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CHAPTER 1

INTRODUCTION

Insect herbivory is endemic within forested ecosystems throughout the world. For the most part, extensive defoliation is not common and the growth and vigor of the majority of forest trees is rarely compromised. The introduction of exotic species significantly influences stand dynamics, as these new invaders often are not subjected to the controls that are present in their native habitats. As a result, outbreak populations may occur more frequently and their effect on individual trees and whole stands can be devastating.

One of North America's most well known introduced defoliators, and arguably the most important in the United States, is the European gypsy moth *(Lymantria dispar* L.) (Lepidoptera: Lymantriidae). The gypsy moth was inadvertently introduced into the United States between 1868 and 1869. Despite numerous attempts to halt its spread, the gypsy moth has expanded it's range to include most of the northeastern United States, south to Virginia and west to Michigan and Ohio (McManus and McIntyre, 1981). Spot infestations have also been found in Arkansas, North Carolina, Tennessee, Washington and Oregon, and what is termed the "generally infested area" continues to expand into the southeastern United States (USDA, 1995).

The gypsy moth is a voracious defoliator and feeds on a wide range of forest and ornamental trees and shrubs. Studies in the early 19th century listed over 400 different species as possible hosts (Mosher, 1915). As the potential threat to the forest resource from extensive defoliation became apparent, scientists attempted to quantify the relationships between defoliation, and subsequent tree growth and mortality. The majority of this work concentrated on northeastern hardwood stands. However, population expansion continued to bring the insect into contact with stand types that had never been subjected to a gypsy moth outbreak. This prompted renewed interest in host susceptibility studies, and laboratory feeding trials were conducted with previously untested southern tree species (Barbosa et al., 1983; Berisford et al., 1993). These studies have shown sweetgum (*Liquidambar styraciflua* L.) to be extremely susceptible to defoliation (Barbosa et al., 1983). Loblolly pine (*Pinus taeda* L.) cannot support first instar larvae; however, the development, survival and fecundity of later instar larvae on pine foliage is excellent (Barbosa et al., 1983; Rossiter, 1987; Berisford et al., 1993). Therefore, stands containing mixtures of loblolly pine, oaks (*Quercus* spp.) and sweetgum may prove as susceptible to defoliation outbreaks as pure hardwood stands. The effect of defoliation on the growth of individual species within these mixtures, and their vulnerability to mortality remains to be proven.

Mixed pine-hardwoods account for 9 percent of the total timberland in the southeastern United States (Sheffield et al., 1989). In the absence of management, these stands are an intermediate seral stage in the overall progress of secondary succession from pioneer pine stands to a hardwood climax. Shade-tolerant hardwoods invade pure stands of pine and become integral components of the stand (Cooper, 1989). As the pines age and are lost to lightning, fire, or insect attacks, these stands eventually progress to a pure hardwood climax (Walker, 1994). In recent years increasing public pressure to manage "biologically diverse" stands, coupled with the expense of maintaining pure pine plantations, has resulted in expanded interest in the management of mixtures of pines and hardwood. However, in order to effectively manage mixed stands we must gain a thorough understanding of how they function. This includes studying species interactions, competition for resources and responses to disturbance. The need for this type of information is readily identifiable. The introduction of an exotic pest with the destructive potential of the European gypsy moth into a vast area of potentially susceptible cover types only increases the urgency with which it must be obtained.

LIFE HISTORY OF *LYMANTRIA DISPAR* L.

The European gypsy moth belongs to the family Lymantriidae of the order Lepidoptera, and like other members of the Lepidoptera, damage to trees occurs during the larval stage (Little, 1972). The Lymantriidae are known as tussock moths because of the prominent hairs that are present during the larval stage (Leonard, 1981). As with other Lepidoptera, the gypsy moth undergoes complete metamorphosis, and only one generation of the gypsy moth occurs annually (Little, 1972).

Eggs are laid by the female in late summer in bark crevices, the underside of branches, and in other sheltered locations. However, when populations are large and competition is high, eggs may be laid on any available substrate. Diapause occurs in the egg stage with the larvae overwintering in the protective egg mass. Egg hatch occurs in early spring, usually from late April to mid-May (McManus et al., 1989), is dependent upon temperature, and has been found to frequently coincide with bud-break of local hardwoods (Leonard, 1981; McManus et al., 1989). Male larvae pass through five instars before pupation, while females pass through six instars (Leonard, 1981).

Upon hatching, larvae instinctively climb to the top of the trees or other objects upon which the egg mass was laid, spinning silk threads as they move. When they can go no further they drop from the threads and are dispersed by the wind (Leonard, 1981; McManus et al., 1989). This dispersal behavior only occurs in favorable conditions; if temperatures are below 7 ° C, or it is raining, larvae will remain on or near the egg mass (Leonard, 1981). During the first three instars larvae feed and rest in the tree crowns (McManus et al., 1989). From the fourth instar onward, larvae move up and down the tree according to light intensity and population density (McManus et al., 1989). If populations are low, larvae feed in the crown during the night and move down the tree to bark crevices and other sheltered locations on the ground during the day. When population levels are high, intraspecific competition for food increases and larvae will feed continuously, day and night. Pupation occurs in late June to early July and lasts for approximately 7 to 14 days (Leonard, 1981; McManus et al., 1989). Male moths are generally the first to emerge from pupation. Once their wings have hardened they begin flying in search of a mate. Females are flightless and generally remain close to the site of their pupation (Leonard, 1981). A potent pheromone is emitted by the female, and it has the ability to attract males from considerable distances. Females are generally monogamous while males are polygamous (Leonard, 1981). After mating, the female lays her eggs in a mass which are covered with brown hairs shed from her abdomen. Both male and female moths live for approximately seven days.

STUDY OBJECTIVES

1) To determine the susceptibility to gypsy moth defoliation of loblolly pines and selected hardwoods growing in pure and mixed stands on the Atlantic Coastal Plain of Virginia and Maryland.

2) To determine the effect of gypsy moth defoliation on mortality of loblolly pines and selected hardwoods growing in pine and mixed stands on the Atlantic Coastal Plain of Virginia and Maryland.

DESIGN OF THE STUDY

Criteria Used in Plot Selection

This study was initiated in the fall of 1991. Between 1992 and 1993 research plots were established in forty-seven mixed pine-hardwood stands throughout the Atlantic Coastal Plain physiographic provinces of Virginia and Maryland (Figure 1.1). Stands were selected that contained mixtures of loblolly pines and oaks, or mixtures of loblolly pines and sweetgum.

A study stand was defined as a unique combination of species, age class, density and site quality. Study stands were selected based on a number of criteria, the most important being stand composition. A wide range of stand compositions was desired in both stand types, from pure hardwood to pure pine. Therefore, during plot establishment, stands were selected that fell within the following ranges:

<u>a) Loblolly pine/oak</u>	**<u>b) Loblolly pine/sweetgum</u>**
>80% pine - <20% oak	>80% pine - <20% sweetgum
60-80% pine - 20-40% oak	60-80% pine -20-40% sweetgum
40-60% pine - 40-60% oak	40-60% pine - 40-60% sweetgum
20-40% pine - 60-80% oak	20-40% pine - 60-80% sweetgum
<20% pine - >80% oak	<20% pine - >80% sweetgum

Additional selection criteria included the following:

- each stand had a well-developed crown structure,
- stands represented medium-quality forest sites, based on pine site index,
- prior defoliation by the gypsy moth was minimal, or no defoliation had occurred,
- stands were on the "leading edge" of the gypsy moth infestation.

Plot Design and Vegetation Measurements

Within each of the forty-seven stands, three sample plots were established at a minimum separating distance of 50 meters. Thus, there were a total of one hundred and forty-one plots within the entire study. Each plot was circular in shape and encompassed 400 m^2 (0.04 ha). On each plot the following variables were measured at time of establishment and annually thereafter, for all woody stems greater than or equal to 5 cm dbh: species, total height, diameter, crown class, crown condition and percent defoliation. Initial stand data was collected as plots were

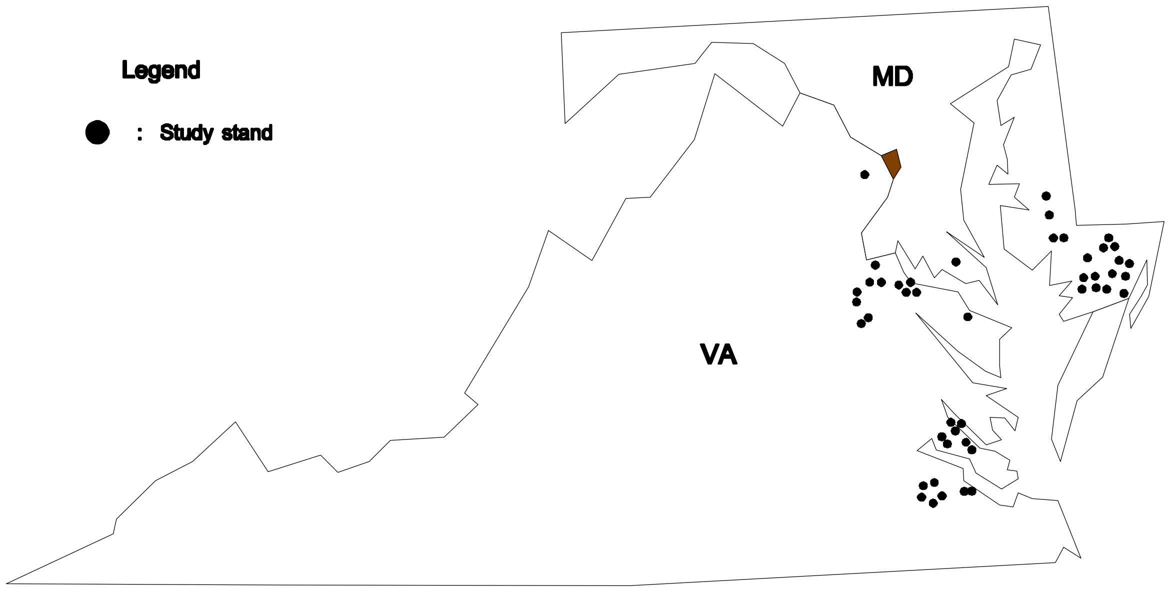

Figure 1.1. Map of Virginia and Maryland showing the location of study stands within the Atlantic Coastal Plain physiographic province.

established in 1991, 1992 and 1993. Annual measurements were taken during the summer months through 1996.

In the fall of each year, subsequent to leaf abscission, an intensive visual survey was used to determine the size of the gypsy moth population based on the number of egg masses within the stand. Three 0.01 ha temporary plots were established within the 0.04 ha overstory plot and the method described by Liebhold et al., (1994) was used to estimate the number of living egg masses per hectare. The center of each 0.04 ha plot was used as plot center for the 0.01 ha egg mass plot.

Percent defoliation was measured using a visual estimate of individual tree defoliation. At the time of peak defoliation within each stand, each tree was independently assessed and placed into one of the following five defoliation classes: none=0-10%, light=11-30%, moderate=31-60%, heavy=61-90%, and complete=91-100%. To account for differences in tree and crown size, a weighted estimate of average defoliation based on tree diameter was used for stands, individual species and host preference classes (Herrick and Gansner, 1986).

SUMMARY

The remaining chapters of this dissertation contain the following information. Chapter 2 contains a thorough review of the literature. It is intended to bring together the available information regarding the effects of defoliation on individual trees and forest stands, and to furnish information on past regional trends in defoliation and mortality. Chapter 3 addresses some commonly asked questions concerning tree mortality subsequent to gypsy moth defoliation. First, is there an association between initial stand composition and subsequent tree mortality? Second, how does site quality influence tree mortality? And finally, do mortality rates in areas experiencing initial outbreaks differ from those undergoing subsequent outbreaks? Chapter 4 describes the susceptibility of mixed pine-hardwood stands of the Atlantic Coastal Plain to gypsy moth defoliation, while Chapter 5 examines the effects of defoliation on tree mortality within these stands. Chapter 6 provides a summary of the dissertation and includes tables and figures that should be useful to forest managers who are attempting to make decisions concerning forest management activities as the gypsy moth moves into the southeastern United States.

