 2.—Changes in stand basal area (ft^2/acre) over time by species group and disturbance type for Old-Series tracts in central Connecticut

		1927	1937	1957	1967	1977	1987	1997	2007
Oak	Fire	32	16	40	49	47	53	63	65
	Multi	26	39	54	43	45	50	59	68
	Single	16	22	34	36	33	37	44	48
Maple	Fire	10	8	11	15	18	22	24	26
	Multi	10	11	12	14	17	18	18	17
	Single	10	11	11	13	15	17	18	19
Birch	Fire	16	13	16	20	20	22	21	23
	Multi	15	18	17	18	21	24	25	26
	Single	27	32	34	34	36	35	36	38

Repeated measures ANOVA indicated stand basal area was not independent of the interaction of survey year and disturbance type (F=10.16, df=14, P<0.001). There were distinct responses of the species groups to the different disturbance regimes (Table 2). After the 1932 wildfire, basal area of all species groups steadily increased through 2007 except for a slight decrease of oak basal area between 1967and 1977. However, while there were slight increases for maple and birch (16 and 10 ft^2/acre, respectively) over the subsequent 65 years; oak basal area increased by 49 ft^2/acre during the same period.

Basal area steadily increased on transects that had only single-year defoliations with a couple of temporary declines for oak and birch between 1967 and 1987. Again, the basal area increase for oak over the 80-year period (32 $ft^{2/}$acre) was greater than for maple and birch (9 and 11 ft^2/acre), but with less difference between species groups.

The multi-year defoliations caused a decrease of oak basal area between 1957 and 1967. During the first defoliation period, oak basal area mortality averaged 36 and 12 percent on transects defoliated by multi-year and single-year events, respectively. In addition, oak accounted for 74 percent of basal area mortality on multi-year defoliation transects compared with only 31 percent on single-year defoliation transects. Oak basal area did not recover to 1957 levels until after 1987. The increase of oak basal area over the past 20 years, 18 ft^2/acre from 1987 to 2007, was greater than the total increase over 80 years for maple and birch, 7 and 11 ft^2/acre, respectively.



In 2007, oaks were predominant in diameter classes greater than 14 inches, but were notably sparse in the smaller diameter classes (Fig. 3). Conversely, more shade-tolerant maples and beech accounted for most stems smaller than 6 inches.

Figure 3.—Distribution of stems among diameter classes in 2007 for Old-Series tracts in central Connecticut.

Ingrowth

Ingrowth patterns were strikingly different between the three disturbance regimes over the past 80 years, but had merged to similar values of 14 to 24 stems per acre per decade (SA^{10}) by 1997 to 2007 (Fig. 4). After 1932, the wildfire transects had a sharp pulse of ingrowth to more than 500 SA^{10} between 1937and 1957 before falling to less than 50 SA^{10} in the subsequent decades. As noted above, this pulse of ingrowth was not unexpected as the wildfire killed 82 percent of stems, mostly in the pole- and sapling-size classes, providing abundant growing space for new trees (Ward and Stephens 1989).

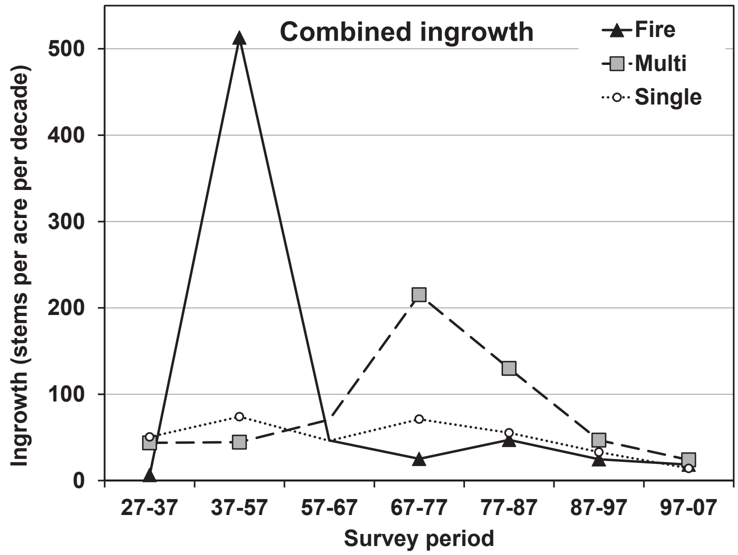


Figure 4.—Ingrowth (stems per acre per decade) by disturbance type and period for Old-Series tracts in central Connecticut. Disturbance types: FIRE-wildfire in 1932, MULTI-repeated multi-year defoliations, and SINGLE-single-year defoliations.

Ingrowth rates on transects with single- and multi-year defoliations were similar during the 1927-1967 periods. On transects that did not have a disturbance that dramatically increased mortality (i.e., single-year defoliation transects), ingrowth rates have fluctuated from 74 SA^{10} between 1937 and 1957 and 14 SA^{10} between 1997 and 2007. Mortality was much higher between 1957 and 1977 on the tracts that had multi-year defoliations than on the tract that had single-year defoliation (Stephens 1971). Similar to the wildfire, but at lower intensity and over a longer period, the increased mortality initiated by multi-year defoliations led to an increase of ingrowth from 53 SA^{10} between 1927 and 1957 to 215 SA^{10} during the 1967 to 1977 period by releasing growing space. With the appearance of the gypsy moth fungus (*Entomophaga maimaiga*) in 1989 that has mostly controlled gypsy moth (Andreadis and Weseloh 1990), increased mortality caused by large-scale defoliation ceased and ingrowth rates declined to 24 SA^{10} for the 1997 to 2007 period.

