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European Gypsy Moth (*Lymantria dispar* L.) Outbreaks: A Review of the Literature

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Abstract

The literature on tree mortality following outbreaks of European gypsy moth was reviewed. The trends in defoliation and mortality and the influence of defoliation on mortality of individual trees and forest stands have been summarized via a regional perspective. The literature showed that: certain tree species are defoliated at higher rates than other species, and frequently suffer greater mortality than less susceptible species; as the intensity (amount of foliage removed) and duration (number of consecutive episodes) of defoliation increases, the amount of tree mortality increases; trees in the lower canopy (those in the suppressed and intermediate crown classes) have a greater probability of being defoliated and dying than trees in the upper canopy (dominants and codominants); and tree mortality tends to increase rapidly during the second year after defoliation.

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Introduction

Following its introduction to Massachusetts in 1869, the European gypsy moth (*Lymantria dispar* L.) has expanded considerably. Currently, its range comprises the entire Northeastern United States as well as portions of North Carolina, Virginia, West Virginia, Ohio, and Michigan (Liebhold et al. 1997). Recently observed reductions in the total area defoliated notwithstanding, the impact of gypsy moth defoliation and subsequent tree mortality on eastern forests continues to be an area of concern (USDA For. Serv. 1995). Such concern is based on observed reductions in tree growth, flowering, and fruiting, and possible tree mortality. Within the urban/forest interface, problems associated with gypsy moth outbreaks are exacerbated by aesthetic and nuisance concerns due to large numbers of wandering larvae and to health risks associated with larval hairs (Montgomery and Wallner 1988).

The amount of defoliation that occurs and its affect on tree physiology is dependent on a number of interrelated factors, for example, tree species, which directly influences the probability and degree of individual-tree defoliation. Certain species are more susceptible than others to defoliation and frequently are defoliated at much higher rates (Liebhold et al. 1995). Tree species also differ in the degree of vulnerability following defoliation. The highly susceptible oaks (*Quercus* spp.) frequently survive repeated defoliation while the less susceptible eastern hemlock (*Tsuga canadensis* L. Carr) can die following a single defoliation (Campbell and Sloan 1977; Twery 1991). Abiotic stresses such as drought, fire, and ice damage also increase the vulnerability of trees. In fact, organisms that attack the weakened tree cause the majority of the mortality that follows defoliation. *Armillaria* spp., a root rot fungus, and *Agilus bilineatus*, the twolined chestnut borer, are examples of secondary agents that cause significant tree mortality in eastern forests (Wargo 1977; Dunbar and Stephens 1975; Dunn et al. 1986).

The extensive literature on the effects of defoliation and mortality from the gypsy moth in the United States includes numerous studies of the bioecology of this insect, control methods, and the effects of defoliation on individual trees and forest stands. In this report we have attempted to summarize this information, with emphasis on trends in defoliation and mortality in the New England States, Pennsylvania, New York, New Jersey, Virginia, West Virginia, and Michigan.

New England

The Melrose Highlands Study

As the source of the original gypsy moth infestation, Massachusetts and the surrounding New England states suffered extensive defoliation and mortality during the early part of the 20th century. The Gypsy Moth Laboratory of the Bureau of Entomology and Plant Quarantine at Melrose Highlands, Massachusetts, conducted one of the first intensive studies of the extent of damage to forest trees from the gypsy moth. Between 1911 and 1931, extensive records

of defoliation and tree condition were collected (Campbell and Sloan 1977). In 1911 and 1912, 264 circular plots (0.07 ha) were established in mixed-oak stands from Cape Cod, Massachusetts, to Kennebunk, Maine (Campbell and Valentine 1972; Campbell and Sloan 1977). Within each plot, species and dominance class were recorded for all trees 7.6 cm and larger in diameter at breast height (dbh). Individual-tree defoliation (based on visual estimates), tree condition, and egg-mass density were determined annually; tree diameters were recorded in 1912 and 1921. Of the original 264 plots, 75 were removed from the study by 1913; 122 plots were maintained through 1921 and 55 were maintained until 1931. We do not have descriptions of the procedures or criteria that were used to estimate defoliation and determine tree condition. As a result, the exact meaning of "ocular estimates" of defoliation, and of trees in "good, fair, or poor" condition is not known (Campbell and Valentine 1972). Nonetheless, the Melrose Highlands data have been the primary source for numerous studies.

The earliest known reference to this data set was by Minott and Guild (1925), whose study was based on records of 37 species comprising 14,610 trees. Each tree was assigned to one of four defoliation classes. Favored species averaged 33.6 percent defoliation per year, while defoliation of species not favored by young larvae averaged 8.8 percent per year; partially favored species averaged 10.2 percent and unfavored species averaged 1.9 percent. Yearly foliage loss of white (*Q. alba* L.), northern red (*Q. rubra* L.), scarlet (*Q. coccinea* Muenchh.), and black (*Q. velutina* Lam.) oaks averaged 36.5 percent and 47 percent of these trees were dead at the end of the 10-year study period. Minott and Guild were unable to separate mortality caused by the gypsy moth from that due to what they termed "...crowding and suppression." Also, they provided no data on egg-mass levels, so it is impossible to determine whether population levels were consistent across all study sites.

Baker (1941) provided a detailed description of defoliation and mortality using the Melrose Highlands data. His analysis was based on plots with 38 species comprising 13,357 trees. Baker also referred to an additional research plot established in 1915 in a stand of young eastern white pine (*Pinus strobus* L.) and coppice hardwoods that had experienced a single, heavy defoliation that year. Information was collected on height, percent defoliation, and the percentage of old and new foliage consumed for 310 pine trees. These trees were examined annually until 1924 at which time percent mortality was recorded. Baker noted the difficulty in distinguishing "normal" mortality from that attributable to the gypsy moth. However, he believed that the observed mortality of dominant trees during this period was abnormal and "...would not have occurred on such a wide scale in the absence of the gypsy moth." Results of his study show that favored species experienced an average defoliation of 37 percent versus 10 percent for unfavored species. Although there was a general pattern of increasing defoliation that resulted in increased mortality, most of the heavy mortality was in stands that experienced defoliation ranging from 21 to 80 percent. Mortality of favored species was 30 percent compared to 13 percent for unfavored species. Among

Table 1.—Effect of crown condition, crown class, and frequency of defoliation on 5-year stem mortality in a composite mixed stand of oaks following a single, heavy defoliation^a

Crown condition	Crown class		Tree mortality		
	Dominant	Intermediate/Suppressed	Baseline ^b	One defoliation	Two defoliations
----- Percent -----					
Good	3	12	1	7	22
Fair	—	—	3	19	50
Poor	22	41	9	36	55

^aFrom Campbell and Sloan (1977).

^bTrees used for the baseline mortality estimate had not been severely defoliated for at least 5 years; rates were calculated at the end of an additional 5-year period.

favorable species, 33 percent of dominants were killed, while only 7 percent of dominant trees of unfavored species died. This indicated that most of the mortality among unfavored species was in the smaller size classes. An outbreak of *Agrilus bilineatus* from 1912 to 1915 coupled with heavy defoliation, drought, and infection by *Armillaria* probably increased the vulnerability of trees to mortality (Baker 1941). In the mixed white pine-hardwood plot that experienced a single defoliation episode, the pines showed a trend toward increasing mortality with increasing defoliation; mortality was greatest among trees that experienced defoliation ranging from 81 to 100 percent.

During the 1970's, interest in the Melrose Highlands data was rekindled. In 1972, Campbell and Valentine published a series of projection tables of annual and cumulative mortality rates and the condition of surviving trees for various species and species groups based on their defoliation history. Although their primary goal was the prediction of tree condition subsequent to defoliation, mortality rates for individual species also were discussed. After 12 years and at least two defoliations, average mortality of individual species was 58 percent for white oak, 55 percent for gray birch (*Betula populifolia* Marsh.), 46 percent for both black and scarlet oak, 27 percent for northern red oak, 26 percent for eastern white pine, and 25 percent for red maple (*Acer rubrum* L.). Intraspecific mortality rates were highest among trees in the suppressed crown class and lowest among dominant trees. Trees in good crown condition prior to heavy defoliation had lower mortality than those in poor condition. Defoliation seemed to accelerate the decline of pioneer gray birch stands, giving weight to the cohort senescence theory. Campbell and Valentine also observed an increase in the white pine component in mixed stands of oak-white pine and gray birch-white pine.