LITERATURE CITED

Barbosa, P.; M. Waldvogel; P. Martinat; L.W. Douglas. 1983. Developmental and reproductive performance of the gypsy moth, Lymantria dispar (L.) (Lepidoptera: Lymantriidae), on selected hosts common to mid-Atlantic and southern forests. Environ. Entom. 12: 1858-1862.

Berisford, C.W.; T.J. Lanigan; M.J. Dalusky; M.E. Montgomery. 1993. Effects of southern tree hosts and climate on gypsy moth survival and development. P.23 *in* Proc. U.S. Department of Agriculture Interagency Gypsy Moth Research Forum 1993. Fosbroke, S.L.C., K.W. Gottschalk (eds.). USDA For. Serv. Gen. Tech. Rep. NE-179.

Cooper, A.W. 1989. Ecology of the pine-hardwood type. P.3-8 *in* Proc. of pine-hardwood mixtures: a symposium on management and ecology of the type. Waldrop, T.A. (ed.). USDA For. Serv. Gen. Tech. Rep. SE-58.

Herrick, O.W. and D.A. Gansner. 1986. Rating forest stands for gypsy moth defoliation. USDA For. Serv. Res. Paper NE-583. 4 p.

Leonard, D.E. 1981. Bioecology of the gypsy moth. P. 9-29 *in* The gypsy moth: Research toward integrated pest management, Doane, C.C., and M.L. McManus (eds.). USDA For. Serv. Tech. Bull. 1584.

Liebhold, A.; K. Thorpe; J. Ghent; D.B. Lyons. 1994. Egg mass sampling for decision-making: a user's guide. USDA For. Serv. Forest Health Protection. NA-TP-04-94. p.8-9

Little, V.A. 1972. General and Applied Entomology, 3rd Edition. Harper & Row, Publishers, Inc. New York, London. 527 p.

McManus, M. L. and T. McIntyre. 1981. P. 1-7 *in* The gypsy moth: Research toward integrated pest management, Doane, C.C., and M.L. McManus (eds.). USDA For. Serv. Tech. Bull. 1584.

McManus, M.; N. Schneeberger; R. Reardon; G. Mason. 1989. Gypsy moth. USDA For. Serv. For. Insect. Dis. Leaflet. 162. 13 p.

Mosher, F.H. 1915. Food plants of the gypsy moth in America. Agric. Inf. Bull. 250. 39 p.

Rossiter, M. 1987. Use of a secondary host by non-outbreak populations of the gypsy moth. Ecology 68(4):857-868.

Sheffield, R.M.; T.W. Birch; E.C. Leatherberry; W.H. McWilliams. 1989. The pine-hardwood resource in the eastern United States. P.9-19 *in* Proc. of pine-hardwood mixtures: a symposium on management and ecology of the type. Waldrop, T.A. (ed.). USDA For. Serv. Gen. Tech. Rep. SE-58.

United States Department of Agriculture. 1995. Forest insect and disease conditions in the United States, 1994. USDA For. Serv. For. Pest Man. Washington, D.C. 74 p.

Walker, L.C. 1994. The southern pine region. P. 271-333 *in* Regional silviculture of the United States, 3rd edition, Barrett, J.W. (ed.). John Wiley & Sons, Inc. New York.

CHAPTER 2

Defoliation and mortality associated with outbreaks of the European gypsy moth (*Lymantria dispar* L.): A regional review of the literature

INTRODUCTION

Following its introduction to Massachusetts in 1869, populations of the European gypsy moth (*Lymantria dispar* L.) have expanded considerably and currently cover an area from Maine to Virginia and west to Ohio. The recently observed reductions in 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, 1995). For the forest manager concerns regarding defoliation outbreaks are due to observed reductions in tree growth, reductions in flowering and fruiting and possible tree mortality. Within the urban/forest interface, in addition to the effects on trees the problems associated with gypsy moth outbreaks can be expanded to both aesthetic and nuisance concerns associated with large numbers of wandering larvae, and possible health risks associated with their urticating hairs (Montgomery and Wallner, 1988).

The amount of defoliation that occurs and its affect on tree physiology is dependent upon a number of interrelated factors. The primary determinant is tree species, as this directly influences the probability of individual tree defoliation. Certain species are more susceptible to defoliation and are frequently defoliated at much higher rates than tree that are resistant or immune to defoliation (Liebhold et al., 1995). Species also exhibit varying vulnerabilities following defoliation. Susceptible oaks (*Quercus* spp.) are frequently able to survive repeated defoliation, while eastern hemlock (*Tsuga canadensis* L. Carr), a resistant species, will die after a single defoliation (Campbell and Sloan, 1977; Twery, 1991). Abiotic stresses such as drought, fire or ice damage, also increase the vulnerability of trees. However, tree mortality following defoliation is most often due to secondary-action organisms rather than as a direct result of the loss of foliage. *Armillaria* spp., a root rot fungus, and *Agrilus bilineatus*, the two-lined chestnut borer are the two organisms most commonly blamed for tree mortality in eastern forests (Wargo, 1977; Dunbar and Stephens, 1975; Dunn et al., 1986).

The literature characterizing the effects of defoliation and mortality in the United States is quite extensive. Much has been written concerning the bioecology of the insect, methods of control, and the effects of defoliation on individual trees and forest stands. Yet there is no single source that brings this information together in a readable format. The purpose of this review is to provide such a source and to furnish information on past regional trends in defoliation and mortality. The papers reviewed in the following sections represent those that are considered to be the most relevant to our discussion. Each section is presented in chronological order and relates to a specific geographic region of the eastern and north-central United States. Where appropriate, multiple discussions of a single collection of data have been combined.

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. Consequently, one of the first truly intensive studies to determine the extent of damage attributable to the gypsy moth was conducted by the Gypsy Moth Laboratory of the former Bureau of Entomology and Plant Quarantine at Melrose Highlands, Massachusetts. Between 1911 and 1931 extensive records of defoliation and tree condition were collected (Campbell and Sloan, 1977). In 1911 and 1912 two hundred and sixty-four 0.07 hectare circular plots were established from Cape Cod, MA, to Kennebunk, ME, in mixed oak forest stands (Campbell and Valentine, 1972; Campbell and Sloan, 1977). Within each plot, the species and dominance class for all trees 7.6 cm and greater in diameter were recorded. Individual tree defoliation (the ocular estimate of two observers), tree condition, and egg mass density were collected annually, while tree diameters were recorded in 1912 and 1921. Of the original 264 plots, 75 were removed from the study by 1913; however, 122 plots were maintained through 1921, and 55 were maintained until 1931. Neither the procedures that were used to estimate defoliation, nor the criteria used to determine tree condition have been located. Therefore reference is often made to "ocular estimates" of defoliation, and of trees in "good, fair, or poor" condition, with no way of determining exactly what is meant (Campbell and Valentine, 1972). Nonetheless, these records have served as a source of information for a number of important studies. Also, while individual authors cite

Melrose Highlands as the origin of their data, slight variations in content (such as numbers of trees and plots) are apparent.

The earliest available reference to this data set was by Minott and Guild in 1925. Their work was based on records of 14,610 trees comprising 37 species. Trees were assigned to 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 per year and unfavored species averaged 1.9 percent per year. 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 at the end of the ten year period 47 percent of these trees were dead. Minott and Guild were unable, however, to separate mortality caused by the gypsy moth from that caused by what they termed " ... *crowding and suppression*". In addition, information on egg mass levels were not published, thus it is impossible to ascertain whether population levels were consistent across all study sites.

Baker (1941) gave an in-depth description of defoliation and mortality using the Melrose Highlands data. His analysis described plots containing 13,357 trees in 38 tree species, figures that differ slightly from the work of Minott and Guild (1925). Reference was also made to an additional research plot established in 1915 in a stand of young eastern white pine (*Pinus strobus* L.) and sprout hardwoods that had experienced a single heavy defoliation in that year. Information was collected for 310 pines, including height, percent defoliation and the percentage of old and new foliage consumed; trees were examined annually until 1924 and percent mortality recorded. As is often the case, Baker noted the difficulty in distinguishing "normal" mortality from that attributable to the gypsy moth. However, he asserted that the observed mortality of dominant trees during this time period was definitely abnormal, and "... *would not have occurred on such a wide scale in the absence of the gypsy moth*" (Baker, 1941). Results of his study show that favored species experienced an average of 37 percent defoliation, while unfavored species averaged only 10 percent defoliation. While there was a general pattern of increasing defoliation resulting in increased mortality, the majority of the heavy mortality occurred in stands that experienced in the range of 21 to 80 percent defoliation. Favored species experienced a 30 percent rate of mortality, compared to a rate of 13 percent among unfavored species. Among favored species, 33 percent of dominants were killed, while only 7 percent of dominant trees of the unfavored species died. This indicated that the majority of the mortality among unfavored species occurred in the smaller size classes. An outbreak of *Agrilus bilineatus* from 1912 to 1915, coupled with heavy defoliation, drought, and infection by *Armillaria* spp., probably increased the vulnerability of trees to mortality (Baker, 1941). In the mixed eastern white pine-hardwood plot that experienced a single defoliation episode, the pines exhibited a definite trend toward increasing levels of mortality with increasing defoliation; mortality was greatest in the range of heaviest defoliation, 81 to 100 percent.

During the 1970's interest in the Melrose Highlands data was rekindled and several authors re-analyzed it during this period. In 1972 Campbell and Valentine produced a series of projection tables outlining annual and cumulative mortality rates and the condition of surviving trees, for various species and species groups, based on defoliation history. Though their primary goal was the prediction of tree condition subsequent to defoliation, mortality rates for individual species were also discussed. After twelve years and at least two defoliations, average mortality of individual species was as follows, 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 rates than those classified to be in poor condition. The authors stated that defoliation appeared to accelerate the decline of pioneer gray birch stands, giving weight to the cohort senescence theory. They also noted an increase in the eastern white pine component in mixed stands of oak-eastern white pine and gray birch-eastern white pine. These trends were not documented, but were based on the authors' observations during their analysis of the data.

Campbell and Sloan's monograph (1977) is often considered the definitive description of stand responses to the gypsy moth. Utilizing 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, thus the authors utilized the 122 plots that were observed during this time period for their analysis of changes in stand composition. 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 five years, and rates were calculated at the end of an additional five year period. This was then compared to the five-year mortality rates for mixed oaks that had been subjected to a single severe defoliation, and those subjected to two consecutive heavy defoliations (Table 2.1). 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, and within the respective tree condition classes, dominant trees had a lower rate of mortality than intermediate/suppressed trees (Table 2.1). Campbell and Sloan 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. The results were even more pronounced among trees that were originally classified as being in poor condition; 69 percent of the resistant species were killed compared to 36 percent of the mixed oaks. In terms of the impact on the forest as a whole, 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 of the total basal area. These figures also take into account losses due to cutting during this time period. When this is taken on a tree basis, approximately 42 percent of oak stems were killed, and in total more than 29 percent of all trees present in 1911 were dead by 1921. In their report, Campbell and Sloan made a number of important points. The gypsy moth outbreak resulted in massive mortality of oak trees and 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 that contained 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 basal

Table 2.1: The effect of crown condition, crown class and frequency of defoliation episodes on five year stem mortality rates in a composite mixed stand of oaks (*Quercus rubra*, *Q. velutina*, *Q. coccinea*, *Q. alba*); mortality rates for crown condition were calculated following a single heavy defoliation, while those for defoliation frequency were calculated following a single severe defoliation and two consecutive heavy defoliations. From Campbell and Sloan (1977).

