DEFOLIATION AND OAK MORTALITY IN SOUTHERN NEW ENGLAND

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Abstract—Crown class and diameter of 4088 upland oaks have been monitored at 10-year intervals since 1927. Plots had three episodes of moderate to heavy defoliation: 1961-1964, 1971-1972, and 1981. Primary defoliators were gypsy moth, canker worm, and elm spanworm. Mortality peaked during the period of 1957-1967 when there were three years of defoliation. Mortality was higher for white oaks than red oaks, and higher for lower canopy trees than for upper canopy trees. Since the end of the multi-year defoliations in 1972, mortality rates for both species groups and all crown classes have fallen to pre-defoliation levels. Mortality was related to tree vigor for red oaks with higher mortality for slower growing trees. The longer term impact of multi-year defoliation events in oak dominated forests is to accelerate mortality of less vigorous oaks in the lower canopy and slower growing trees in the upper canopy.

INTRODUCTION

Gypsy moth (*Lymantria dispar*) has spread to at least seventeen eastern states since its accidental introduction outside of Boston in the late 1800's (Morin and others 2005). Gypsy moth is well established on the eastern and northern portions of the central hardwood region. Although the national "Slow the Spread" program has greatly reduced the rate of expansion (Sharov and others 2002), gypsy moth will probably be found throughout the region before 2050.

Gypsy moth has a wide host range (Liebhold and others 1995). However, increased mortality and reduced growth of oak (*Quercus* spp.) species have accounted for most of the economic and ecological damage caused by this alien pest. Mortality is usually highest for smaller trees in the lower canopy (suppressed and intermediate crown classes) than for larger trees (Brown and others 1979, Campbell and Sloan 1977, Kegg 1973, but see Stalter and Serrao 1983). Much of the mortality following defoliation has been attributed to secondary agents, such as twolined chestnut borer (*Agrilus bilineatus*) and shoestring root rot (*Armillaria mellea*), that attack weakened trees (Baker 1941, Dunbar and Stephens 1975).

The short term impacts of gypsy moth defoliation are well-documented. Oak diameter growth decreases by 30-60 percent during outbreaks (Baker 1941, Brown and others 1979, Campbell and Garlo 1982, Muzika and Liebhold 1999). Earlier studies noted that diameter growth and tree health recovered 2-10 years after heavy defoliation (Campbell and Garlo 1982, Campbell and Sloan 1977, Muzika and Liebhold 1999).

The objectives of this study were: (1) document the effect of multi-year defoliations on oak mortality and diameter growth, (2) analyze how mortality was influenced by crown and vigor classes, and (3) examine the longer term impacts (20+ years) of multi-year defoliations on mortality and growth of upland oaks.

STUDY AREAS

Study plots were the Cabin (40 acres), Cox (50 acres), and Reeves Tracts (40 acres) in Meshomasic State Forest, Connecticut. Most of the land was cleared for pasture or cultivation by the mid-1800's. The current forests developed following farm abandonment and cessation of charcoal cutting in the early 1900's. The forests were estimated to be 20 to 40-years-old in 1927 (Hicock and others 1931).

Stand composition and structures are typical of most second-growth forests, not only in central Connecticut, but of much of the eastern extension of the central hardwood forest. Upland oaks are predominant in the upper canopy. Upland oaks have accounted for more than half the upper canopy basal

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area since the first inventory (Ward and others 1999). The mean diameter of upper canopy trees increased from five inches in 1927 to over fourteen inches in 1997. Maple (*Acer* spp.) and birch (*Betula* spp.) are predominant in the lower canopy.

The plots are on the western edge of the Eastern Highlands of Connecticut, a region of metamorphic rocks and glaciated soils. The topography of the plots is gently rolling with elevations ranging from 300 to 550 feet above mean sea level. Soils are very stony to extremely stony, fine sandy loams derived from granite, gneiss, and schist glacial tills, and are acidic to strongly acidic (pH 4.5-6.0). The area is in the northern temperate climate zone with average annual precipitation of 44 inches.

Defoliation

The plots were subjected to three episodes of defoliation between 1961-1982. The guidelines of Gottschalk (1993) were used to describe defoliation severity in this paper: light (< 30 percent), moderate (30-60 percent), and heavy (> 60 percent). Aerial surveys indicated moderate to heavy defoliation of Cox, Cabin, and Reeves during 1961-1963 by gypsy moth and canker worm (*Paleacrita vernata*). The plots were heavily defoliated by gypsy moth and elm spanworm (*Ennomos subsignarius*) during 1971-1972. All plots were once again heavily defoliated by gypsy moth in 1981. Only Cabin was lightly defoliated in 1982. The duration of each defoliation episode decreased over time, but defoliation intensity was greatest in 1981. A fourth gypsy moth infestation began in 1989, but was limited by the gypsy moth fungus (*Entomophaga maimaiga*).