Campbell and Sloan's (1977) monograph is considered by many as the definitive description of stand responses to the gypsy moth. Using data from the Melrose Highlands study, they summarized inter- and intraspecific responses of individual trees and a composite mixed stand of oaks

(northern red, black, scarlet, and white oak) following defoliation. The period from 1911 to 1921 saw a sustained gypsy moth outbreak, so the authors analyzed the 122 plots that were observed during those years. Campbell and Sloan provided a baseline rate of mortality (number of trees) for the composite mixed stand. Trees used for this estimation had not been severely defoliated for at least 5 years, and rates were calculated at the end of an additional 5-year period. This was then compared to the 5-year mortality rates for mixed oaks that had been subjected to a single, severe defoliation and those subjected to two consecutive heavy defoliations (Table 1). Five-year mortality rates for dominant and intermediate/suppressed oaks showed a similar pattern. Those in good condition fared better than those in poor condition following a single, heavy defoliation; dominant trees had a lower rate of mortality than intermediate/suppressed trees (Table 1). Campbell and Sloan (1977) also found that following a single heavy defoliation, mortality of resistant species was greater than that of mixed oaks. Resistant species in good condition prior to defoliation experienced 12 percent mortality, while only 7 percent of the mixed oaks originally rated in good condition were lost. Results were even more pronounced among trees that were originally classified as in poor condition; 69 percent of the resistant species were killed compared to 36 percent of the mixed oaks. The authors estimated that between 1911 and 1921, defoliation by the gypsy moth resulted in a 35-percent reduction in basal area of oaks, and a 16-percent reduction in total basal area. These figures also take into account losses due to cutting during this period. On a per-tree basis, nearly 42 percent of oak stems were killed, and more than 29 percent of all trees present in 1911 were dead by 1921. Campbell and Sloan concluded that the gypsy moth outbreak resulted in massive mortality of oak trees, and that changes in basal area were closely associated with the original stand composition. The greater the original percentage of oak a stand contained in 1911, the less total basal area that stand contained in 1921. The composite stand with more than 66 percent oak in 1911 lost 47 percent of its original basal area by 1921; where the composite stand originally contained between 33 and 66 percent oak, there was a 26-percent loss

Table 2.—Effect of crown condition on 5-year stem mortality rates of dominant and intermediate/suppressed trees, mixed oaks, and resistant species following a single, heavy defoliation in a composite mixed stand of oaks^a

Crown condition	Tree mortality			
	Dominant	Intermediate/ suppressed	Mixed oaks	Resistant species
	----- Percent -----			
Good	3	12	7	12
Poor	22	41	35	70

^aFrom Campbell (1979).

in basal area. The composite stand with less than 33 percent oak lost 21 percent of its original basal area, and stands with no oaks and less than 20 percent susceptible species lost 11 percent of the original basal area.

Tree condition and crown position also influenced the probability of mortality subsequent to defoliation. When trees were rated visually as in good condition prior to defoliation, their likelihood of surviving was much greater than trees rated as poor. Dominant trees weathered a defoliation episode better than intermediate/suppressed trees; the authors likened this result to “a thinning from below.”

The frequency of defoliation also increased mortality; two successive defoliations killed more trees than a single episode. Different mortality rates among host preference classes and crown classes resulted in smaller numbers of susceptible species and intermediate/suppressed trees in the forest in 1921. There also were significant intraspecific differences. Within a single species, some trees were consistently defoliated at a much higher rate than their counterparts; consequently, these trees also died at a much higher rate. Campbell and Sloan pointed out that defoliation tended to be greater during the initial stage of the outbreak, and that the changes they observed were similar to “those that might be expected from natural selection.”

Campbell (1979) used the Melrose Highlands data to emphasize the interrelationships among insects, trees, and biophysical factors. The data were sorted into trees that had experienced light defoliation (less than 75 percent) and heavy defoliation (75+ percent), and a baseline rate of “normal” mortality for a composite mixed stand of oaks (northern red, scarlet, black, and white oak) was established. The effect of crown condition, crown class, and species composition on cumulative percent mortality during a 5-year period following a single, heavy defoliation is shown in Table 2. Campbell’s results indicate that a single, heavy defoliation within a predominantly oak stand killed primarily the less vigorous intermediate and suppressed trees, many of which would not have survived anyway.

However, two heavy defoliations may result in the death of otherwise healthy, dominant oaks. Campbell observed that

following two successive defoliations, 22 percent of oaks originally rated in good condition were dead after 5 years. When defoliation of resistant species occurred, it often had a far greater effect than the defoliation of susceptible species, particularly among trees in poor condition. An unexpected result was the apparent greater resistance to mortality exhibited by white pine compared to red maple. Following a single, heavy defoliation, mortality of red maple was considerably higher than that of eastern white pine. Campbell (1979) attributed this observation to “...basic differences in either tree physiology or specific timing of events connected with defoliation.” By 1921, interspecific differences in mortality had created stands that contained about one-third fewer susceptible species than were present prior to the outbreak; this probably rendered them less susceptible to future outbreaks.

Other Studies

In 1932, Cape Cod experienced an intense defoliation episode. That year, in cooperation with the Melrose Highlands Gypsy Moth Laboratory and the Harvard Forest, Hall (1935) studied the relative resistance of Cape Cod pitch pine (*P. rigida* Mill.) to gypsy moth defoliation. He determined that pitch pine was defoliated only after all other more palatable species had been consumed. Nearly all of the foliage that was eaten consisted of second- or third-year needles. By contrast, the gypsy moth fed on new and old needles of white pine, red pine (*P. resinosa* Ait.) and spruce (*Picea* spp.), apparently resulting in increased mortality. Hall also described two red pine plantations: one had been sprayed and suffered no damage; the other was completely defoliated and experienced nearly total mortality. On the basis of this information, Hall determined that pitch pine on Cape Cod was relatively resistant to the gypsy moth and should be considered in future management prescriptions for that area. His study includes one of the earliest descriptions of conifer defoliation by the gypsy moth; and provides insight into apparent differences in susceptibility among conifer species.

In 1952, the Plant Pest Control Branch of the Bureau of Entomology and Plant Quarantine evaluated the gypsy moth problem (Perry 1955). Part of the assessment focused on stumpage losses due to mortality and growth loss due to

Table 3.—Estimated losses in merchantable timber to mortality from gypsy moth in New England States, 1932-52^a

State	Area defoliated (75 to 100%)	Tree mortality ^b			Estimated value of stumpage killed		
		Total	Pulpwood	Sawtimber	Pulpwood	Sawtimber	Total
	<i>ha</i>	<i>Percent</i>	<i>m³</i>		<i>Cost</i>		
Maine	102,926	18	921,708	162,138	618,031	412,020	1,030,051
New Hampshire	189,230	18	1,317,998	198,615	883,755	505,008	1,388,763
Vermont	3,927	18	31,260	4,120	20,961	10,476	31,437
Massachusetts	632,190	18	2,798,024	240,222	1,134,382	610,800	1,745,182
Connecticut	2,884	9	11,478	1,515	10,262	3,852	14,114
Rhode Island	7,871	9	19,581	2,067	8,753	5,256	14,009
Total	939,028	—	5,100,049	608,667	2,676,144	1,547,412	4,223,556

^aFrom Perry (1955).