Crown Condition	**Crown Class**		**Tree Mortality**		
	Dominant	**Inter/Suppr.**	**Baseline**[a]	**One Defoliation**	**Two Defoliations**
	%				
Good	3	12	1	7	22
Fair	--	--	3	19	50
Poor	22	41	9	36	55

[a] Trees used for the baseline mortality estimate had not been severely defoliated for at least five years and rates were calculated at the end of an additional five year period.

area loss. The composite stand that contained less than 33 percent oak lost 21 percent of its original basal area, and in stands that contained both no oaks and less than 20 percent susceptible species 11 percent of the original basal area was lost. Tree condition and crown position also influenced the probability of mortality subsequent to defoliation. When trees were visually rated to be in "good" condition prior to defoliation their likelihood of surviving was much greater than trees rated in "poor" condition. Dominant trees weathered a defoliation episode better than intermediate/suppressed trees, so much so that the authors likened the results of defoliation to the " *... equivalent of a thinning from below*". The frequency of defoliation also increased mortality; two successive defoliations killed more trees than a single episode. Differential 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 were also 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. In concluding their discussion, Campbell and Sloan pointed out that defoliation was inclined to be greater during the initial stage of the outbreak, and the changes that they observed were similar to " *.... those that might be expected from natural selection*".

In 1979 Campbell used the Melrose Highlands data to emphasize the interrelationships that occur between the insect, trees, and biophysical factors. The data were sorted into trees that had experienced light defoliation (less than 75 percent) and heavy defoliation (75 percent or higher), and a baseline rate of "normal" mortality for a composite mixed stand of oaks (northern red, scarlet, black, and white oak) was given. The effect of crown condition, crown class, and species composition on cumulative percent mortality during a five year period following a single, heavy defoliation is given in Table 2.2. Campbell's results indicate that a single heavy defoliation within a predominantly oak stand killed mainly the less vigorous intermediate and suppressed trees, many of which would not have survived anyway. Two heavy defoliations however, 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 five years. When defoliation of resistant species occurred, it often had a far greater effect than the defoliation of susceptible species, especially if the trees were in poor condition. An unexpected result was the apparent greater resistance to mortality exhibited by eastern white pine compared to red maple. Following a single heavy defoliation, mortality of red maple was considerably higher than mortality of eastern white pine. The author attributes 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 approximately one-third less of the susceptible species than were present prior to the outbreak; this in turn probably rendered them less susceptible to future outbreaks (Campbell, 1979).

Other Studies

In 1932, Cape Cod, MA, experienced an extremely intense defoliation episode (Hall, 1935). In the same year, in cooperation with the Melrose Highlands Gypsy Moth Laboratory and the Harvard Forest, Hall (1935) conducted a study to determine the relative resistance of Cape Cod pitch pine (*P. rigida* Mill.) to gypsy moth defoliation. He determined that pitch pine was

Table 2.2: The effect of crown condition on five year stem mortality rates of dominant trees, intermediate/suppressed trees, mixed oaks and resistant species following a single heavy defoliation in a composite mixed stand of oaks (*Quercus rubra*, *Q. velutina*, *Q. coccinea*, *Q. alba*). From Campbell and Sloan (1979).

Crown Condition	**Tree Mortality**			
	Dominant	**Intermediate/ Suppressed**	**Mixed Oaks**	**Resistant Species**
	------------------ % ------------------			
Good	3	12	7	12
Poor	22	41	35	70

defoliated only after all other more palatable species had been consumed. In addition, the majority of foliage that was eaten consisted of second or third year needles; only in exceptional cases were new needles consumed. In contrast, the gypsy moth fed upon both the new and old needles of eastern white pine, red pine *(P. resinosa* Ait.) and spruce (*Picea* spp.), apparently resulting in increased mortality. Hall also described two red pine plantations, one which had been sprayed and suffered no damage; the other was completely defoliated and experienced almost 100 percent mortality. Based on this information, he determined that pitch pine on Cape Cod was relatively resistant to the gypsy moth and should be considered in future management prescriptions for the area. This study is one of the earliest descriptions of conifer defoliation by the gypsy moth; it also provides some insight into apparent differences in susceptibility among conifer species.

In 1952, an appraisal of the gypsy moth problem was conducted by the Plant Pest Control Branch of the Bureau of Entomology and Plant Quarantine (Perry, 1955). It included a section focusing on stumpage losses due to mortality, and growth loss due to defoliation that encompassed the years 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. Eastern white pine and eastern hemlock also suffered mortality, but on a lesser scale. Perry's appraisal also discussed the unpublished work of J.N. Summers in eastern New England, and G. C. Tierney in the Connecticut River Valley area of Massachusetts in 1947. Summers et al. studied more than 186 gypsy moth infested forest areas from 1912 to 1921 and observed mortality rates of approximately 33 percent. Tierney estimated mortality losses for the period 1935 to 1946, based on 33 areas totaling 1,046 hectares. During this ten-year period each area experienced an average of two years of 75 to 100 percent defoliation. Average mortality for the total area was approximately 37 percent. The 1952 study also incorporated a field evaluation during which 84 forested areas were examined for mortality losses. These areas had a history of heavy defoliation and were considered to be representative of areas described as 75 to 100 percent defoliated in published annual reports. Many areas experienced 75 to 100 percent defoliation for two years with an average annual mortality rate ranging from 12 to 18 percent; total mortality averaged approximately 24 percent on a volume basis. Based on Tierney's work and on the 1952 field inspection, the author derived an " ... *expectable mortality loss* ..." of 18 percent for every 0.4 hectare area reported as 75 to 100 percent defoliated in the last 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 hectares amounted to 5,100,049 m^3 of pulpwood and 608,667 m^3 of merchantable sawtimber with an estimated value of $4,223,556 (Table 2.3). Using the implicit price deflators for gross national product, this is equivalent to a value of approximately $20,419,030 in 1990 dollars (United States, President, 1990).

Turner (1963) evaluated the work of House (1960), in a short summary of gypsy moth defoliation effects in New England. The study conducted by House concentrated on the effects of defoliation on eastern white pine and is the most detailed of the four described by Turner. Two sets of plots were established in 1953 and 1954 in areas of severe defoliation of eastern white pine and eastern hemlock; these included both plots that experienced defoliation and undefoliated check plots. The plots established in 1953 were located in Connecticut and Maine; those

Table 2.3. Estimated mortality losses from gypsy moth to merchantable timber in the New England States from 1932 to 1952. From Perry, 1955.

State	Area Defoliated, 75 and 100 percent	Tree Mortality			Estimated Value of Stumpage Killed		
		Total	Pulpwood	Sawtimber	Pulpwood	Sawtimber	Total
	ha	%	m^3		$		
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

[a] The 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.

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. Eastern white pine and eastern hemlock were the major species within the stands; northern red and white oak, other northern hardwoods, spruce, and fir (*Abies* spp.) were minor components (Table 2.4). Defoliated plots on both areas were subjected to a single, severe, (90-100 percent) defoliation followed by five years without significant defoliation. At the end of the five year period, cumulative stem mortality of eastern white pines on the 1953 plots was 8 percent, and 17 percent on the 1954 plots. Trees that were completely stripped or had 90 percent of their foliage removed exhibited the highest mortality rates (Table 2.4). Approximately 67 percent of all eastern white pine mortality occurred in the two years following defoliation. Only 11 percent of the total killed were dominant and codominant trees, 42 percent were in the suppressed crown class and 16 percent were intermediates. Based on this information the author 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*"; in other words the trees succumbed to competition-induced mortality. While significant mortality was described, recovery of defoliated eastern white pines was also observed. Five years after the defoliation episode, 31 percent of stems that were completely defoliated had normal crowns and another 47 percent had reached a level described as approximately 80 percent of full crown. Essentially, the plots established in 1954 were pure eastern white pine stands, yet they suffered extensive defoliation and significant mortality. Since the data available to us does not indicate the presence of "susceptible" species

Table 2.4: Five year mortality rates observed in defoliated and undefoliated stands in New England; trees were defoliated either 100 or 90 percent. From House (Turner, 1963)

	Stand Composition (%)			**Stem Mortality (%)**	
	Eastern White Pine	**Eastern Hemlock**	**Red/White Oaks**	**Eastern White Pine**	**Eastern Hemlock**
	---------- % ----------				
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

within the defoliated stands, we must assume that larvae became established in adjacent forested areas prior to moving onto the more resistant eastern 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 eastern white pine, pitch pine, scarlet oak, white oak 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 two years of heavy defoliation (60 to 100 percent) during 1971 and 1972, followed by a single year of medium defoliation (20 to 60 percent) in 1973, and one year of low defoliation (0 to 20 percent) in 1974. Defoliation during 1975 was negligible. Oaks were subjected to higher levels of defoliation in the mixed oak stand (greater than 60 percent) than in either oak-pine or mixed hardwood stands, and 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 three 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 was also apparent; ninety percent of all dead stems and 63 percent of the total basal area loss was in the suppressed and intermediate crown classes. In their concluding remarks, Brown et al. stated 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 were also subjected to intensive defoliation in 1981 and 1982. Brown et al. (1988) described the mortality of eastern white pine that occurred in mixed stands during the outbreak. Infested and control stands of three types were studied, oak-pine, pine-oak and pine; conditions on all sites were described as similar with site index below 60 for oaks. Eastern white pine occurred only as an understory component in oak-pine stands, in the overstory in pine-oak stands, and as the dominant species in pure pine stands. 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, RI, and the Pachaug State Forest in Voluntown, CT. Defoliation of suppressed and intermediate eastern white pines was severe (75-100 percent) in 1981; 85 percent of all understory eastern white pines in the oak-pine type were defoliated, 94 percent in the pine-oak type, and 41 percent in the pure pine type. Dominant and codominant eastern white pines experienced only light defoliation. Brown et al. suggested that the small stand size and close proximity to susceptible stands contributed to defoliation in what would normally be considered a resistant stand type. Following defoliation, the majority of eastern white pine mortality in all stand types consisted of 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. Eastern white pines in the overstory were essentially unaffected and basal area losses were negligible (0 percent in the mixed stands, 3.2 percent in the pine stand). On a total stand basis oak-pine stands were hit the hardest, losing 33.7 percent of the original eastern 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. Based on these results the authors suggested that silvicultural practices to encourage movement of eastern white pines from understory to canopy positions would result in reduced mortality. Though defoliation of oaks was severe in the mixed stands, the mortality observed was comparable to that in the control stands. As these areas were previously infested during a severe outbreak in 1970-74 (Brown et al., 1988), it is possible that many of the vulnerable oaks were killed prior to the 1981-82 infestation, thereby explaining the observed low mortality.

In 1981 extensive areas of eastern hemlock and eastern white pine were defoliated following a large outbreak in western Connecticut. The subsequent mortality of these two species was described in three papers by Stephens (1984, 1987, 1988). Four stands were examined, an oak-pine stand in which the eastern white pine understory had been released by removing half of the oak overstory; a hardwood-hemlock stand in which eastern hemlock was present in both the overstory and understory; and two hardwood-pine stands in which eastern 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 onto the eastern white pine and eastern hemlock within the stands. Conifers that suffered the most extensive defoliation were dominant eastern hemlocks (84 percent mean defoliation), and suppressed eastern white pine (80 percent mean defoliation). While individual eastern hemlocks within each of the four crown classes were completely stripped, none of the eastern white pines experienced 100 percent defoliation. Consequently, Stephens noted that eastern hemlock had a higher vulnerability than eastern white pine, and the vulnerability of intermediate and suppressed trees was greater than that of dominants or codominants (Table 2.5). The author implicated competition-induced mortality as a possible cause by stating " ... *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 appeared to have a

Table 2.5: Percent stem mortality of eastern white pine and eastern hemlock in western Connecticut stands three years after a heavy defoliation. From Stephens (1988).