Not only did each of the three disturbance types have different ingrowth patterns over the past 80 years, the species composition of ingrowth also differed by disturbance type (Table 3). On transects that had had only single-year defoliation episodes, maple has been the predominant ingrowth species for every period over the past 80 years. Birch and maple had similar ingrowth rates before the multi-

Table 3.—Stand ingrowth (stems per acre per decade) over time by species group and disturbance type

		1927 -1937	1937 -1957	1957 -1967	1967 -1977	1977 -1987	1987 -1997	1997 -2007
Oak	Fire	0	244	11	2	15	2	1
	Multi	13	2	1	8	11	2	1
	Single	18	17	4	4	5	4	2
Maple	Fire	2	154	26	15	15	12	10
	Multi	15	23	35	85	34	12	7
	Single	20	44	29	48	39	18	7
Birch	Fire	4	114	9	9	17	12	8
	Multi	15	19	35	122	85	33	16
	Single	12	13	13	20	12	10	5

year defoliation episodes; but subsequently, birch ingrowth has been much higher than maple, 207 and 119 SA[10] between 1967 and 1987. There is also evidence that these defoliations permanently increased American beech ingrowth.

A different species response was observed on the wildfire transects where oak was the predominant species in the two decades following the fire. Other studies have also noted that oak responds well to fire (Ward and Brose 2004). Indeed, fire or a fire-surrogate such as mowing or herbicide may be necessary to obtain adequate oak regeneration (Brose et al. 2006).

DISCUSSION: DISTURBANCE AND STAND DEVELOPMENT

This study found that disturbances had long-term impacts on forest composition, especially for new ingrowth. Oak density was twice as high on transects burned by the 1932 wildfire than on unburned transects (Table 1). Maple density was highest and it was the most numerous species on transects that had had only single-year defoliation episodes. In contrast, birch density was highest and it was the most numerous species on multi-year defoliation transects. It is worth noting that the most severe disturbance (fire) was the most favorable for oak, the intermediate disturbance (multi-year defoliations) favored birch, and the mildest disturbance (single-year defoliation) favored maple.

The increasing dominance of the oak species group as measured by basal area (Table 2) and continued dominance of oaks in the larger diameter classes (Fig. 3) were predicted by development of a canopy stratified by shade tolerance (Oliver 1978, Ward and Stephens 1993). This suggests that opportunities to recruit oak regeneration will persist for several decades, if not a century, for longer lived species such as northern red and white oak; but these opportunities will not persist for shorter lived oak species, such as black and scarlet oak, that are approaching their lifespans in these 110-year-old stands (Johnson and Abrams 2009). Oak ingrowth (Table 3) and density (Table 1) have continued to decline in the absence of fire (Table 3). Consequently, oaks were a small component of both the sapling-and pole-size classes, 2 and 9 percent, respectively (Fig. 4).

Changes in disturbance regimes, specifically a decrease in fire return intervals and intensity, have been linked to conversion of oak-dominated forests to more mesophytic species in the eastern United States and Canada (Nowacki and Abrams 2008). Because short-term studies have differed on whether fire benefits oak (Brose et al. 2006), there has been a question of the utility of fire to maintain a significant oak component in hardwood forests. The single, intense wildfire in 1932 caused a pulse of ingrowth dominated by oak (Table 3). More than 70 years later, oak density on the wildfire transects was double that of transects not burned (Table 1). Another study also found that oak density was higher in areas burned 5to 51 years earlier than in adjacent unburned areas (Brown 1960). It will be several decades before fire studies established beginning in the 1990s have comparable data.

These observations indicate that maintaining oak will require active management, such as prescribed burning, mowing, or herbicide to allow development of oak regeneration competitive with maple, beech, and birch before a disturbance that removes the upper canopy (Brose et al. 2008). As noted above, partial cutting and similar disturbances such as multi-year defoliation episodes benefit non-oak species and should be minimalized in stands where management objectives include maintaining an oak component. Until there is change toward more active management and less partial cutting, oak will continue to decline and these forests will become increasingly dominated by more mesophytic species.

By contrast, increases of birch ingrowth (Table 3) and density (Table 1) were associated with mortality of upper canopy trees following multi-year defoliation episodes between 1957 and 1977. The number of trees killed by defoliation was similar to those removed during partial cutting (Ward 2007). Short-term studies (<8 years) west of the Appalachians reported that red maple dominated regeneration following defoliation induced mortality in oak stands (Allen and Bowersox 1989, Fajvan and Wood 1996, Hix et al 1991, Muzika and Twery 1995). Whether our results east of the Appalachians are specific to a local geographical region or are more representative to longer term trends will not be known until similar studies are conducted west of southern New England.

As with the shift from chestnut to oak forests in the early 1900s, the emergence of a forest dominated by mesophytic hardwoods will alter the economic, ecological, and esthetic values of the forest. The consequences of these changes will last well into the 21st century. Historically, oak has been more economically valuable than maple and birch for its higher price, lower cull rates, and higher per acre volume growth. The shift from oak will also affect many wildlife and insect populations - discriminating against those species dependent on oak and favoring those species associated with maple and birch. Changes in esthetic values are important because of increased public use of the forested landscape for both home sites and recreation. The leaves and flowers of maple and birch are more colorful than oak. However, faster growing oaks and pines are more likely to have the "big tree" characteristics that the public associates with mature forests.

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