^bThe following conversion factors were used to convert English units reported in the original article to the metric units reported here: 6 board feet = 1 cubic foot; 1 standard cord = 79 cubic feet; 1 cubic meter = 35.3145 cubic feet.

defoliation from 1933 to 1952. Results indicated that both oak and pine-oak forests were affected, with oaks absorbing most of the damage. Northern red, scarlet, and black oaks were the most vulnerable following defoliation; white and chestnut (*Q. prinus* L.) oaks were the least vulnerable. White pine and hemlock also suffered mortality but to a lesser degree. Perry referred to the unpublished work of J.N. Summers and others in eastern New England and G. C. Tierney in the Connecticut River Valley area of Massachusetts. Summers studied more than 186 gypsy moth-infested forest areas from 1912 to 1921 and observed mortality rates of about 33 percent. Tierney estimated mortality for a 10-year period (1935 to 1946) based on 33 areas totaling 1,046 ha. During this period, each area experienced an average of 2 years of 75-to 100-percent defoliation. Average mortality for the total area was 37 percent.

Perry's (1955) study included field evaluations of mortality in 84 forested areas with a history of heavy defoliation and that were considered representative of areas described in published annual reports as having suffered defoliation rates of 75 to 100 percent. Many areas that experienced this amount of defoliation for 2 years had an average annual mortality rate of 12 to 18 percent (about 24 percent on a volume basis). On the basis of Tierney's work and the 1952 field evaluations, Perry estimated an "expectable mortality loss" of 18 percent for every 0.4-ha area that incurred defoliation of 75 to 100 percent during the previous 20 years. Utilizing this annualized rate, related stand volumes and relevant stumpage values, it was estimated that between 1933 and 1952, gypsy moth-related mortality on 939,028 ha affected 5,100,049 m³ of pulpwood and 608,667 m³ of merchantable sawtimber with an estimated value of \$4,223,556 (Table 3). According to the "Economic Report of the President" for 1990, this is equivalent to \$20,419,030 in 1990 dollars.

Turner (1963) evaluated the work of House (1960) in a summary of the effects of gypsy moth defoliation in New England. House's study focused on the effects of defoliation on white pine. Two sets of plots were established in 1953 and 1954 in areas of severe defoliation of white pine and hemlock; these included defoliated and undefoliated check plots. The plots established in 1953 were located in Connecticut and Maine; those established in 1954 were located in southeastern New Hampshire and southwestern Maine. Species composition was typical of unmanaged stands in the central and transitional hardwood-white pine-hemlock forests of New England. White pine and hemlock were the major species within the stands, while northern red and white oak, other northern hardwoods, spruce, and fir (*Abies* spp.) were minor components (Table 4). Defoliated plots on both areas were subjected to a single, severe defoliation (90 to 100 percent) followed by 5 years with no significant defoliation. At the end of the 5-year period, cumulative stem mortality of white pines was 8 percent on the 1953 plots and 17 percent on the 1954 plots. Trees that were completely stripped or had 90 percent of their foliage removed had the highest mortality rates (Table 4). Two-thirds of all white pine mortality occurred in the 2 years following defoliation. Only 11 percent of the total killed were dominant and codominant trees; 42 percent were in the suppressed class and 16 percent were intermediates.

Turner concluded that: "in the absence of any planned management ... defoliation by gypsy moth merely hastened a natural and widespread process—death of white pine by prolonged suppression;" that is, the trees succumbed to competition-induced mortality. The recovery of defoliated white pines was also observed. Five years after the defoliation episode, 31 percent of stems that were completely defoliated had normal crowns and the crown level of another 47 percent had reached 80 percent. The plots established in 1954 were pure white pine stands, yet they

Table 4.—Five-year mortality rates for trees in defoliated (90 to 100 percent) and undefoliated stands in New England^a

Item	Stand composition			Stem mortality	
	Eastern white pine	Eastern hemlock	Red/white oaks	Eastern white pine	Eastern hemlock
----- Percent -----					
1953 Plots					
Defoliated	69	14	11	19	68
Undefoliated	80	15	5	0	0
1954 Plots					
Defoliated	95	5	0	39	66
Undefoliated	93	0	7	0	0

^aFrom Turner (1963).

suffered extensive defoliation and significant mortality. Since the data available to us does not indicate the presence of “susceptible” species within the defoliated stands, we must assume that larvae became established in adjacent forested areas prior to moving on to the more resistant white pine.

Between 1972 and 1975, Brown et al. (1979) studied defoliation and mortality in mixed oak, oak-pine, and mixed hardwood stands in Rhode Island. Mixed oak stands contained scarlet, white, and black oak; oak-pine stands contained white pine, pitch pine, scarlet oak, white, and black oak; and mixed hardwood stands contained scarlet, white, black, and northern red oak, beech (*Fagus grandifolia* Ehrh.), birches, red maple, and hickories (*Carya* spp.). Oaks comprised 98 percent of the basal area in mixed oak stands, 60 percent in oak-pine stands and 29 percent in mixed hardwood stands. The sites experienced 2 years of heavy defoliation (60 to 100 percent) (1971 and 1972), followed by medium defoliation (20 to 60 percent) in 1973, and low defoliation (0 to 20 percent) in 1974. Defoliation was negligible in 1975. Oaks were subjected to higher levels of defoliation in the mixed oak stand (more than 60 percent) than in either oak-pine or mixed hardwood stands; this was reflected in the observed mortality within each stand type. The mixed oak type lost 17.4 percent of its original basal area over the 3-year period, while the oak-pine type lost 6.7 percent and the mixed hardwood type lost 5.0 percent. The effect of crown position also was apparent; 90 percent of all dead stems and 63 percent of the total loss of basal area was in suppressed and intermediate trees. Brown et al. concluded that “...reduced defoliation and low mortality rates in the oak-pine and mixed hardwood stands attest to the importance of species composition” in determining susceptibility to gypsy moth defoliation.

Rhode Island forests also were subjected to intensive defoliation in 1981 and 1982. Brown et al. (1988) described the mortality of white pine in mixed stands during the outbreak. Infested and control stands of three types (oak-pine, pine-oak, and pine) were studied. Conditions on all sites were described as similar. The site index was below 60

for oaks. White pine was an understory component in oak-pine stands, in the overstory in pine-oak stands, and the dominant species in stands of pure pine. The major oak species within the mixed stands included white, scarlet, and black oak. Stands were located in the Arcadia State Forest in Richmond and Exeter Counties and Scituate, Rhode Island, and the Pachaug State Forest in Voluntown, Connecticut. Defoliation of suppressed and intermediate white pines was severe (75 to 100 percent) in 1981; 85 percent of all understory white pines in the oak-pine type were defoliated, 94 percent were defoliated in the pine-oak type, and 41 percent were defoliated in the pure pine type. Dominant and codominant white pines experienced only light defoliation. Brown et al. (1988) suggested that small stand size and proximity to susceptible stands contributed to defoliation in what otherwise would be considered a resistant stand type.

Following defoliation, most of the white pines that were killed in all stand types were understory stems. Oak-pine stands lost 42.5 percent of the original understory basal area; pine-oak stands lost 38.7 percent and pure pine stands lost 43.2 percent. White pines in the overstory were essentially unaffected and basal-area losses were negligible. On a total stand basis, oak-pine stands were hit the hardest, losing 33.7 percent of the original white pine basal area. Pine-oak stands lost 12.7 percent; while in pure pine stands only 7.3 percent of the original basal area died. The authors suggested that silvicultural practices that encourage the movement of white pine from the understory to canopy would reduce mortality. Although defoliation of oaks was severe in mixed stands, the mortality observed was comparable to that in control stands. Because these areas had been infested during a severe outbreak in 1970-74 (Brown et al. 1988), many of the vulnerable oaks may have been killed prior to the 1981-82 infestation. This would explain the low mortality that was observed.