Species	**Crown Class**				
	Suppressed	**Intermediate**	**Codominant**	**Dominant**	**Total**
	--------------------	--------------------	%	--------------------	--------------------
Eastern white pine	26	7	0	0	17
Eastern hemlock	44	47	40	19	43

notable influence on the mortality of eastern hemlock. Intermediate and suppressed trees that were defoliated 90 percent or less, had a much lower probability of dying compared to trees that experienced 100 percent defoliation. Stephens also suggested that the mortality of eastern hemlock was a direct result of defoliation, and not due to secondary factors such as insects or disease. He did not believe, however, that extensive pure stands of eastern hemlock or eastern white pine would be susceptible to defoliation. Instead, he stated that foliage loss is likely to occur only where these resistant species grow either in mixed stands with susceptible species, or where large areas of susceptible species are growing in close proximity to pure stands. Following heavy defoliation, both overstory and understory eastern hemlock appeared to be extremely vulnerable to mortality, while vigorous overstory eastern white pine would be expected to survive with little impact.

Stephens and Ward (1992) reported on stand dynamics within unmanaged mixed hardwood stands in the Eastern Highlands of Connecticut over a period of sixty 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 estimated to be between 20 and 40 years for all tracts. Trees were inventoried every decade, beginning in 1926-27 and ending in 1987. Records of tree mortality were initiated in 1937 on all tracts. A single exception to this method was a portion of the Turkey Hill tract on which a wildfire burned in 1932; in 1934 this area was re-inventoried and tree mortality was included at this time. 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 life-span 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 constituted 30 percent of the total number of major species present, maples contributed 28 percent and birches approximately 20 percent. Examples of 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. Over the course of sixty years, the forests were subjected to three significant defoliation episodes. During the decade 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 these were not identified). The Cox, Cabin and Reeves tracts were partially defoliated between 1961 and 1963; in 1964 the Turkey Hill tract suffered partial defoliation. During the period from 1967 to 1977, gypsy moth and elm spanworm (*Ennomos subsignarius* Hübner) defoliated all areas; the Cox tract suffered the most defoliation and the Turkey Hill tract the least. Between 1977 and 1987 the gypsy moth was the primary defoliator. All four areas were heavily defoliated in 1981; the Cabin tract was subjected to minor defoliation in 1982. Defoliation was described only in very general terms; the amount of defoliation on each tract was estimated by aerial survey and actual amounts for all six decades were not provided. However, the authors described the decade from 1957 to 1967 as experiencing the most disturbance due to a combination of defoliation and an extended drought. Mortality was separated into periodic mortality (the 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 greatest contributor to total mortality (basal area basis) during the sixty year period was the oak group; of the five major oak species affected, white and chestnut oaks suffered the greatest loss. During the decade from 1957 to 1967, periodic basal area mortality among the red oak group ranged from 18 to 26 percent, while mortality among white and chestnut oaks ranged from 54 to 66 percent. During the same time period, periodic mortality (stems basis) of the oak group increased from 37 to 70 percent. Periodic canopy mortality during the sixty year study period varied by species group. Birches and maples experienced high levels of canopy mortality during the early portion of the study, and relatively low levels during 1957-67. However, from 1967 to 1987 these two groups lost more canopy trees than either the oak or the other species groups. Mortality among the oaks was greatest during 1957 to 1967 (25 percent of the basal area and 32 percent of the stems), and subsequently decreased in following years. During the first thirty years (1927 to 1957), much of the observed loss was among smaller canopy trees, while in the decade from 1957 to 1967 it was the larger oaks that died. When all four sites were combined, the total periodic basal area mortality was greatest during the period from 1937 to 1957 (30 percent). During the three subsequent decades, all periods during which defoliation occurred, total periodic basal area mortality decreased; from 24 percent in 1957-67, to 15 percent in 1967-77, to 10 percent in 1977-87. It appears that gypsy moth defoliation has become a regular disturbance feature in the forest, perhaps increasing the rate of stand development, and thus 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, and in 1920 approximately 104,085 hectares near Somerville, NJ, were affected (McManus and McIntyre, 1981).

Kegg (1971) described defoliation-induced oak mortality within a northern hardwood forest. The outbreak began in the Morristown National Historical Park, NJ, in 1966 in a single two hectare tract, and increased during the next three years. In 1968 and 1969 all susceptible tree species were defoliated 50 to 100 percent. The gypsy moth population subsequently collapsed and only minor defoliation occurred in 1970. In evaluating the effects of the outbreak, Kegg utilized a 0.4 hectare permanent plot established in 1967, and one-hundred 0.04 hectare sample plots established in 1970. The species most affected by the infestation included oaks and American beech, which sustained repeated defoliations. The more resistant hardwoods, including black birch, red maple, and hickories, usually 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 0.4 hectare 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 three years of defoliation 69 percent of all oaks had died. Sample plot data revealed that oaks experienced the highest rate of stem mortality (28 percent), with a resultant basal area loss of 22 percent. Stem mortality of all other hardwoods was equal to 5 percent or less. In his analysis Kegg separated trees into four size classes (15 to 32, 33 to 47, 48 to 65, and ≥ 66 cm) rather than the more familiar crown classes. Stem mortality was most pronounced in the smallest class (49 percent) and largest class (46 percent). The 33 to 47 cm class had 25 percent mortality while the 48 to 65 cm class had 21 percent mortality. Kegg concluded that following repeated gypsy moth defoliation oaks were the most vulnerable species, with mortality occurring when defoliation levels exceeded 70 percent. He also suggested that in the long-term the effects of future outbreaks would be less severe due to the removal of susceptible tree species.

Kegg continued to evaluate gypsy moth defoliation in New Jersey and subsequently described defoliation-induced oak mortality in the Newark Watershed (Kegg, 1973, 1974). During a five year period, (1968-72), 7,231 hectares of primarily oak forest were defoliated three times. In 1968, approximately 405 hectares sustained 50-75 percent defoliation. During the next two years, the majority of the susceptible tree species on the entire area sustained 75-100 percent defoliation. In 1971-72 the population collapsed and defoliation was negligible. Five species of oak (white, northern red, chestnut, black, and scarlet) were found within the study area and these constituted 63 percent of the total number of trees observed. As a result, oaks experienced the greatest mortality, a loss of approximately 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, oak mortality averaged approximately 6 percent (on a stem basis), defoliation increased this rate significantly. In 1969 mortality of oaks equaled 14 percent, in 1970 this figure increased to 38 percent, in 1971 it had risen to 58 percent, and in 1972 oak mortality was 63 percent. Mortality among resistant species remained at pre-defoliation levels (less than 6 percent), and this was cited as evidence that defoliation was the primary causal agent in the observed oak mortality. Using Kegg's data for initial and final basal area the oak basal area loss noted above (56 percent) was calculated; the 44 percent figure reported in the original article was actually the percentage still living after defoliation.

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, approximately 30 percent of the stand basal area consisted of pine species, mainly pitch pine and shortleaf pine (*P. echinata* Mill.); the red and white oak groups comprised the remainder. Stand age was estimated to be between 40 and 55 years. The authors' estimated individual tree defoliation within each of 20 permanent 0.04 hectare plots between 1972 and 1976. The gypsy moth outbreak occurred in 1972 and 1973, during which the oaks suffered extensive defoliation and the pines were moderately defoliated. During 1974 to 1976, the pines remained undefoliated while the oaks were moderately defoliated by associated phytophages. Three years after the final gypsy moth defoliation, increment cores were extracted from the living trees. Radial growth of the oaks was severely reduced both during and subsequent to the defoliation episodes. In 1976 mean annual radial growth of trees in the both the red and white oak groups was less than 80 percent of the growth in the five year period prior to the outbreak (1965 to 1970). Conversely, pines increased their growth to approximately 165 percent of that prior to 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 approximately 12 percent of the original oak basal area and approximately 8 percent of the pine.

Stalter and Serrao (1983) studied mortality following gypsy moth defoliation within an oak-dominated forest on the Greenbrook Sanctuary, NJ. Three sites were examined; a wet site, a mesic site and a dry site. 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 2.6). The outbreak began in 1979 and ended in 1981 after three successive defoliation episodes. Oaks were preferentially defoliated and suffered approximately 90 percent defoliation each year. Northern red oak was the dominant oak species within the forest, comprising 47 percent of all oaks present and as a result also experienced the greatest stem mortality (32%). No chestnut oaks were lost and mortality of white oak (1%) and black oak (4%) were negligible. Large, old trees and small, suppressed trees died at the highest rates, results that are similar to those reported in other areas of New Jersey (Kegg, 1973). Mortality of red oak was low on the dry site (4 percent of the original basal area) and high on both the wet site (75 percent) and the mesic site (100 percent). This confirms previous observations (Stalter and Serrao, 1983), that trees on drier sites are comparatively better able to tolerate physiological stress than trees of the same species growing on mesic sites. Stalter and Serrao (1983) did not single out gypsy moth defoliation as the primary causal agent in the observed mortality; rather, they identified multiple factors including the intensity and duration of defoliation, secondary organisms, drought, and the influence of site.

Table 2.6: Species composition as a percentage of stand basal area, on three sites within the Greenbrook Sanctuary, NJ, prior to defoliation by the gypsy moth. From Stalter and Serrao (1983).

Species	**Site Type**		
	Wet	**Mesic**	**Dry**
	% of BA		
Quercus rubra	27.2	20.0	41.4
Q. alba	--	--	5.9
Q. velutina	--	--	2.4
Q. prinus	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

Pennsylvania

During 1932 the gypsy moth entered the Wilkes-Barre-Scranton area of Pennsylvania (McManus and McIntyre, 1981). Subsequent eradication attempts failed and the whole state is currently considered to be generally infested.

The Pocono Mountains

Gypsy moth defoliation and subsequent mortality in the Pocono Mountains region of Pennsylvania is chronicled in a series of papers spanning almost two decades (Gansner and Herrick, 1979; Gansner et al., 1983; Gansner et al, 1993). The first description of the 1970's outbreak in the Pocono Mountains was made by Gansner and Herrick (1979). One hundred and forty-three plots were established in 1971, and mortality of all trees 7.6 cm (DBH) and greater was recorded every year for a five year period. Moderate to heavy defoliation was observed from 1971 to 1973, with populations collapsing in 1974 and 1975 prior to another increase in 1976. The authors noted that mortality was unevenly distributed among the affected plots; heavy mortality was observed in only a small percentage of stands, with the majority experiencing minor losses. For the five 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 (actual oak basal area ranged from zero to 100 percent).

Gansner et al. (1983) revisited the plots described by Gansner and Herrick (1979), and characterized changes in stand composition during an eight year period, beginning in 1971. Following the removal of some plots due to cutting, development, and insect control, the authors used a total of 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 13 percent, but by 1979 growth had moved the mean basal area back to pre-outbreak levels (19.5 m^2/ha). Defoliation reduced the proportion of oaks within the affected stands, while the proportion of more resistant hardwood species increased. The oak component, however, was still the largest in 1979. While there was not a significant overall change in basal area within the plots during the study, one-tenth lost more than 30 percent of their basal area and a small number lost more than 50 percent. Much of this mortality occurred in overstocked stands, among small, low grade trees. By 1979, the number of overstocked plots had been reduced from 24 percent to 17 percent, while the number of fully stocked plots barely changed (63 percent in 1971 and 62 percent in 1979).