PROCEDURES

Field Measurements

The study plots were established in 1927. Each plot had six to fourteen transects, and each transect had ten to twenty transect segments (66 by 16.5 feet). Transects were spaced 264 feet apart. Transect centerlines were permanently located by stakes at two chain intervals. Trees were mapped on transect segments. During each inventory, the species, diameter, and crown class of each tree was recorded. Minimum dbh (diameter at 4.5 feet) was 0.6 inches in 1927 and 1937; since 1957 the minimum dbh has been 0.5 inches. The plots were not inventoried in 1947. Individual trees were matched with data from previous inventories using their location, species, and diameter. To increase the sample size of larger stems, the transect width was increased to 33 feet in 1957 for all stems with diameters of at least ten inches. These larger trees in the outer strips were measured and mapped concurrently with the stems in the inner, original strips. More complete details of the plots and sampling can be found in Ward and others (1999).

Data Analysis

Preliminary analysis following defoliation episodes found survival and growth differed between the white oak subgenera (*Leucobalanus*) and the red oak subgenera (*Erythrobalanus*). Species in the *Leucobalanus* subgenera include white (*Quercus alba*) and chestnut oak (*Q. prinus*). Species in *Erythrobalanus* subgenera include northern red (*Q. rubra*), black (*Q. velutina*), and scarlet oak (*Q. coccinea*). In the analysis and discussion that follows, these groups will be referred to as the white oak and red oak groups, respectively.

To allow direct comparisons of mortality rates in this study and other published studies, mortality rates were converted to 10-year values. Differences in mortality rates among periods (intersurvey intervals) were tested using procedures by Neter and others (1982, p 325-329). Analysis of variance was used to examine influence of species group, crown class, and periods on diameter growth. Tukey's HSD test was used to determine whether diameter growth differed among periods and species group for each crown class. Differences were considered significant at $P \leq 0.05$.

RESULTS AND DISCUSSION

Before Defoliation

Mortality rates for upper canopy trees (dominant and codominant crown classes) were lower than mortality rates for lower canopy trees (intermediate and suppressed) during the thirty-years before multiple years of defoliation (table 1). During this period, mortality of upper canopy trees averaged less than 5 percent per decade compared with more than 60 percent per decade for suppressed oaks.

Table 1—Mortality rates of oaks in southern New England by survey period and crown class at beginning of period

Species group and period	Crown class at beginning of period[a]			
	Dominant	Codominant	Intermediate	Suppressed
	Mortality rate (percent per decade)			
Red oaks				
1937–57	3a	5b	26a	60b[b]
1957–67	11b[b]	44c[b]	79b	78c[b]
1967–77	12b	35c	43a	69bc
1977–87	5a	4ab	24a	33a
1987–97	2a	2ab	31a	54b
White oaks				
1927–37	1a	4a	18a	61b
1937–57	2a	11a	31a	71b
1957–67	55c	76b	84b	89c
1967–77	10b	13a	33a	46ab
1977–87	5ab	5a	31a	33a
1987–97	0a	3a	9a	60b
	Sample size			
Red oaks				
1927–37	325	238	361	562
1937–57	239	230	233	353
1957–67	540	144	81	167
1967–77	514	74	14	35
1977–87	424	101	21	21
1987–97	382	140	29	72
White oaks				
1927–37	151	165	336	1,032
1937–57	98	136	196	625
1957–67	161	88	56	167
1967–77	78	15	9	26
1977–87	64	22	16	66
1987–97	53	29	11	113

[a] Column values for a given species group and crown class with the same letter were not significantly different at $p \leq 0.05$.
[b] Red oak and white oak mortality were significantly different at $p \leq 0.05$.

Similar mortality rates (converted to 10-year basis) were found in other stands that were not defoliated. In New York, mortality of northern red oak between ages 24-64 years varied by crown class; 5 percent for dominant and codominant trees, 33 percent for intermediate trees, and 70 percent for suppressed trees (Lorimer 1981). Another study in New York and Massachusetts found mortality of 21-41 year-old upper canopy trees was 3-4 percent compared with 55-59 percent for suppressed trees (Lorimer 1984). In West Virginia, mortality was much higher for intermediate than codominant or dominant 55-year-old northern red oaks (Trimble 1974).

Before defoliation, mortality rates of upper canopy trees did not significantly differ between the white and red oak groups (table 1). Diameter growth of red oaks was significantly greater than for white oaks within a given crown class, except for suppressed trees between 1927-1937 (table 2). Average annual diameter growth of red oaks between 1927-1957 was 0.17 inches compared with 0.12 inches for upper canopy white oaks.