In 1981, extensive areas of hemlock and white pine were defoliated following a large outbreak in western Connecticut. Stephens (1984, 1987, 1988) described in three studies, the subsequent mortality of these species. Four stands were

Table 5.—Percent stem mortality of eastern white pine and eastern hemlock in western Connecticut stands 3 years after a heavy defoliation^a

Species	Suppressed	Intermediate	Codominant	Dominant	Total
White pine	26	7	0	0	17
Hemlock	44	47	40	19	43

^aFrom Stephens (1988).

examined, an oak-pine stand in which the white pine understory had been released by removing half of the oak overstory; a hardwood-hemlock stand in which hemlock was present in both the overstory and understory; and two hardwood-pine stands in which white pine was present in both the overstory and understory (Stephens 1988). All of the stands were heavily defoliated by the gypsy moth in 1981; susceptible species were completely defoliated and larvae then moved on to white pine and hemlock within the stands. Conifers that suffered the most extensive defoliation were dominant hemlocks (84 percent mean defoliation), and suppressed white pine (80 percent). While individual hemlocks within each of the four crown classes were completely stripped, none of the white pines experienced total defoliation. Stephens noted that hemlock had a higher vulnerability than white pine, and that the vulnerability of intermediate and suppressed trees was greater than that of dominants or codominants (Table 5). Stephens implicated competition-induced mortality as a possible cause, stating that the "... lack of mortality among dominant and codominant white pine and the slow increase in mortality of intermediate and suppressed trees suggests any effect of defoliation was simply to accelerate mortality, which would have occurred eventually."

Slight variations in defoliation intensity seemed to have a notable influence on hemlock mortality. Intermediate and suppressed trees that experienced defoliation of 90 percent or less had a much lower probability of dying than trees that were completely stripped. Stephens also suggested that the mortality of hemlock was a direct result of defoliation as opposed to secondary factors such as insects or disease. However, he did not believe that extensive pure stands of hemlock or white pine would be susceptible to defoliation. Rather, he stated that foliage loss is likely only where these resistant species grow in mixed stands with susceptible species, or where large areas of susceptible species grow near pure stands. Following heavy defoliation, both overstory and understory hemlock seemed highly vulnerable to mortality, while vigorous overstory white pine would be expected to survive with little impact.

Stephens and Ward (1992) reported on the dynamics of unmanaged mixed hardwood stands in the Eastern Highlands of Connecticut over a period of 60 years. Transect data from four forest tracts were described. Three sets of transects were established in 1927 (Cabin, Cox, and Reeves), and one was established in 1926 (Turkey Hill). Stand age at the time of transect establishment was an estimated 20 to 40 years for all tracts. Trees were inventoried every decade beginning in 1926-27 and ending in 1987.

Beginning in 1937, tree mortality was recorded on all tracts except for a portion of the Turkey Hill tract that was ravaged by wildfire in 1932. In 1934, this area was reinventoried and tree mortality was recorded.

The tracts were described as representative of forests of this region. Some portions had been cleared for agriculture and then reverted to forest cover; other areas were never cleared but were subjected to repeated timber harvests. Trees were separated into major and minor species based on their potential lifespan and position in the canopy. Major species were further subdivided into four groups: oaks, including northern red, black, scarlet, white, and chestnut; maples, including sugar and red; birches, including black (*B. lenta* L.) and yellow (*B. alleghaniensis* Britton); and other species, which included all other major tree species. Oaks accounted for 30 percent of the total number of major species present; maples contributed 28 percent and birches accounted for nearly 20 percent. Minor species included American chestnut (*Castanea dentata* Marsh), flowering dogwood (*Cornus florida* L.), and bluebeech (*Carpinus caroliniana* L.). Each tract was also separated into four soil drainage classes: wet, moist, medium-moist, and dry.

During the 60-year period analyzed, the forests were subjected to three significant defoliation episodes. From 1957 to 1967, gypsy moth and spring cankerworm (*Paleacrita vernata* Peck) were the primary defoliators of all four areas (defoliation by other species was mentioned but not identified). The Cox, Cabin and Reeves tracts were partially defoliated between 1961 and 1963; in 1964, the Turkey Hill tract suffered partial defoliation. From 1967 to 1977, gypsy moth and elm spanworm (*Ennomos subsignarius* Hübner) defoliated all four areas; the Cox tract suffered the most defoliation and the Turkey Hill tract the least. Between 1977 and 1987, gypsy moth was the primary defoliator. Each area was heavily defoliated in 1981; the Cabin tract was subjected to minor defoliation in 1982. Defoliation was described only in general terms; the amount of defoliation on each tract was estimated by aerial survey but actual amounts for all 6 decades were not provided. However, Stephens and Ward (1992) stated that the decade from 1957 to 1967 experienced the most disturbances due to a combination of defoliation and an extended drought.

Mortality was separated into periodic mortality (overall mortality during one decade), and periodic canopy mortality (mortality of canopy trees during one decade) expressed on both a stem and volume basis. The oak group accounted for the most mortality (basal-area basis) during the 60-year

period. Of the five major oak species affected, white and chestnut oaks suffered the greatest loss. Periodic basal-area mortality among white and chestnut oak ranged from 54 to 66 percent, while mortality among the red oak group ranged from 18 to 26 percent. During the same period, periodic mortality (stem basis) of the oak group increased from 37 to 70 percent. Periodic canopy mortality varied by species group during the entire study period. From 1957 to 1967, birches and maples experienced low canopy mortality following high levels in the early years of the study. From 1967 to 1987, birch and maple lost more canopy trees than the oaks or other species groups. Mortality among the oaks was greatest from 1957 to 1967 (25 percent of the basal area and 32 percent of the stems) and decreased in subsequent years. From 1927 to 1957, much of the observed loss was among smaller canopy trees; from 1957 to 1967, mortality was high among the larger oaks. When all four sites were combined, total periodic basal-area mortality was greatest (30 percent) from 1937 to 1957. During the 30 years that followed, a period during which defoliation occurred, total periodic basal-area mortality decreased: 24 percent in 1957-67, 15 percent in 1967-77, and 10 percent in 1977-87. Gypsy moth defoliation apparently is a regular disturbance feature in the forest, perhaps increasing the rate of stand development and hastening the death of weaker trees.

New Jersey and New York

Gypsy moth infestations in New York State were first discovered in Geneva in 1913 and the Westchester area in 1914 (McManus and McIntyre 1981). New Jersey's infestations apparently originated from a shipment of blue spruce trees imported from the Netherlands. By 1920, 104,085 ha near Somerville were affected (McManus and McIntyre 1981).

Kegg (1971) described defoliation-induced oak mortality within a northern hardwood forest in New Jersey. The outbreak began in the Morristown National Historical Park in 1966 in a single, 2-ha tract and increased during the next 3 years. In 1968 and 1969, all susceptible tree species suffered defoliation ranging from 50 to 100 percent. The gypsy moth population subsequently collapsed and defoliation was minor in 1970. Kegg evaluated a 0.4-ha permanent plot established in 1967 and 100 sample plots (0.4 ha) established in 1970. Species most affected by the infestation included oaks and American beech, which sustained repeated defoliations. Most of the more resistant hardwoods, including black birch, red maple, and hickories, experienced a single defoliation. Prior to defoliation, oaks comprised 24 percent of all trees within the stand. During the course of the outbreak, oak mortality increased with each successive year of defoliation. Within the permanent plot, mortality of oak stems totaled 6 percent prior to 1967. By the spring of 1968 it had increased to 17 percent, and following 3 years of defoliation, 69 percent of all oaks had died. Sample-plot data revealed that oaks had the highest rate of stem mortality (28 percent) with a resulting loss in basal-area of 22 percent. Stem mortality of all other hardwoods was 5 percent or less. Kegg separated trees into four size classes (15 to

32, 33 to 47, 48 to 65, and 66 cm). Stem mortality was greatest in the smallest class (49 percent) and largest class (46 percent). Mortality in the other classes ranged from 21 to 25 percent. Kegg found that following repeated defoliation, oaks were the most vulnerable species, with mortality occurring when defoliation levels exceeded 70 percent. He suggested that the long-term effects of future outbreaks would be less severe due to the removal of susceptible tree species.