Gansner et al. (1993) utilized several comprehensive forest inventories in their description of the impact of more than two decades of gypsy moth defoliation in the Pocono's. Actual defoliation records were not provided, but the outbreaks 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, while other hardwoods and softwoods both averaged 8 percent mortality. The authors noted that mortality was highly variable among individual plots, some lost 100 percent of the original oak volume while in others mortality was negligible and oak volume actually increased. Variations between species and among crown classes were also observed, with increased mortality among smaller, low quality trees. Thus, the authors concluded that following gypsy moth defoliation smaller, lower quality oaks suffered the highest mortality rate. Volumes in trees less than 25 cm in diameter declined, but increases in the larger diameter classes apparently compensated for this loss. Overall, between 1965 and 1989 the total volume of growing stock increased 60 percent; and in 1989 oak volume comprised 43 percent of the total inventory, the same proportion that was present in 1965.

Central Pennsylvania, Ridge & Valley Province

Herrick and Gansner (1987) have provided an excellent overview of the defoliation and mortality that occurred in central Pennsylvania in the early 1980's. In 1978 more than 600 plots, 0.04 hectares in size, were established between Carlisle and State College, PA, in forest stands that had 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 covered a wide range; site characteristics, such as slope and elevation were also quite variable. Between 1978 and 1984, there were three years in which defoliation was significant. Ocular 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 either light (<30 percent), moderate (30-59 percent), or heavy (∃60 percent) defoliation. In 1980 defoliation of all plots averaged 17 percent. In 1981 the average increased to 39 percent with almost half of the plots experiencing moderate or heavy defoliation, while in 1982 average defoliation was reduced to 22 percent. Defoliation intensity and frequency differed from plot to plot. While 25 percent of the plots received at least one heavy defoliation, only 2 percent received two heavy defoliations; in addition, approximately half of the plots received no defoliation at all. As a result, mortality was also unevenly distributed throughout the plot network; a large number of plots lost a small number of trees while a few plots lost a large number of trees. Susceptible species suffered the highest losses. Twenty-two percent of all oaks present in 1978 had been killed by 1984. Oaks also contributed more to total mortality than all other hardwood and softwood species. Approximately 51 percent 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. In their discussion the authors showed a direct relationship between cumulative mortality and mean defoliation levels. Those plots with less than 10 percent defoliation had mortality rates of 13 percent; as defoliation increased to more than 40 percent, mortality also increased to 28 percent. Herrick and Gansner also highlighted the fact that mortality rapidly increases two years following a major defoliation, a trend which has been observed in other studies (Campbell and Sloan, 1977).

Gansner (1987) used the Central Pennsylvania data set to summarize the influence of site productivity on tree mortality subsequent to defoliation. Approximately 15,000 trees (7.6 cm DBH and above) were separated by site classes, and cumulative mortality rates were recorded during the period from 1979 through 1985. Site index was based on the age and height of dominant northern red oaks, and three classes were identified: poor (SI less than 16.8 meters), medium (SI 16.8 to 22.8 meters), and good (SI 22.9 meters and above). Results of this analysis showed the highest mortality occurring on good sites and the lowest mortality on poor sites (Table 2.7). Gansner proposed two theories to explain his observations; the first was that trees on poor sites were physiologically better adapted to endure stresses such as defoliation. This is consistent with information reported by Stalter and Serrao (1983). The second was that secondary agents such as *Armillaria* and *Agrilus bilineatus* are less active on poor sites. There does not appear to be much evidence to support this theory however. In fact, the opposite

Table 2.7 Influence of site quality on stem and basal area mortality subsequent to defoliation in Central Pennsylvania. From Gansner (1987).

Site Index	**Stem Mortality**		**Basal Area Mortality**	
	Oaks	**Total**	**Oaks**	**Total**
---------- m ----------	---------- % ----------			
≥ 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

appears to be true, with pathogenicity of *Armillaria* increasing with reductions in site quality (Kile et al., 1991). Also, Dunbar and Stephens (1975) found *Agrilus bilineatus* to play a major role in oak mortality on sites that were located on dry ridges, and upper slopes with thin rocky soils.

The Central Pennsylvania data set described above (Herrick and Gansner, 1987) was also used by Feicht et al. (1993) in their description of changes in stand condition following thirteen years of gypsy moth infestation. In 1986 a 228 plot subset of those originally established in 1978 was selected to facilitate the collection of more data on the long-term effects of defoliation. The sub-sample was approximately equally divided between those plots which had received at least one severe defoliation episode (>60 percent), those which had received only moderate defoliation (30-60 percent), and those experiencing only low levels of defoliation (<30 percent). The areas containing the study plots consisted of primarily mixed oak forests located in the Tuscarora and Bald Eagle State Forests of Central Pennsylvania. 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. During the thirteen year period of study there were two gypsy moth outbreaks. In 1981 thirty-four percent of the plots experienced severe defoliation, while in 1986 eighteen percent were severely defoliated. In 1986, twenty-six plots were sprayed as part of Pennsylvania's annual suppression program and the authors noted that had this not occurred the percentage of plots receiving a severe defoliation during that year would have been higher. Each plot within the sub-sample was then placed within a defoliation class based on the intensity and duration of episodes to which it had been exposed. During 1978 to 1985, 43 percent of the plots were subjected to patterns of defoliation that placed them in the low to moderate defoliation classes. Fifty-seven percent of the plots experienced at least one severe defoliation, two moderate defoliation episodes, or some greater combination (e.g. one year heavy and one year moderate or three years moderate defoliation). During 1985 to 1990, 64 percent of plots were placed in low to moderate defoliation classes, and 36 percent were placed in classes experiencing higher levels of defoliation. Overall, only 22 percent of all plots were severely defoliated for more than one year and 26 percent were never subjected to more than low defoliation. The authors then classified overstory mortality (basal area loss per acre) as either low (<15 percent), moderate (15-30 percent), or severe (>30 percent). Oak species were preferentially defoliated and consequently suffered greater mortality than non-oak species; 65 percent of all trees killed during the study were oaks. The majority (76 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 of severe defoliation (or less) 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 slightly reduced 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) in that overall stocking levels were not significantly affected during 1978 to 1985, but duration and intensity of the defoliation episodes had a direct effect on tree mortality.

Western Pennsylvania, Appalachian Plateau

Fosbroke and Hicks (1989) described gypsy moth defoliation and mortality in southwestern Pennsylvania oak stands from 1985 to 1989. Two hundred and thirty-seven plots, 0.04 hectares in size, were established in defoliated and undefoliated stands. Forest stands consisted of mixed hardwoods with red maple and chestnut oak being 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. Though they contained more oak prior to the gypsy moth outbreak, defoliated stands had a lower mean stand density (27.1 m^2/ha) compared to undefoliated stands (32.1 m^2/ha). Mean stand defoliation ranged from a low of 9 percent in 1988 to a high of 50 percent in 1986. Oaks sustained the greatest defoliation, averaging 62 percent for the four 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 four years of gypsy moth activity, 24 percent of the trees in defoliated stands had died, while undefoliated stands had lost 11 percent of their original number. Thirty percent of the original oak basal area was lost, a 39 percent stem mortality rate. The effect on individual species was greatest among scarlet, black and chestnut oak. Initially, mortality rates appeared to be influenced by site condition; stands on poor sites (less than SI 18.3 for northern red and white oak), sites with steep slopes (greater than 15 percent), and southern aspects all exhibited greater mortality than their respective counterparts. However, the authors 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.

The Pennsylvania Damage Appraisal Surveys

Beginning in 1981, the state of Pennsylvania through the Division of Forest Pest Management, the Division of Forest Advisory Services, and the individual forest districts, has conducted a gypsy moth damage appraisal survey every three years (Quimby, 1991). Areas included in the survey are those which have suffered an outbreak in the preceding three year period. Due to fluctuations in the gypsy moth population, the total area affected by defoliation in the three years prior to each survey has varied considerably. In 1984 this area encompassed approximately 1.7 million hectares, in 1987 it was reduced to approximately 972,000 hectares, while in 1990 it was back up to approximately 2.5 million hectares (Quimby, 1991). However, the portion of the defoliated area that was actually affected by moderate or heavy tree mortality during each of the three periods has steadily fallen. In 1984 approximately 17 percent of the defoliated area experienced more than 15 percent mortality, in 1987 only 11 percent was affected, and in 1990 this figure was reduced to 2 percent (Quimby, 1991).

Quimby (1987) described both the 1984 damage appraisal survey and results of a ten year study of fifty-seven permanent plots established in 1970. Within the damage appraisal survey, trees were separated by species and size (pulpwood and sawtimber) and stands were classified as containing either moderate (<30 percent) or heavy (> 30 percent) mortality. Approximately 280,000 hectares of forest-land were surveyed. Oak (northern red, black, scarlet, white, and chestnut) was the dominant species group, accounting for approximately 75 percent of the pulpwood and 90 percent of the sawtimber. Consequently, this group also experienced the greatest losses following defoliation. Among sawtimber-sized trees, oak mortality (volume basis) in stands containing moderate mortality averaged 34 percent; in stands containing heavy mortality it rose to a mean of approximately 58 percent. In both cases scarlet oak exhibited the greatest mortality, 46 percent in the moderate and 72 percent in the heavy stands. Conifers and hickories also exhibited notable mortality. Both comprised only about one percent of the total species composition, but conifers suffered a 40 percent loss in the pulpwood class, while hickories lost 40 percent in the sawtimber class. The total value loss of all timber based on average 1984 stumpage prices was estimated to be approximately $100 million dollars.

Quimbys' 1989 report described a damage appraisal conducted in 1988 by the Western Forest Pest Management Area. This area was defoliated during 1984-87 but was not included in the 1987 damage appraisal survey. Approximately 8,865 hectares were surveyed, and forest stands separated into moderate (15 to 30 percent) and heavy (>30 percent) mortality classes. Variable-radius plots were used to tally species, diameter, height and vigor of both pulpwood and sawtimber trees. In those stands classified as moderate mortality, pulpwood mortality on a volume basis averaged approximately 25 percent, and sawtimber mortality averaged approximately 29 percent. In heavy mortality stands, pulpwood mortality averaged 24 percent, while sawtimber mortality averaged approximately 48 percent. As was observed in the 1984 damage appraisal, the oak component experienced the greatest losses. In moderate mortality stands, a larger proportionate volume of oak pulpwood was lost (34 percent) than oak sawtimber (29 percent). While in heavy mortality stands, proportionate losses of oak sawtimber were greater (47 percent) than oak pulpwood (37 percent). The total value of dead stumpage throughout the survey area was estimated at approximately $8.8 million dollars.