During the Period of Multi-Year Defoliations

The three consecutive years of moderate to heavy defoliation, 1961-1963, were the first known defoliation episodes on these plots. Mortality rates increased significantly during this period (table 1). Significant increases were noted for both the red oak and white oak groups, and for all crown classes. Mortality of dominant and codominant white oaks increased to 55 and 76 percent, respectively. This was significantly higher than the mortality rates of dominant and codominant red oaks. Mortality of all dominant and codominant red oaks remained higher than pre-defoliation levels during 1967-77 when there were two consecutive years of defoliation. Interestingly, mortality of codominant white oaks decreased to values similar to, and not significantly different from, pre-defoliation values.

Table 2— Annual diameter growth of oaks in southern New England by period and crown class at beginning of period

Species group and period	Crown class at beginning of period[a]			
	Dominant	Codominant	Intermediate[b]	Suppressed
	inches per decade			
Red oaks				
1927–37	0.24d[b]	0.15d[b]	0.09a[b]	0.04a
1937–57	0.17c[b]	0.11bc[b]	0.08a[b]	0.06a[b]
1957–67	0.12a[b]	0.07a	0.05a	0.04a
1967–77	0.11a[b]	0.08ab	0.07a	0.07a
1977–87	0.14b	0.10abc	0.07a	0.05a
1987–97	0.15bc	0.12c	0.10a	0.03a
White oaks				
1927–37	0.18d	0.12b	0.07a	0.03a
1937–57	0.10abc	0.08a	0.04a	0.02a
1957–67	0.08a	0.06a	0.01a	0.03a
1967–77	0.09ab	0.05a	0.02a	0.04a
1977–87	0.12bc	0.09ab	0.04a	0.04a
1987–97	0.13c	0.11ab	0.05a	0.02a

[a] Column values for a given species group and crown class with the same letter were not significantly different at $p \leq 0.05$.
[b] Red oak and white oak diameter growth were significantly different at $p \leq 0.05$.

Mortality differed among species during 1957-1967 (table 3). Red oaks (northern red, black, and scarlet) in the dominant crown class had lower mortality rates during this period than white and chestnut oaks. In the codominant crown class, mortality of northern red and scarlet oak were lower than for white and chestnut oak. Northern red and black oaks in the suppressed crown class had lower mortality than white oak. Thus, when crown class is included as a factor, the red oak group had lower mortality than the white oak group.

Other studies differ on relative mortality rates among species during and immediately following defoliation (table 4). Because these studies did not present mortality rates by crown position for individual species and because mortality is much higher for trees in the lower canopy than for trees in the upper canopy, the observed differences in species mortality rates in other studies may reflect the proportion of each species that was in lower canopy in each study.

Diameter growth of upper canopy red oaks, but not white oaks, decreased during the initial period of defoliation (table 2). Growth rates for dominant and codominant red oaks decreased by 30 and 35 percent, respectively. Red oak diameter growth during the pre-defoliation period (1937-1957) was 23-30 percent lower than the previous period (1927-1937). Multi-year defoliations reduced oak (primarily black oak) diameter growth by 32-40 percent (Brown and others 1979). Other studies found diameter growth reductions for both red and white oaks following defoliation (Campbell and Garlo 1982, Muzika and Liebhold 1999).

Mortality rates of lower canopy (intermediate and suppressed) oaks increased during the initial period of defoliation (table 1). Mortality rates were similar to pre-defoliation values during the second period of defoliation. Other studies have also reported higher mortality for lower canopy oaks (Brown and others 1979, Campbell and Sloan 1977, Kegg 1971). It should be recalled that mortality of suppressed oaks was high prior to defoliation (table 1), and it is likely that defoliation merely accelerated demise of this crown class. Surprisingly, multi-year defoliations did not have a significant impact on diameter growth of lower canopy trees (table 2). This may be because mortality was higher for the slowest growing trees (table 5).

Table 3—Mortality rates between 1957–67 of oaks in southern New England by species and crown class in 1957

	Crown class in 1957[a]			
Species	Dominant	Codominant	Intermediate	Suppressed
		Mortality rate (percent per decade)		
Northern red oak	10a	38a	77a	79a
Black oak	12a	53ab	82a	76a
Scarlet oak	13a	44a	82a	87ab
White oak	40b	72b	83a	92b
Chestnut oak	67c	82b	90a	80ab
		Sample size		
Northern red oak	303	72	53	94
Black oak	133	45	17	58
Scarlet oak	104	27	11	15
White oak	70	50	46	132
Chestnut oak	91	38	10	35

[a] Column values for a given species group and crown class with the same letter were not significantly different at $p \leq 0.05$.