Kegg also described defoliation-induced oak mortality in the Newark Watershed (Kegg 1973, 1974). From 1968 to 1972, 7,231 ha of primarily oak forest were defoliated three times. In 1968, more than 400 ha sustained defoliation ranging from 50 to 75 percent. During the next 2 years, most of the susceptible tree species on the entire area sustained defoliation of 75 to 100 percent. In 1971-72, the population collapsed and defoliation was negligible. Five species of oak (white, northern red, chestnut, black, and scarlet) accounted for 63 percent of the total number of trees observed. As a result, oaks experienced the greatest mortality, a loss of 56 percent of the original basal area and 63 percent of the original stem density. Species in the white oak group lost a larger number of individuals (69 percent) than those in the red and black oak group (43 percent). Prior to the gypsy moth outbreak, average oak mortality was about 6 percent on a stem basis; defoliation increased this rate significantly. In 1969, oak mortality was 14 percent. Mortality increased to 38 percent in 1970, 58 percent in 1971, and 63 percent in 1972. Mortality among resistant species remained at pre-defoliation levels (less than 6 percent); this was cited as evidence that defoliation was the primary causal agent of the oak mortality.

Campbell and Garlo (1982) discussed short-term stand responses following two successive gypsy moth defoliations in the pine-oak communities of southern New Jersey. In their study, about 30 percent of the stand basal area consisted of pine species, primarily pitch and shortleaf pine (*P. echinata* Mill.); the red and white oak groups comprised the remainder. Stand age was estimated at 40 to 55 years. The authors' estimated individual-tree defoliation within each of 20 permanent plots (0.04 ha) between 1972 and 1976. The outbreaks occurred in 1972 and 1973, during which the oaks suffered extensive defoliation and the pines were moderately defoliated. From 1974 to 1976, the pines remained undefoliated while the oaks were moderately defoliated by associated phytophages. Three years after the final defoliation episode, increment cores were extracted from living trees. Radial growth of the oaks was reduced severely both during and following the defoliation episodes. In 1976, mean annual radial growth of trees in both the red and white oak groups was less than 80 percent of the growth in the 5-year period prior to the outbreak (1965 to 1970). Conversely, pines increased their growth to approximately 165 percent of that before the outbreak. According to the authors, the pines may be at an advantage following defoliation as evidenced by their increased growth. Mortality following the outbreak claimed nearly 12 percent of the original oak basal area and 8 percent of the pine.

Table 6.—Species composition (as a percentage of stand basal area) at three sites within Greenbrook Sanctuary, New Jersey, prior to defoliation by gypsy moth^a

Species	Site type		
	Wet	Mesic	Dry
	----- % of BA -----		
<i>Quercus rubra</i>	27.2	20.0	41.4
<i>Q. alba</i>	—	—	5.9
<i>Q. velutina</i>	—	—	2.4
<i>Q. prinus</i>	3.1	—	1.0
Susceptible hardwoods	—	—	0.3
Resistant hardwoods	18.5	3.0	23.6
Resistant conifers	25.2	20.9	—
Immune hardwoods	26.2	55.9	25.4

^aFrom Stalter and Serrao (1983).

Stalter and Serrao (1983) studied mortality following gypsy moth defoliation within an oak-dominated forest within Greenbrook Sanctuary in New Jersey. Three sites were examined: wet, mesic, and dry. Unfortunately, other than these generic descriptions, no quantitative information on soil drainage or site quality was presented. Four species of oak (northern red, white, chestnut, and black) were present within the forest, but not all species were found on all sites (Table 6). The outbreak began in 1979 and ended in 1981 after three successive defoliation episodes. Oaks suffered defoliation of about 90 percent each year. Northern red oak was the dominant oak species within the forest, accounting for 47 percent of all oaks present. This species also experienced the most stem mortality (32 percent). No chestnut oaks were lost and mortality of white and black oak was negligible (1 and 4 percent, respectively). Large, old trees and small, suppressed trees died at the highest rates. This result was similar to that reported for other locations in New Jersey (Kegg 1973). Mortality of red oak was low on the dry site (4 percent of original basal area) and high on the wet site (75 percent) and mesic site (100 percent). This confirms previous observations (Stalter and Serrao 1983) that trees on drier sites better tolerate physiological stress than trees of the same species on mesic sites. Stalter and Serrao did not suggest that gypsy moth defoliation was the primary causal agent of the observed mortality. Rather, they identified multiple factors, including the intensity and duration of defoliation, secondary organisms, drought, and the influence of site.

Pennsylvania

In 1932, the gypsy moth was reported in the Wilkes-Barre-Scranton area of Pennsylvania (McManus and McIntyre 1981). Subsequent eradication attempts failed and today the entire state is considered as generally infested.

Pocono Mountains

Gypsy moth defoliation and subsequent mortality in the Pocono Mountains region of Pennsylvania during the 1970's

has been chronicled in a series of papers spanning nearly 2 decades (Gansner and Herrick 1979; Gansner et al. 1983, 1993). In 1971, 143 plots were established and annual mortality of trees 7.6 cm and larger in dbh was recorded over a 5-year period. Defoliation was moderate to heavy from 1971 to 1973, with populations collapsing in 1974 and 1975 prior to another defoliation episode in 1976. Gansner and Herrick noted that mortality was distributed unevenly among the affected plots; mortality was heavy in only a small percentage of stands. For the 5-year period, mortality averaged 13 percent of the original number of trees and 13 percent of the original basal area. Oaks averaged 56 percent of the basal area prior to defoliation.

Gansner et al. (1983) revisited the plots described by Gansner and Herrick (1979), and characterized changes in stand composition from 1971 to 1979. Following the removal of some plots due to cutting, development, and insect control, the authors used 131 plots in their analysis. Gypsy moth populations caused moderate defoliation from 1976 to 1978 and collapsed in 1979. Between 1971 and 1979, the number of trees killed averaged 45 per acre (13 percent), but growth had offset most of the loss in mean basal area, which returned to pre-outbreak levels (19.5 m²/ha). Defoliation reduced the proportion of oaks within the affected stands, while the proportion of more resistant hardwood species increased. The oaks remained the largest component in 1979. While there was no significant overall change in basal area within the plots during the study, one-tenth lost more than 30 percent of their basal area and several lost more than 50 percent. Much of this mortality was in overstocked stands among small, low-grade trees. By 1979, the percentage of overstocked plots had been reduced from 24 to 17, while the percentage of fully stocked plots barely changed (63 in 1971 versus 62 in 1979).

Gansner et al. (1993) used data from several comprehensive forest inventories of the Pocono's in evaluating the impact of more than 2 decades of gypsy moth defoliation. Actual defoliation records were not provided, but the outbreaks

Table 7.—Effect of site quality on stem and basal-area mortality following defoliation in central Pennsylvania^a

Site index (m)	Stem mortality		Basal-area mortality	
	Oaks	Total	Oaks	Total
	----- Percent -----			
≥ 22.9	28	21	24	19
16.8 - 22.8	26	21	23	20
< 16.8	18	14	13	12
All sites	23	19	20	17

^aFrom Gansner (1987).

were characterized as typically cyclical, with peaks in the early 1970's and 1980's. Twelve percent of the original timber volume was lost between 1972 and 1976 (Gansner and Herrick 1979). Between 1978 and 1989 cumulative mortality averaged 10 percent; oaks experienced the greatest loss at 13 percent. Mortality was highly variable among individual plots. Some lost 100 percent of the original oak volume, while mortality was negligible and oak volume increased in others. Differences between species and among crown classes also were observed, with increased mortality among smaller, low-quality trees. The authors concluded that smaller, lower quality oaks suffered the highest mortality following gypsy moth defoliation. Volumes in trees less than 25 cm in diameter declined but increases in the larger diameter classes apparently compensated for this loss. Between 1965 and 1989, the total volume of growing stock increased by 60 percent; in 1989, oak volume accounted for 43 percent of the total inventory, the same proportion observed in 1965.