The 1991 report by Quimby described the 1990 damage appraisal survey in detail; it also provided a concise summary of relevant data from the previous surveys and examined some stands that underwent defoliation in the 1970's. For the 1990 survey, areas in which heavy tree mortality had occurred subsequent to the last survey, and which had also been defoliated by the gypsy moth were identified; this encompassed 42,773 hectares. Forest stands were then separated into areas of moderate (15 to 30 percent) or heavy (>30 percent) stand mortality through aerial sketch-mapping. This was followed by a ground survey using variable-radius plots. Those trees which were alive or appeared to have died since the last survey (within three years) were then categorized by species, diameter, number of sixteen-foot logs (sawtimber), number of eight-foot bolts (pulpwood), and mortality. Of the total volume killed, nearly 98 percent consisted of assorted oak species (northern red, white, chestnut, and scarlet). In stands with moderate mortality, 34 percent of the oak pulpwood and 60 percent of the oak sawtimber was killed; stands with heavy mortality lost an average of 24 percent of oak pulpwood and 63 percent oak sawtimber. The total value of stumpage killed was estimated to be $28.3 million dollars. Quimby (1991) also discussed the reassessment of nineteen stands in eastern and central Pennsylvania in which plots were established in 1970. Each stand contained between one and five 0.04 hectare plots; between 1970 and 1979 these were examined biannually and individual tree defoliation, tree vigor and number of egg masses present were recorded. In 1990 the stands were remeasured, however, due to logging and other disturbances some had been destroyed. Where this occurred, variable-radius plots were established in nearby areas to evaluate stand change. Between 1970 and

1990 there were two gypsy moth epidemics, one during 1971 to 1973, and another between 1981 and 1982. During this period ten stands received at least two or more moderate or heavy defoliations. In the first ten years of observation oak mortality following a single defoliation averaged 18 percent, after two defoliations mean oak mortality rose to 89 percent, and following three defoliations mean oak mortality was 98 percent. Over the twenty year period average oak mortality was slightly lower; a single year of defoliation resulted in 14 percent mortality, two years increased the rate to 38 percent and three years resulted in an average of 48 percent. Four plots with original oak compositions ranging from 22 to 78 percent suffered a 100 percent loss of oak after two or three defoliation episodes. Changes in species composition and shifts in diameter classes occurred due to the loss of oak and subsequent replacement by large numbers of smaller trees. However, the overall effect of these episodes on total stand basal area was negligible, regardless of the number of defoliation episodes or the amount of mortality. Quimby also 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, have rendered these stands less susceptible to future gypsy moth outbreaks*".

As mentioned previously, the total area defoliated prior to each damage appraisal survey was variable. However, Quimby (1991) noted that the variation in estimated mortality between damage surveys was relatively small. From 1981 to 1990 the average percent mortality for sawtimber was 37 percent, ranging from a low of 33 percent in 1987 to a high of 42 percent in 1984. The average percent mortality for pulpwood during this period was 34 percent; the low of 27 percent occurred in 1987 and the high of 39 percent occurred in 1984. The high levels of mortality observed in the 1984 survey 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 a small gypsy moth infestation was discovered in Shenandoah National Park, in the Blue Ridge Mountains of Virginia (Ravlin and Fleischer, 1989). During the next two decades gypsy moth populations increased dramatically and approximately two thirds of the state is currently considered to be generally infested (Davidson et al., 1994).

Gypsy moth larvae were first detected in Jefferson County, West Virginia in 1978; however, it was not until 1985 that the first episodes of noticeable defoliation were 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). Though the gypsy moth has been active in West Virginia for two decades and in Virginia for nearly three decades, there are relatively few sources which specifically document its' impact within this region.

Virginia

In 1992, Tigner produced a report for the Virginia Department of Forestry describing defoliation and mortality in Virginia (Davidson et al., 1994). A portion of this report 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 (from 0 to 3 defoliation episodes) were identified in 1988 using historical data. Stand size ranged from 6.5 to 46.2 hectares. 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-defoliation through to post-defoliation. Instead he compared stands with either zero, one, two, or three defoliations, thus data was 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; chestnut, white, scarlet, black and northern red. In Clarke County, undefoliated stands averaged 20 percent oak mortality, a single defoliation raised mortality to 23 percent, two defoliations increased the rate to 30 percent, and following three defoliations 50 percent of the original oak basal area had been killed. The mortality of other hardwood and softwood species was actually greater in undefoliated stands than in those receiving one, two, or three defoliation episodes, but remained below 15 percent. Undefoliated stands on the Lee Ranger District of the GWNF averaged 8 percent oak mortality. Following a single defoliation this figure increased to 24 percent, after two episodes oak mortality averaged 32 percent, and when stands were subjected to three defoliations 37 percent of the original oak basal area was killed. As was observed in the Clarke County data, mortality within the group of other hardwood and softwood species did not appear to be significantly influenced by the 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 forests in both areas had displayed considerable mortality among oaks as a result of an extended drought in many counties of northern Virginia, and this is listed as a probable contributing factor in the observed mortality subsequent to defoliation.

Shenandoah National Park, has been the site of significant gypsy moth activity since the insects introduction to Virginia. However, I was unable to locate any literature or data that provides a synthesis of the progression of the outbreaks within the park and any resultant impacts. The information that is available comes from a combination of the work of Potts and Teetor (1989), Tigner's (1992) report of the impact of defoliation on Virginia's hardwood forests, and Kasbohm's (1994) description of the infestation's influence on the black bear population in the Park.

Potts and Teetor (1989) used defoliation information from aerial photographs to facilitate a ground survey using transects and 0.04 hectare plots to estimate mortality (stem basis) following both a single defoliation and two episodes. Baseline mortality, not attributable to the gypsy moth, was established through an independent study and this figure was then subtracted from gross mortality estimated both one and two years after initial and subsequent defoliations. Following a single defoliation the mortality of red and white oak, black birch, black locust (*Robinia pseudoacacia* L.) and basswood (*Tilia americana* L.) were all equal to or below 7 percent; only chestnut oak appeared to be adversely impacted with mortality approaching 14 percent. Resistant and immune species, such as hickories, red maple, and yellow poplar, were essentially unaffected. The authors noted a similar pattern subsequent to the second defoliation episode. Oaks were the most severely affected species; white oaks suffered 35 percent mortality, red oaks 40 percent and chestnut oak 42 percent. The effect on pines appeared to be minimal as mortality in stands defoliated twice and those defoliated only once both averaged approximately 13 percent. Potts and Teetor pointed out, however, that lack of additional baseline mortality information for pine species leaves the effect of gypsy moth defoliation on pine mortality unclear. The authors concluded that the short-term impacts of defoliation have been limited to the oak component, and this was exacerbated by a drought that had been affecting the area since 1985.

Tigner (1992) also described the results of a monitoring study initiated in 1974 in the western Madison County portion of Shenandoah National Park. Fixed-radius 0.04 hectare plots were used to evaluate mortality among trees 15.2 cm DBH and larger. 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, ranging in age from fifty to more than one-hundred and fifty years old. Stands were located on moderate to poor, upper slope sites with site indexes of 15.2 to 18.3 meters. In 1982 and 1984, light defoliation by loopers (Geometriidae) was observed within all the study plots; in 1984 this was concentrated primarily on the white oaks. Gypsy moth defoliation first occurred in 1987, but this was considered negligible and plots were subjected to only a single heavy (61-100 percent) episode in 1989, followed by two years of light (0-30 percent) or negligible defoliation. In addition to stress from defoliation, stands had also been exposed to a prolonged drought, and a severe winter storm in 1980 which resulted in large numbers of damaged 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. Gypsy moth defoliation increased mortality rates among trees in the intermediate and suppressed crown classes; this trend was also present prior to defoliation but on a much smaller scale. Because white oaks and other non-oak species had a larger proportion of their number among these crown classes, they experienced more loss than the red oaks. Among species groups however, mortality of the oak component was much higher than among other species. During the defoliation episodes, 84 percent of the trees studied were severely or moderately defoliated; 77 percent were subjected to a single episode, while the rest experienced two episodes. This group of defoliated trees then lost 11 percent of its original number, ostensibly 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. The study used eighteen sites that had been established in 1987 as part of a permanent Long Term Ecological Monitoring System. These sites, consisting primarily of chestnut and red oak stand types, were located in the North and Central Administrative Districts of the park. Noticeable defoliation occurred in 1985 and continued through 1989, with the majority of sites receiving a single defoliation episode. However, in the North District large areas were subjected to two or three defoliations during 1986 to 1989. Sixty percent of the chestnut oak and 45 percent of the red oak stands suffered heavy defoliation (>60 percent) during the study period. As the duration of defoliation episodes increased, tree mortality also increased. Sites that did not experience defoliation lost an average of 2.6 percent of the original number of oak stems. Following a single episode of defoliation, this rate increased to a mean of approximately 4.7 percent, and those sites subjected to two to three episodes averaged a 17.6 percent loss. At the extreme, a single site lost approximately 85 percent of its original density during 1987 to 1990. The only other species groups that lost a significant number of trees were the maples (mean =11.9 percent) and hickories (mean = 8.9 percent); however, this was restricted to areas that suffered two to three defoliation episodes.

West Virginia

In 1991, Atkins and Smallwood produced a report describing defoliation and mortality in West Virginia, from 1985 to 1990. The data used was taken from damage appraisals conducted throughout the state by the West Virginia Division of Forestry. Aerial defoliation estimates were used to separate areas into three classes; light (0 to 29 percent), moderate (30 to 59 percent) and heavy (≥ 60 percent). Areas that had been moderately or heavily defoliated were then subjected to a visual ground inspection of individual trees. These ground inspections were carried out at the end of the second growing season following initial defoliation and consisted of variable-radius plots. Trees were classified by species, size class, vulnerability to mortality, and actual mortality. Oak species comprised from 65 to 88 percent of the total stocking of 1,841 hectares examined. Following a single defoliation, actual stand mortality averaged 16 percent of the original basal area; rates increased with duration of the defoliation episode, and the oak component suffered the highest mortality. Following two defoliations, mortality increased to 23 percent, and three defoliations resulted in a rate of 26 percent. In terms of the monetary value lost, Atkins and Smallwood determined that following moderate to heavy defoliation of 32,978 hectares, approximately 594,657 m^3 of timber, worth nearly 17 million dollars was killed.

Michigan

The gypsy moth was first discovered in Lansing, Michigan in 1954 (McManus and McIntyre, 1981). However, it was not until 1982 that significant defoliation was observed (Hart, 1990). Since then, yearly defoliation levels have steadily increased with a high in 1992 of approximately 288,425 hectares of Michigan's forests were defoliated (USDA, 1995).

Information describing defoliation-induced mortality in forest stands in Michigan is scarce. Hart (1990) described a study initiated in 1986 to evaluate the influence of defoliation on bigtooth (*Populus grandidentata* Michx.) and quaking aspen (*P. tremuloides* Michx.) in Michigan. The study area was located in Midland County, MI, and consisted of six stands of mixed northern hardwoods. All six areas were subjected to defoliation episodes during 1985 to 1989; defoliation was most severe in 1986. Three stands were aerially sprayed with *Bacillus thuringiensis* in 1986, 1987, and 1988, and the author noted that these areas were defoliated at a slightly lesser intensity than the other areas. Twenty-five variable-radius plots were used to evaluate damage to both aspen species. Diameters, heights, tree condition, and an ocular estimation of percent defoliation were measured for individual trees. Aspen comprised five percent of the total inventory, the actual data used for the evaluation consisted of 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 completely defoliated, the other was stripped of more than 80 percent of its foliage. Mortality was not distinguishable by crown class; sub-dominants, co-dominants and dominants were killed at almost equal rates. Of the three bigtooth aspen trees killed, only one was in good condition prior to defoliation; it was subsequently completely defoliated. Mortality in sprayed stands was not discussed. The author also pointed out the role of secondary organisms in mortality subsequent to defoliation. Species of *Armillaria* were observed on 89 percent of the dead trees, and 53 percent also showed signs of attack by species of wood-boring insects (*Agrilus* and *Saperda* spp.).

SUMMARY

The intent of this regional review is to provide a synthesis of the current knowledge regarding the relationships between gypsy moth defoliation and subsequent tree mortality. Though the information that was used spans a time period of almost one hundred years and involves the work of many scientists the following consistencies among studies were observed.

- Susceptible tree species are defoliated at higher rates than resistant species, and frequently suffer greater mortality than resistant 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 understory (those in the suppressed and intermediate crown classes) have a greater probability of being defoliated and dying, than trees in the overstory (dominants and codominants).
- Tree mortality tends to rapidly increase during the second year after defoliation.

LITERATURE CITED

Atkins, J.M., and H. Smallwood. 1991. Gypsy moth damage in West Virginia, 1985-1990, and predicted future impact. West Virginia Division of Forestry, Tech. Rep. 91-1. 6 p.