Table 4—Summary of previous research on mortality rates of oak species following gypsy moth defoliation

Study	CHO	WHO	BLO	SCO	NRO	State
Kegg (1971)	11	38	16	39	36	NJ
Kegg (1973)	66	84	48	27	41	NJ
Dunbar and Stephens (1975)	80	42	27	33	32	CT
Campbell and Sloan (1977)	—	42	48	35	16	MA
Stalter and Serrao (1983)	0	1	4	—	46	NJ
Fosbroke and Hicks (1989)	44	35	46	57	31	PA
Herrick and Gansner (1987)	23	23	33	28	14	PA
Average	37	38	32	37	31	
Median	34	38	33	34	32	

CHO = chestnut oak; WHO = white oak; BLO = black oak; SCO = scarlet oak; NRO = northern red oak; NJ = New Jersey; CT = Connecticut; MA = Massachusetts; PA = Pennsylvania.
— = not applicable.

Table 5—Mortality rates between 1957–67 of oaks in southern New England by diameter growth and crown class immediately before multi-year defoliations[a]

Species group	Annual growth	Crown class at beginning of period[b]			
		Dominant	Codominant	Intermediate	Suppressed
		percent per decade			
Red oaks					
	≤ 0.05	—	60b	96b	94b
	0.05 – 0.10	35c[c]	58b[c]	75a	84b
	0.10 – 0.15	13b[c]	35a	50a	38a
	> 0.15	4a[c]	16a	—	—
White oaks					
	≤ 0.05		82ab	90a	95a
	0.05 – 0.10	66a	85b	70a	88a
	0.10 – 0.15	55a	56a	—	—
	> 0.15	44a	—	—	—

— = not applicable.
[a] Diameter growth was the average of the 1937–57 period.
[b] Column values for a given species group and crown class with the same letter were not significantly different at $p \leq 0.05$.
[c] Red oak and white oak mortality were significantly different at $p < 0.05$.

As was noted above, diameter growth of red oaks was higher than for white oaks prior to the period of multi-year defoliations (table 2). Thus, higher mortality of white oaks following defoliation may be related to lower vigor, more than to the ability of white oaks to successfully recover from (cope with) multiple defoliations. Mortality was higher for oaks with poor crowns than for those with good crowns (Campbell and Sloan 1977, Gansner and Herrick 1984).

For red oaks, but not white oaks, tree vigor was a good predictor of upper canopy tree mortality between 1957-1967 (table 5). Red oaks with annual diameter growth of at least 0.1 inch had lower mortality rates during the period of multi-year defoliations than slower growing trees (table 2). For example, mortality was 16 percent for codominant red oaks that had annual diameter growth of 0.15 inch compared with 60 percent for codominant red oaks that had annual diameter growth of less than 0.05.

After Defoliations

Although there was heavy defoliation in 1981, there have been no sequential years of defoliation since 1971-1972. The defoliation in 1981 did not induce the higher mortality of the earlier, multi-year defoliations (table 2). Indeed, mortality rates for both red and white oaks during 1977-1987 fell to values similar to, or lower than, those before the first defoliations in the 1960's.

Mortality continued to decrease during the next ten years, 1987-1997, except for both red and white oaks in the suppressed crown class. Many of the oaks in the suppressed crown class became established in the canopy gaps formed following the mortality pulse during the 1960's. The increased mortality between 1987-1997 can probably be attributed to competition from the more shade tolerant maple and birch that became established at the same time.

Diameter growth quickly recovered following the end of multi-year defoliations. Diameter growth of codominant red and white oaks during 1987-1997 were similar to, or higher than, growth before 1957-1967 (table 2). Following multi-year defoliations, diameter growth of red and white oaks recovered to eighty percent of pre-defoliation levels within two years of defoliation episodes (Campbell and Garlo 1982), and full recovery was noted after 10 years (Campbell and Sloan 1977). Other studies have also noted oak stands are capable of quickly recovering once defoliation severity and frequency have subsided (Feicht and others 1993, Gansner and others 1983, Muzika and Liebhold 1999).

Stand basal area of oaks has increased steadily since 1927, except during the periods of multi-year defoliations (Ward and others 1999). The decrease in basal area between 1957-1967 was evenly distributed among lower canopy oaks and upper canopy white oaks. Basal area of upper canopy red oaks increased slightly during this period. The longer term impacts of multi-year defoliations have been to nearly eliminate lower canopy oaks (both red and white oaks) and to reduce the proportion of white oaks relative to red oaks. Because mortality of upper canopy red oaks was less than that for to white oaks, and because the diameter growth of surviving red oaks increased once defoliations ceased, total oak basal area is now higher than before the period of multi-year defoliations.

ACKNOWLEDGMENTS

As with all long-term studies, we are indebted to the two generations of scientists and field technicians who preceded us. We thank H.W. Hicock, M.F. Morgan, H.J. Lutz, H. Bull, and H.A. Lunt for the foresight in establishing these permanent forest research plots; G.R. Stephens for maintaining the research from 1957-1987; and the Division of Forestry, Connecticut Department of Environmental Protection for preserving the study areas. This research was partly funded by McIntire-Stennis Project CONH-553.

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