Central Pennsylvania

Herrick and Gansner (1987) have provided an excellent overview of defoliation and mortality in central Pennsylvania during the early 1980's. In 1978, more than 600 plots (0.04 ha) were established between Carlisle and State College in forest stands with no prior history of gypsy moth infestation. As would be expected with a plot network of this size, values for tree diameter, basal area per hectare, and stand age, slope, and elevation were highly variable. Between 1978 and 1984, there were 3 years in which defoliation was significant. Visual estimates of individual-tree defoliation (to the nearest 10 percent) were used to calculate plot averages. These averages were then used to assign plots an annual rating of light (less than 30 percent), moderate (30 to 59 percent), or heavy (60+ percent) defoliation. In 1980, average defoliation for all plots was 17 percent. In 1981, defoliation increased to 39 percent with nearly half of the plots experiencing moderate or heavy defoliation. Defoliation was reduced to 22 percent in 1982. Twenty-five percent of the plots received at least one heavy defoliation; only 2 percent received two heavy defoliations. Mortality also was distributed unevenly throughout the plot network; many plots lost few trees while several plots lost many trees. Twenty-two percent of all oaks present in 1978 had been killed by 1984. Oaks contributed

more to total mortality than all other hardwood and softwood species. About half of all trees sampled were oaks; total mortality of all trees during the study was 17 percent, with oaks accounting for 63 percent of this figure. Herrick and Gansner (1987) found a direct relationship between cumulative mortality and mean defoliation levels. Plots with less than 10 percent defoliation had mortality rates of 13 percent; as defoliation increased to more than 40 percent, mortality also increased (28 percent). The authors also reported that mortality increases rapidly 2 years following a major defoliation. Campbell and Sloan (1977) observed the same trend.

Gansner (1987) used the central Pennsylvania data to summarize the influence of site productivity on tree mortality following defoliation. They separated about 15,000 trees (7.6 cm and larger in dbh) by site class, and cumulative mortality rates were recorded during 1979 to 1985. Site index was based on the age and height of dominant northern red oaks. Three classes were identified: poor (SI less than 16.8 m), medium (16.8 to 22.8 m), and good (22.9+ m). Mortality was highest on good sites and the lowest on poor sites (Table 7). Gansner proposed two theories to explain his observations: 1) trees on poor sites were physiologically better adapted to endure stresses such as defoliation, consistent with information reported by Stalter and Serrao (1983); and 2) secondary agents such as *Armillaria* and *Agilus bilineatus* are less active on poor sites. In fact, the opposite appears to be true, as the pathogenicity of *Armillaria* increases with reductions in site quality (Kile et al. 1991). Also, Dunbar and Stephens (1975) found that *Agilus bilineatus* played a major role in oak mortality on sites located on dry ridges and upper slopes with thin rocky soils.

Feicht et al. (1993) also used the central Pennsylvania data set in their description of changes in stand condition following 13 years of gypsy moth infestation. In 1986, a 228-plot subset of those originally established in 1978 was selected to facilitate the collection of additional data on the long-term effects of defoliation. The subsample was divided about equally between plots that received at least one severe defoliation episode (more than 60 percent), those that were only moderately defoliated (30 to 60 percent), and those that experienced only low levels of defoliation (less than 30 percent). The study plots were in primarily mixed oak forests

located in the Tuscarora and Bald Eagle State Forests. Information on tree defoliation and vigor was collected annually from 1978 to 1990, and regeneration surveys were conducted in 1989 and 1992, the latter for evaluation of understory response to overstory mortality. Defoliation was recorded on an individual-tree basis for all years except 1985, and was estimated to the nearest 10 percent.

There were two gypsy moth outbreaks during the 13-year study period. In 1981, 34 percent of the plots experienced severe defoliation; 18 percent were severely defoliated in 1986, when 26 plots were sprayed as part of Pennsylvania's annual suppression program. The authors noted that had spraying not occurred, the percentage of plots that were severely defoliated that year would have been higher. Each plot within the subsample was assigned a defoliation class. From 1978 to 1985, 43 percent of the plots were in the low-to moderate-defoliation classes; 57 percent of the plots experienced at least one severe defoliation, two moderate defoliation episodes, or some greater combination (e.g., 1 year heavy and 1 year moderate or 3 years moderate). From 1985 to 1990, 64 percent of the plots were in the low or moderate class. Only 22 percent of all plots were severely defoliated for more than 1 year and 26 percent were subjected only to low defoliation.

Feicht et al. (1993) classified overstory mortality (basal-area loss per acre) as low (less than 15 percent), moderate (15 to 30 percent), or severe (31+ percent). The preferred oaks suffered higher mortality than non-oak species; 65 percent of all trees killed during the study were oaks. Seventy-six percent of the plots experienced low mortality, though 17 percent lost more than 30 percent of their original basal area. On a whole-plot basis, basal area showed a consistent decline as defoliation intensity and duration increased. When tree growth was included, the plots that had received only a single year (or less) of severe defoliation exhibited a short-term increase in basal area prior to a subsequent decline. The overall effect of defoliation on overstory stocking levels was negligible; the number of overstocked and fully stocked stands was reduced slightly while the number of understocked stands increased by approximately 5 percent. The authors concluded that their analysis supported the original conclusions of others (Herrick and Gansner 1988; Gottschalk 1989), that is, overall stocking levels were not significantly affected from 1978 to 1985, but the duration and intensity of the defoliation had a direct effect on tree mortality.

Western Pennsylvania

Fosbroke and Hicks (1989) described gypsy moth defoliation and mortality in southwestern Pennsylvania oak stands from 1985 to 1989; 237 plots (0.04 ha) were established in defoliated and undefoliated stands in Cambria and Somerset Counties. Forest stands consisted of mixed hardwoods; red maple and chestnut oak were the dominant species. Prior to defoliation, 41 percent of the basal area of the undefoliated stands consisted of chestnut, northern red, white, black, and scarlet oak; the defoliated stands contained 63 percent oak. Although there were more oaks in defoliated stands prior to

the gypsy moth outbreak, these stands had a lower mean stand density (27.1 m²/ha) compared to undefoliated stands (32.1 m²/ha). Mean stand defoliation ranged from 9 percent in 1988 to 50 percent in 1986. Oaks sustained the greatest defoliation, averaging 62 percent for the 4-year period. Mortality increased with both the duration of defoliation and increasing oak basal area. Stands with less than 60 percent of their basal area in oaks had losses that were comparable to undefoliated stands; those with more than 60 percent oak showed a distinct increase in mortality. Following 4 years of gypsy moth activity, 24 percent of the trees in defoliated stands had died, while undefoliated stands had lost 11 percent of the original trees. Thirty percent of the original oak basal area was lost, a stem mortality rate of 39 percent. The effect on individual species was greatest among scarlet, black, and chestnut oak. Initially, mortality rates seemed influenced by site condition; stands on poor sites (less than SI 18.3 for northern red and white oak), sites with steep slopes (>15 percent), and southern aspects all had greater mortality than their respective counterparts. However, Fosbroke and Hicks (1989) concluded that their results were due more to site factors influencing stand composition rather than a site/mortality relationship, as stands with the aforementioned characteristics tended to have a large oak component.

Pennsylvania Damage Appraisal Surveys

Beginning in 1981, the Pennsylvania Bureau of Forestry, Division of Forest Pest Management and individual forest districts have conducted a gypsy moth damage appraisal survey every 3 years (Quimby 1991). Areas included in the survey have suffered an outbreak in the preceding 3-year period. Due to fluctuations in the gypsy moth population, the total area affected by defoliation in the 3 years prior to each survey has varied considerably. For example, this area encompassed 1.7 million ha in 1984, about 970,000 ha in 1987 and nearly 2.5 million ha in 1990 (Quimby 1991). However, the portion of the defoliated area actually affected by moderate or heavy tree mortality during each of the three periods has fallen steadily. In 1984, nearly 17 percent of the defoliated area experienced more than 15 percent mortality versus 11 percent in 1987 and only 2 percent in 1990 (Quimby 1991).