Baker, W.L. 1941. Effect of gypsy moth defoliation on certain forest trees. J. For. 39:1017-1022.

Brown, J.H., D.B. Halliwell, and W.P. Gould. 1979. Gypsy moth defoliation: impact in Rhode Island forests. J. For. 77:30-32.

Brown, J.H., V.B. Cruickshank, W.P. Gould, and T.P. Husband. 1988. Impact of gypsy moth defoliation in stands containing white pine. North. J. Appl. For. 5:108-111.

Campbell, R.W. 1979. Gypsy moth: forest influence. USDA Agric. Inf. Bull. 423. 44 p.

Campbell, R.W., and A.S. Garlo. 1982. Gypsy moth in New Jersey pine-oak. J. For. 80:89-90.

Campbell, R.W., and R.J. Sloan. 1977. Forest stand responses to defoliation by the gypsy moth. For. Sci. Monogr. 19. 34 p.

Campbell, R.W., and H.T. Valentine. 1972. Tree condition and mortality following defoliation by the gypsy moth. USDA For. Serv. Res. Pap. NE-236. 331 p.

Davidson, C.B., J.E. Johnson, and T.C. Tigner. 1994. Gypsy moth defoliation and tree mortality in Virginia. P. 75-83 *in* Proc. 1992 national gypsy moth review., Marshall, P. (ed.) Indiana Department of Natural Resources, Divisions of Forestry and Entomology/Plant Pathology.

Dunbar, D.M., and G.R. Stephens. 1975. Association of two-lined chestnut borer and shoestring fungus with mortality of defoliated oak in Connecticut. For. Sci. 21:169-174.

Dunn, J.P., T.W. Kimmerer, and G.L. Nordin. 1986. Attraction of the twolined chestnut borer, *Agrilus bilineatus* (Weber) (Coleoptera: Buprestidae), and associated borers to volatiles of stressed white oak. Can. Entom. 118(6):503-509.

Feicht, D.L., S.L.C. Fosbroke, and M.J. Twery. 1993. Forest stand conditions after 13 years of gypsy moth infestation. P. 130-14 *in* Proc. 9th Central Hardwood Forest Conf., Gillespie, A.R., G.R. Parker, P.E. Pope, and G. Rink (eds.). USDA For. Serv. Gen. Tech. Rep. NC-161.

Fosbroke, D.A., and R.R. Hicks, Jr. 1989. Tree mortality following gypsy moth defoliation in southwestern Pennsylvania. P. 74-80 *in* Proc. 7th Central Hardwood Forest Conf., Rink,G., and C.A. Budelsky (eds.). USDA For. Serv. Gen. Tech. Rep. NC-132.

Gansner, D.A. 1987. Site productivity and tree mortality on new frontiers of gypsy moth infestation. USDA For. Serv. Res. Note. NE-340. 3 p.

Gansner, D.A., and O.W. Herrick. 1979. Forest stand losses to gypsy moth in the Poconos. USDA For. Serv. Res. Note. NE-273. 5 p.

Gansner, D.A., O.W. Herrick, P.S. DeBald, and R.E. Acciavatti. 1983. Changes in forest condition associated with gypsy moth. J. For. 81(3):155-157.

Gansner, D.A., S.L. Arner, R.H. Widmann, and C.L. Alerich. 1993. After two decades of gypsy moth, is there any oak left? North. J. Appl. For. 10(4):184-186.

Gottschalk, K.W. 1989. Effects of previous stand management on mortality following gypsy moth defoliation: preliminary results. P. 573-578 *in* Proc. Fifth Biennial Southern Silvicultural Research Conf., Miller, J.H. (comp.) USDA For. Serv. Gen. Tech. Rep. SO-74.

Hall, R.C. 1935. Cape Cod pitch pine: Its resistance to gipsy moth defoliation and its advantages as a forest tree. J. For. 33:169-172

Hart, J.H. 1990. Effect of gypsy moth on aspen in Michigan. P. 173-176 *in* Proc. 1989 Aspen Symp., Adams, R.D. (ed.) USDA For. Serv. Gen. Tech. Rep. NC-140.

Herrick, O.W. and D.A. Gansner. 1987. Gypsy moth on a new frontier: forest tree defoliation and mortality. North. J. Appl. For. 4:128-133.

Herrick, O.W. and D.A. Gansner. 1988. Changes in forest condition associated with gypsy moth on new frontiers of infestation. North. J. Appl. For. 5(1): 59-61.

Hicks, R.R. Jr., and D.A. Mudrick. 1994. 1993 Forest Health, a status report for West Virginia. West Virginia Department of Agriculture, Charleston, WV. 68 p.

House, W.P. 1960. Gypsy moth-white pine damage study. Final report. USDA Agric. Res. Serv. Plant Pest Control Div. Eastern Region. 48 p.

Kasbohm, J.W. 1994. Response of black bears to gypsy moth infestation in Shenandoah National Park, Virginia. Ph.D. diss., Virginia Polytechnic Institute and State Univ. 219 p.

Kegg, J.D. 1971. The impact of gypsy moth: Repeated defoliation of oak in New Jersey. J. For. 69:852-854.

Kegg, J.D. 1973. Oak mortality caused by repeated gypsy moth defoliations in New Jersey. J. Econ. Entomol. 66(3):639-641.

Kegg, J.D. 1974. Quantitative classification of forest stands as related to their vulnerability to loss following initial outbreak of the gypsy moth, *Porthetria dispar* (L.), with equations for forecasting basal area losses. M.S. Thesis, Rutgers University. 36 p.

Kile, G.A., G.I. McDonald, and J.W. Byler. 1991. Ecology and disease in natural forests. P. 102-121 *in* Armillaria root disease, Shaw, C.G. III. and G.A. Kile (eds.). USDA For. Serv. Agric. Handbook 691.

Liebhold, A.M., K.W. Gottschalk, R.M. Muzika, M.E. Montgomery, R. Young, K. O'Day, and B. Kelley. 1995. Suitability of North American tree species to the gypsy moth: a summary of field and laboratory tests. USDA For. Serv. Gen. Tech. Rep. NE-211. 45 p.

McManus, M.L., and T. McIntyre. 1981. Introduction: historical chronology. P. 1-8 *in* The gypsy moth: Research toward integrated pest management, Doane, C.C., and M.L. Mcmanus (eds.). USDA For. Serv. Tech. Bull. 1584.

Minott, C.W., and I.T. Guild. 1925. Some results of the defoliation of trees. J. Econ. Entomol. 18:345-348.

Montgomery, M.E., and W.E. Wallner. 1988. The gypsy moth, a westward migrant. P. 353-375 *in* Dynamics of forest insect populations: patterns, causes, implications, Berryman, A.A. (ed). Plenum Press, New York.

Perry, C.C. 1955. Gypsy moth: Appraisal program and proposed plan to prevent spread of the moths. USDA Tech. Bull. 1124. 27 p.

Potts, R.R. II., and A. Teetor. 1989. Effects of the gypsy moth on the forests of Shenandoah National Park, Virginia. P. 196-198 *in* Proc. 1988 National Gypsy Moth Review. Michigan Dept. of Agric., Pesticide and Plant Pest Management Division.

Quimby, J.W. 1987. Impact of gypsy moth defoliation on forest stands. P. 21-29 *in* Proc. Coping with the gypsy moth in the new frontier: a workshop for forest managers. Fosbroke, S., and R.R. Hicks (eds.). West Virginia Univ. Books, Morgantown.

Quimby, J.W. 1989. Damage appraisal in gypsy moth defoliated woodlands - Western area, 1988. Pennsylvania Bureau of Forestry, Division of Forest Pest Management Report. 3 p.

Quimby, J.W. 1991. Tree mortality following gypsy moth epidemics - 1990. Pennsylvania Bureau of Forestry, Division of Forest Pest Management Report. 50 p.

Ravlin, F.W., and S.J. Fleischer. 1989. The gypsy moth dilemma: For want of a silver bullet. P. 2-5 *in* The Gypsy Moth in Virginia, 1989, Carroll, B.S., and F.W. Ravlin (eds.). Virginia Coop. Ext., Publication 444-028.

Stalter, R., and J. Serrao. 1983. The impact of defoliation by gypsy moths on the oak forest at Greenbrook Sanctuary, New Jersey. Bull. Torrey Bot. Club. 110(4):526-529.

Stephens, G.R. 1984. Heavily defoliated white pine has lower mortality than hemlock. Front. Pl. Sci. Fall 1984:4-5.

Stephens, G.R. 1987. Effect of gypsy moth defoliation on conifers. P. 30-38 *in* Proc. Coping with the gypsy moth in the new frontier: a workshop for forest managers. Fosbroke, S., and R.R. Hicks (eds.). West Virginia Univ. Books, Morgantown.

Stephens, G.R. 1988. Mortality, dieback and growth of defoliated hemlock and white pine. North. J. Appl. For. 5:93-96.

Stephens, G.R., and J.S. Ward. 1992. Sixty years of natural change in unmanaged mixed hardwood forests. Conn. Agric. Exp. Stn. Bull. 902. 63 p.

Tigner, T. 1992. Gypsy moth impact on Virginia's hardwood forests and forest industry. Virginia Dept. of Forestry, Charlottesville, VA. 36 p.

Turner, N. 1963. Effect of defoliation by the gypsy moth. Conn. Agric. Exp. Stn. Bull. 658. 30 p.

Twery, M.J. 1991. Effects of defoliation by gypsy moth. P.27-39 *in* Proc. U.S. Department of Agriculture Interagency Gypsy Moth Research Review 1990. Gottschalk, K.W., M.J. Twery, and S.I. Smith (eds.). USDA For. Serv. Gen. Tech. Rep. NE-146.

USDA, Forest Service. 1995. Forest insect and disease conditions in the United States, 1994. USDA For. Serv., Forest Pest Management. 74 p.

United States. President. 1990. P. 290-291 *in* Economic report of the president transmitted to congress, 1990. Supt. of Docs. U.S. Govt. Print. Off. Washington D.C.

Wargo, P.M. 1977. *Armillariella mellea* and *Agrilus bilineatus* and mortality of defoliated oak trees. For. Sci. 23(4):485-492.

CHAPTER 3

Tree mortality subsequent to defoliation by the European gypsy moth (*Lymantria dispar* L.) in the United States: a review

INTRODUCTION

For more than a century, the European gypsy moth (*Lymantria dispar* L.) (Lepidoptera: Lymantriidae) has been responsible for defoliation outbreaks of varying severity in eastern and central forests of North America. From its first introduction in 1869 to the early 1960's defoliation episodes were concentrated in the northern hardwood and oak forests of New England and the Mid-Atlantic states. As gypsy moth populations have expanded their range further south and west, however, outbreaks in previously undefoliated forest types have become more frequent. The primary effects of gypsy moth defoliation on trees are a reduction in tree growth, reductions in flowering and fruiting, and individual tree mortality. Though all reduce the monetary and aesthetic value of trees and forests, tree mortality is the most easily observed effect, and thus the one that garners the majority of public and scientific attention.

While many species of trees and shrubs are utilized as a food source, gypsy moth larvae exhibit a decided preference for certain species. Consequently, researchers have historically categorized forest trees according to their relative susceptibility to defoliation (Mosher, 1915). These attempts at categorization were essentially for the sake of convenience, for in reality larval feeding preference is a continuum dependent upon various external factors such as population size and the availability of food. One of the most recent classification systems separates trees and shrubs into three groups, those described as either "susceptible", "resistant" or "immune" to defoliation (Montgomery, 1991; Twery, 1991; Liebhold et al., 1995). Susceptible tree species are described as those which are consumed by all larval stages, while resistant species are consumed by only some larval stages or when susceptible species are not available; immune species are rarely if ever consumed by any larval stage (Table 3.1). Their inherent susceptibility or resistance also results in species exhibiting differential growth and mortality responses subsequent to defoliation.