Quimby (1987) described both the 1984 damage appraisal survey and results of a 10-year study of 57 permanent plots established in 1970. For the survey, trees were separated by species and size (pulpwood and sawtimber) and stands were classified as having moderate (less than 30 percent) or heavy (30+ percent) mortality. About 280,000 ha of forestland were surveyed. Oak (northern red, black, scarlet, white, and chestnut) was the dominant species group, accounting for about 75 percent of the pulpwood and 90 percent of the sawtimber. Consequently, this group also experienced the greatest losses following defoliation. Among sawtimber-size trees, average oak mortality (volume basis) in stands containing moderate mortality was 34 percent versus 58 percent in stands with heavy mortality. In both cases, scarlet oak had the greatest mortality—46 percent in moderate stands versus 72 percent in heavy stands. Mortality also was

considerable among conifers and hickories. Both accounted for only 1 percent of total species composition, but conifers lost 40 percent in the pulpwood class and hickories lost 40 percent in the sawtimber class. The total value loss of all timber (based on average 1984 stumpage prices) was estimated at \$100 million.

Quimby (1989) described a 1988 damage appraisal of 8,865 ha by the Western Forest Pest Management Area. Forest stands defoliated from 1984 to 1987, were separated into moderate (15 to 30 percent) and heavy (31+ percent) mortality classes. Variable-radius plots were used to tally species, diameter, height, and vigor of both pulpwood and sawtimber trees. In stands with moderate mortality, average pulpwood mortality (volume basis) was about 25 percent; average sawtimber mortality was nearly 30 percent. In stands with heavy mortality, average pulpwood mortality was 24 percent and average sawtimber mortality was 48 percent. As was observed in the 1984 damage appraisal, the oak component experienced the greatest losses. In stands with moderate mortality, more oak pulpwood was lost (34 percent) than oak sawtimber (29 percent). In stands with heavy mortality, proportionate losses were greater for oak sawtimber (47 percent) than for oak pulpwood (37 percent). The total value of dead stumpage throughout the survey area was estimated at \$8.8 million.

Quimby (1991) also described the 1990 damage appraisal survey. He provided a concise summary of relevant data from the previous surveys and examined stands that were defoliated during the 1970's. For the 1990 survey, areas in which tree mortality had been heavy following defoliation by the gypsy moth were identified (42,773 ha). As before, forest stands were divided into moderate (15 to 30 percent) or heavy (31+ percent) mortality classes. He categorized trees, that were alive or that apparently died since the last survey (within 3 years), by species, diameter, number of 16-foot logs (sawtimber), number of 8-foot bolts (pulpwood), and mortality. Of the total volume killed, nearly all of the trees were oaks (northern red, white, chestnut, or scarlet). In stands with moderate mortality, 34 percent of the oak pulpwood and 60 percent of the oak sawtimber were killed. In stands with heavy mortality, 24 percent of the oak pulpwood and 63 percent of the oak sawtimber died. The total value of stumpage killed was an estimated \$28.3 million.

Quimby (1991) also discussed the reassessment of 19 stands in eastern and central Pennsylvania in which plots were established in 1970. Each stand contained one to five plots (0.04 ha). Between 1970 and 1979, these were examined biannually and individual-tree defoliation, tree vigor, and number of egg masses were recorded. In 1990, the stands were remeasured, though some had been destroyed due to logging and other disturbances. Where this occurred, variable-radius plots were established in nearby areas to evaluate stand change. There were gypsy moth epidemics in 1971-73 and 1981-82. Ten stands experienced two or more moderate or heavy defoliation episodes. In the first 10 years of observation, average oak mortality following a single defoliation was 18 percent. Mean oak mortality rose

to 89 percent after two defoliations and reached 98 percent following three defoliations. Over the 20-year period, average oak mortality was slightly lower: a single year of defoliation resulted in 14 percent mortality, 2 years increased the mortality rate to 38 percent, and 3 years resulted in average mortality of 48 percent. Four plots with original oak compositions ranging from 22 to 78 percent suffered a total loss of oak after two or more defoliation episodes. Changes in species composition and shifts in diameter class occurred due to the loss of oak and subsequent replacement by large numbers of smaller trees. However, the overall effect on total stand basal area was negligible regardless of the number of defoliation episodes or the amount of mortality. Quimby pointed out what he considered to be the beneficial aspects of these changes, namely "...that the increased species diversity, particularly the addition of white pine, hemlock, and white ash, has rendered these stands less susceptible to future gypsy moth outbreaks."

Although the total area defoliated prior to each damage appraisal survey was variable, Quimby (1991) noted that the variation in estimated mortality between damage surveys was relatively small. From 1981 to 1990, the average mortality for sawtimber was 37 percent (range: 33 percent in 1987 to 42 percent in 1984). The average mortality for pulpwood was 34 percent (range: 27 percent in 1987 to 39 percent in 1984). The high levels of mortality in 1984 were attributed to a drought in the early 1980's that probably resulted in increased stress prior to defoliation (Quimby 1987, 1991).

Virginia and West Virginia

In 1969, an infestation of gypsy moth was reported in Shenandoah National Park in the Blue Ridge Mountains of Virginia (Ravlin and Fleischer 1989). During the next two decades, populations of the insect increased dramatically. Today, two-thirds of the state is currently considered as generally infested (Davidson et al. 1994). In West Virginia, gypsy moth larvae were first detected in Jefferson County in 1978. However, it was not until 1985 that noticeable defoliation was reported (Atkins and Smallwood 1991; Hicks and Mudrick 1994). Populations have since spread from the Eastern Panhandle into the northwestern and the southeastern portions of the state (Hicks and Mudrick 1994). Although the gypsy moth has been active in West Virginia for two decades and in Virginia for nearly 30 years, there has been little documentation of the insect's impact on these states.

Virginia

A report from the Virginia Department of Forestry describing defoliation and mortality in Virginia (Tigner 1992) described studies in Clarke County and on the Lee Ranger District of the George Washington National Forest (GWNF). Twenty-four stands in Clarke County that had experienced varying degrees of infestation (as many as three) were identified in 1988 using historical data; stand size ranged from 6.5 to 46.2 ha. Each was inventoried using variable-radius plots, and the number of trees and basal area of individual tree species,

both live and dead, were recorded. Defoliation was estimated using a combination of low-altitude aerial surveys and high-altitude aerial photography. In 1990 a similar survey was conducted on the Lee Ranger District of the GWNF in which 34 stands were identified. Unlike previous studies, the stands Tigner described were not observed from pre- through to postdefoliation. Instead, he compared stands with zero, one, two, or three defoliations, so data were not necessarily obtained from the same plots. For both Clarke County and the GWNF, the data for each of the defoliation periods was pooled prior to analysis. The majority of timberland in both areas was classified as the oak-hickory forest type. Defoliation affected mainly the oaks.

In Clarke County, average mortality of oak in undefoliated stands was 20 percent. A single defoliation raised mortality to 23 percent, two defoliations increased the rate to 30 percent, and 50 percent of the original oak basal area was lost following three defoliations. Mortality of other hardwood and softwood species was greater in undefoliated stands than in those receiving one, two, or three defoliation episodes, but remained below 15 percent. Oak mortality on undefoliated stands on the Lee Ranger District of the GWNF averaged 8 percent. Mortality increased to 24 percent following a single defoliation, 32 percent after two episodes, and 37 percent when stands were subjected to three defoliations. As in Clarke County, mortality within the group of other hardwood and softwood species was not significantly influenced by frequency of defoliation and remained below 10 percent. In both areas, the overall effect of the infestations was a reduction in the live stand basal area of oak species. Prior to defoliation, the oaks in both areas had suffered considerable mortality resulting from an extended drought in many counties of northern Virginia.

Shenandoah National Park has been the site of significant gypsy moth activity since the insect's introduction to Virginia. However, literature that documents the progression of the outbreaks and subsequent impacts within the park is unavailable. The information that is available was obtained from the work of Potts and Teetor (1989), Tigner's (1992) report on defoliation in Virginia's hardwood forests, and Kasbohm's (1994) description of the infestation's influence on the black bear population in Shenandoah National Park.

Potts and Teetor (1989) used defoliation information from aerial photographs to facilitate a ground survey using transects and 0.04-ha plots to estimate mortality (stem basis) following both a single defoliation and two defoliation episodes. Baseline mortality, not attributable to the gypsy moth, was established through an independent study. This figure was then subtracted from gross mortality estimated both 1 and 2 years after initial and subsequent defoliations. Following a single defoliation, mortality of red and white oak, black birch, black locust (*Robinia pseudoacacia* L.) and basswood (*Tilia americana* L.) was 7 percent or less; only chestnut oak seemed adversely impacted, with mortality approaching 14 percent.

Potts and Teetor (1989) noted a similar pattern following the second defoliation episode. Oaks were the most severely

affected species; mortality was 35 percent among white oak, 40 percent among red oak, and 42 percent among chestnut oak. The effect on pines was minimal as average mortality in stands defoliated twice and those defoliated only once was 13 percent. The authors pointed out that the effect of gypsy moth defoliation on pine mortality is unclear because of the lack of data on baseline mortality for pine species. They concluded that the impact of defoliation has been limited to the oak component, and that this was exacerbated by a drought that had been affecting the area since 1985.

Tigner (1992) described the results of a monitoring study initiated in 1974 in the western Madison County portion of Shenandoah National Park. Fixed-radius plots (0.04-ha) were used to evaluate mortality among trees 15.2 cm and larger in dbh. Annual estimates of defoliation and tree condition were conducted from 1974 to 1991 with lapses in data collection in 1975 and 1981. Stands were described as unmanaged, mature oak forests consisting primarily of white and northern red oak that ranged in age from 50 to more than 150 years. Stands were located on moderate to poor, upper slope sites (SI 15.2 to 18.3 m). In 1982 and 1984, light defoliation by loopers (Geometriidae) was observed within all the study plots; in 1984, this was concentrated primarily among white oak. Gypsy moth defoliation first occurred in 1987 but this was considered negligible and plots were subjected to only a single, heavy (61 to 100 percent) episode in 1989 followed by 2 years of light (0 to 30 percent) defoliation. These stands also had been exposed to a prolonged drought, and a severe winter storm in 1980 damaged numerous trees. Prior to gypsy moth defoliation, annual mortality ranged from 0 to 4 percent and was concentrated among trees described as being under some form of stress. Defoliation increased mortality among trees in the intermediate and suppressed classes; this trend also was observed prior to defoliation but on a much smaller scale. White oak and other non-oak species had a larger proportion of stems in these classes than red oak and thus incurred greater losses. However, among species groups, mortality of the oak component was much higher than among other species. During the defoliation episodes, 84 percent of the trees studied were moderately or severely defoliated: 77 percent were subjected to a single episode while the remainder experienced two episodes. This group of defoliated trees lost 11 percent of its original total due to defoliation-induced mortality.

Kasbohm (1994) examined the influence of gypsy moth defoliation and associated tree mortality on black bear populations within the Shenandoah National Park. Eighteen sites that had been established in 1987 as part of the Long Term Ecological Monitoring System consisted primarily of chestnut and red oak stand types located in the Park's North and Central Administrative Districts. Defoliation was noticeable in 1985 and continued through 1989, with most sites undergoing a single defoliation episode. However, in the North District, large areas were subjected to two or three defoliations from 1986 to 1989. Sixty percent of the chestnut oak and 45 percent of the red oak stands suffered heavy defoliation (more than 60 percent) during the study period. As the duration of defoliation episodes increased, tree

mortality also increased. Sites with no defoliation lost an average of 2.6 percent of the original number of oak stems. This rate increased to 4.7 percent following a single episode of defoliation and 17.6 percent after two or three episodes. At the extreme, a single site lost 85 percent of its original density from 1987 to 1990. The maples and hickories were the other species groups that lost a substantial number of trees, 11.9 and 8.9 percent, respectively. These losses occurred in areas that suffered two or three defoliation episodes.

West Virginia

Atkins and Smallwood (1991) described defoliation and mortality in West Virginia from 1985 to 1990. The data for their report were from damage appraisals conducted by the West Virginia Division of Forestry. Aerial defoliation estimates were used to separate areas into three defoliation classes: light (0 to 29 percent), moderate (30 to 59 percent) and heavy (60+ percent). A ground inspection of individual trees was conducted in areas that suffered moderate or heavy defoliation. These inspections, carried out at the end of the second growing season following initial defoliation, included the use of variable-radius plots. They classified trees by species, size class, vulnerability to mortality, and actual mortality. Oak species accounted for 65 to 88 percent of total stocking in the 1,841 ha evaluated. Following a single defoliation, actual stand mortality averaged 16 percent of the original basal area. Mortality increased with duration of a defoliation episode, and the oak component had the greatest losses. Mortality increased to 23 percent following two defoliations and to 26 percent after three episodes. Atkins and Smallwood (1991) estimated that moderate to heavy defoliation of 32,978 ha resulted in the loss of 594,657 m³ of timber worth nearly \$17 million.

Michigan

In Michigan, the gypsy moth was first reported in 1954 in Lansing (McManus and McIntyre 1981). However, it was not until 1982 that significant defoliation was observed (Hart 1990). Since that time, yearly defoliation levels have increased steadily reaching a high of 288,425 ha in 1992 (USDA For. Serv. 1995).

There are few published studies of defoliation-induced mortality in Michigan's forests. Hart (1990) described a study initiated in 1986 to evaluate the influence of defoliation on quaking aspen (*Populus tremuloides* Michx.) and bigtooth aspen (*P. grandidentata* Michx.). Located in Midland County, the study area consisted of six stands of mixed northern hardwoods. All six areas were defoliated from 1985 to 1989; defoliation was most severe in 1986. Three stands were aerially sprayed with *Bacillus thuringiensis* in 1986, 1987, and 1988. Hart noted that these areas were defoliated to a lesser degree than the other areas. Twenty-five variable-radius plots were used to evaluate damage to both aspen species, which accounted for 5 percent of the inventory. Diameter, height, tree condition, and visual estimates of percent defoliation were recorded for 113 quaking aspen and 75 bigtooth aspen trees. Of the trees defoliated in 1986,

cumulative stem mortality of quaking aspen was 14 percent, while bigtooth aspen lost 4 percent of its original density. Fifteen of the 16 quaking aspen trees that died were totally defoliated; the other was stripped of more than 80 percent of its foliage. Mortality was not distinguishable by crown class; subdominants, codominants and dominants were killed at nearly equal rates. Of the three bigtooth aspen trees killed, only one was in good condition prior to defoliation; it was subsequently defoliated completely. Hart (1990) also discussed the role of secondary organisms in mortality following defoliation. Species of *Armillaria* were observed on 89 percent of the dead trees; 53 percent also showed signs of attack by wood-boring insects (*Agrilus* and *Saperda* spp.).

Summary

The following results were consistent among the studies evaluated in this literature review:

- Certain tree species are defoliated at higher rates than other species, and frequently suffer greater mortality than less susceptible species.
- As the intensity (amount of foliage removed) and duration (number of consecutive episodes) of defoliation increases, the amount of tree mortality increases.
- Trees in the lower canopy (those in the suppressed and intermediate crown classes) have a greater probability of being defoliated and dying than trees in the upper canopy (dominants and codominants).
- Tree mortality tends to increase rapidly during the second year after defoliation.

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The literature on tree mortality following outbreaks of European gypsy moth was reviewed. The trends in defoliation and mortality and the influence of defoliation on mortality of individual trees and forest stands have been summarized via a regional perspective. The literature showed that: certain tree species are defoliated at higher rates than other species, and frequently suffer greater mortality than less susceptible species; as the intensity (amount of foliage removed) and duration (number of consecutive episodes) of defoliation increases, the amount of tree mortality increases; trees in the lower canopy (those in the suppressed and intermediate crown classes) have a greater probability of being defoliated and dying than trees in the upper canopy (dominants and codominants); and tree mortality tends to increase rapidly during the second year after defoliation.

Keywords: defoliation, tree mortality, oaks, eastern hardwoods, *Quercus*





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