This notion of susceptibility is also applicable at the stand level, where stand susceptibility refers to the likelihood that defoliation will occur if the gypsy moth is present. Prior research indicates that pure stands of susceptible food species, such as oaks, are more susceptible to defoliation than stands containing mixtures of susceptible, resistant and immune species (Bess et al., 1947; Gottschalk and Twery, 1989; Houston and Valentine, 1977). Once defoliated, these stands are also more likely to suffer some form of damage, most often tree mortality. Stand vulnerability, the probability of damage following defoliation, is thus greater in stands of susceptible species. A generalized theory regarding the influence of species composition on subsequent mortality in gypsy moth defoliated stands first emerged during the late 19th and early 20th century (Forbush and Fernald, 1896; Mosher, 1915; Clement and Munro, 1917). Though no formal experiments had been conducted, it was widely believed that stands containing large numbers of species unfavorable for gypsy moth consumption (i.e. resistant and immune species), would not suffer defoliation and mortality. These ideas were the basis for research regarding possible silvicultural control of the gypsy moth through the removal of favored species from susceptible stands (Clement and Munro, 1917; Baker and Cline, 1936;

Table 3.1: Examples of some trees and shrubs common to the Eastern United States, and their classification according to currently accepted gypsy moth host preference classes; adapted from Montgomery, 1991; Twery, 1991 and Liebhold et al., 1995.

Crown Position	Feeding Preference Class		
	Susceptible	**Resistant**	**Immune**
Overstory	*Betula nigra*	*Acer negundo*	*Abies balsamea*
	Betula papyrifera	*Acer rubrum*	*Abies fraseri*
	Betula populifolia	*Acer saccharum*	*Acer saccharinum*
	Larix decidua	*Betula lenta*	*Aesculus glabra*
	Larix laricina	*Carya* spp.	*Aesculus octandra*
	Liquidambar styraciflua	*Juglans cinerea*	*Aesculus hippocastanum*
	Populus balsamifera	*Juglans nigra*	*Betula alleghaniensis*
	Populus grandidentata	*Picea* spp.	*Catalpa speciosa*
	Pyrus malus	*Pinus* spp.	*Celtis* spp.
	Quercus spp.	*Prunus serotina*	*Fraxinus* spp.
	Salix spp.	*Prunus avium*	*Gleditsia triacanthos*
		Populus deltoides	*Gymnocladus dioicus*
		Sassafras albidum	*Ilex opaca*
		Tsuga canadensis	*Juniperus virginiana*
		Tsuga caroliniana	*Liriodendron tulipifera*
		Ulmus americana	*Magnolia acuminata*
			Morus rubra
			Platanus occidentalis
			Robinia pseudoacacia
			Ulmus rubra
Understory	*Carpinus caroliniana*	*Amelanchier arborea*	*Acer pensylvanicum*
	Corylus americana	*Cornus florida*	*Acer spicatum*
	Crataegus spp.	*Oxydendrum arboreum*	*Cercis canadensis*
	Hamamelis virginiana	*Prunus pensylvanica*	*Diospyros virginiana*
	Ostrya virginiana	*Prunus virginiana*	*Kalmia latifolia*
		Vaccinium spp.	*Rubus* spp.
			Viburnum spp.

Korstian and Ruggles, 1941).

Both past and present silvicultural control methods theorize that a reduction in the percentage composition of susceptible species lowers stand susceptibility (Gottschalk, 1993). Whether the influence of species composition can be extended from a reduction in defoliation to a reduction in tree mortality remains to be seen.

Though species composition often takes center stage in discussions of forest stand susceptibility and vulnerability, descriptions of susceptible and resistant forest types frequently involve references to specific site factors. Susceptible forests have been described as those occurring on dry ridges and sandy plains, where stands are composed mainly of slow-growing, susceptible species and frequently have had a history of both natural and anthropogenic disturbance (Bess et al., 1947; Houston and Valentine, 1985). Conversely, Houston and Valentine (1985) described resistant stands as those found on mesic ridges, slopes, and bottomlands, where stands were primarily mixtures of susceptible and resistant species and moisture was not a limiting factor. These classifications, however, refer only to the likelihood of defoliation; the question is whether these susceptible sites also experience greater tree mortality. References to observed differences in rates of mortality on different sites have been made by a number of scientists (Bess et al., 1947; Campbell and Sloan, 1977; Houston, 1981; Gottschalk and Twery, 1989). Whether this is due to site conditions directly influencing the vulnerability of individual trees or whole stands, or is simply a function of site conditions affecting species composition, and thus defoliation and mortality, is unknown. If these differences can be quantified, the identification and classification of both susceptible and vulnerable stands by site would become feasible.

As gypsy moth populations have expanded from their zone of original introduction, differences have been observed between areas experiencing initial outbreaks as a result of new introductions, and those experiencing subsequent outbreaks from established populations. As a result, some scientists have advanced the theory that mortality rates along the "leading edge" of the gypsy moth infestation are greater than in areas that have experienced long-term infestation. This may be a result of reduced defoliation in the latter, due to the loss of susceptible species; or it may be the result of genetic selection favoring oaks that are better able to survive defoliation (Campbell and Sloan, 1977). Confirmation of a difference may shed some light on these hypotheses; it would also affect decisions made by forest managers concerning control efforts for the gypsy moth under these different conditions.

The previous observations accentuate the importance of three topics of interest to both foresters and entomologists. Is there an association between initial stand composition and subsequent mortality rates of trees defoliated by the gypsy moth? Does site quality influence the mortality rate? Do initial outbreaks in previously uninfested areas inflict more damage than subsequent outbreaks? Though they have been the subject of frequent discussion, these specific questions have not been thoroughly examined through the use of either designed experiments, or through a critical review of the literature. Therefore, the objective of this paper is to provide a critical synthesis of the available literature in order to elucidate the relationship between gypsy moth defoliation and subsequent tree mortality in the forests of the eastern and north-central United States.

FACTORS INFLUENCING TREE MORTALITY FOLLOWING DEFOLIATION

The etiology of individual tree mortality subsequent to insect defoliation is extremely complex. Therefore, prior to a discussion of the effects of gypsy moth defoliation it is prudent to review the relevant factors in detail. Whether a tree succumbs to mortality, or merely experiences a short-term reduction in growth increment following defoliation is dependent upon the following factors: the tree species; the intensity, duration and frequency of defoliation; the tree's physiological condition at the time of defoliation; and the presence of secondary-action organisms such as *Armillaria* spp. and *Agrilus bilineatus* (Weber) (Wargo and Houston, 1974; Dunbar and Stephens, 1975; Houston, 1981; Parker, 1981; Wargo, 1981a). These factors do not act independently; rather it is their action in combination that determines the final outcome. For instance, while healthy oaks are able to recover from defoliation during periods when they are not experiencing other significant stress, defoliation during or following a severe drought has been shown to increase the probability of mortality (Baker, 1941; Campbell and Sloan, 1977). In observations of oak decline following defoliation by the oak leaf roller (*Croesia (Argyrotoxa) semipurpurana* Kearf.) in Pennsylvania, Staley (1965) noted that while defoliation was the primary cause of decline, severity of decline was dependent upon both climatic and edaphic factors.

Defoliation intensity is a measure of the amount of foliage that is lost during a defoliation episode; it is typically expressed as the percentage of foliage removed during the growing season. Past descriptions of defoliation intensity have frequently placed trees into one of three classes; those experiencing less than 30 percent defoliation (*light*), 30 to 60 percent defoliation (*moderate*), or greater than 60 percent (*heavy*) (Gottschalk, 1993). Light defoliation generally results in minimal visual or physiological damage, while moderate and heavy defoliation may cause heavy damage. Susceptible hardwoods, such as oaks, are often completely defoliated during an outbreak, but if not physiologically stressed they are able to recover. Instances of trees undergoing consecutive complete defoliations followed by recovery are not uncommon (Kulman, 1971). As a rule, following heavy defoliation, conifers are more vulnerable than hardwoods. Baker (1941) found that when eastern white pine (*Pinus strobus* L.) defoliation exceeded 80 percent, tree mortality was nearly three times greater than that of trees defoliated less than 80 percent. House (Turner, 1963) observed similar results among both eastern white pine and eastern hemlock (*Tsuga canadensis* L. Carr). The duration of defoliation refers to the number of consecutive annual defoliation episodes that occur in a given time period. Frequency of defoliation refers to the number of defoliation outbreaks that occur in a given time period (i.e., how far apart the outbreaks are, every four to five years or every ten to twelve years). As the number of consecutive episodes increases, the probability of tree mortality rises (Campbell and Sloan, 1977). Following a single heavy defoliation in Pennsylvania, Quimby (1987) reported 18 percent oak mortality; two years of defoliation increased this figure to 89 percent, and after three years of heavy defoliation oak mortality averaged 98 percent.

The greatest single indicator of the likelihood of mortality is physiological condition at the time of defoliation. Research has consistently shown that trees in poor condition suffer greater mortality; for example, suppressed and intermediate trees are frequently killed following a single defoliation (Campbell and Valentine, 1972; Campbell and Sloan, 1977). Starch is an abundant reserve carbohydrate in plants and is an important measure of physiological condition (Parker, 1981; Kozlowski et al. 1991). Artificial defoliation of young black oak (*Quercus* *velutina* Lamarck), white oak (*Q. alba* L.) and sugar maple (*Acer saccharum* Marsh) by Wargo (1981b), revealed a significant reduction in root starch content. Reductions in root starch levels have also been associated with increases in glucose and fructose (Parker and Houston, 1971; Wargo, 1972). Some authors have suggested that these changes are initiated by defoliation and reflect a conversion of starch to sugar (Parker and Houston, 1971; Wargo, 1972, Wargo and Harrington, 1991). This creates conditions that are beneficial to the growth of a number of fungal species, thus defoliation may indirectly encourage increased fungal invasion and subsequent tree mortality (Parker, 1981; Wargo, 1981a).

The fungal organism most frequently cited in references to defoliation-induced mortality is *Armillaria* spp., a root rot fungus. *Armillaria* spp. are ubiquitous in forests throughout North America, and under normal conditions root infection is limited by the host tree (Kile et al., 1991). When stressed by external factors such as defoliation, however, resistance to infection is lowered and the possibility of colonization by *Armillaria* increases (Wargo and Harrington, 1991). Parker and Houston (1971) described an apparent relationship between sugar maple defoliation and subsequent infection by *Armillaria*. They noted that while timing and intensity of defoliation influenced dieback of individual buds and twigs, tree mortality appeared to be due primarily to fungal invasion. Based on examinations of stems and cut stumps, Dunbar and Stephens (1975) concluded that *Armillaria* played only a minor role in oak mortality in Connecticut. However, the results of a study by Wargo (1977) provide evidence that *Armillaria* contributes significantly to oak mortality following gypsy moth defoliation. Examination of the roots and root collars of living, dying and dead trees showed *Armillaria* present in 42 percent of living trees and 96 percent of dead or dying trees (Wargo, 1977). Historically, many authors have described the species responsible for oak mortality as *Armillaria mellea* (Vahl, Quel.); however, recent taxonomic advances have indicated that this assumption is incorrect (Watling et al. 1991). Studies in southwestern Pennsylvania have revealed that the species most commonly affecting mixed oak stands in this region is *Armillaria bulbosa* Barla - synonyms *A. gallica* Marxm. and *A. lutea* Gillet (Twery et al., 1990). Similar relationships were observed in an extensive study of forest sites throughout the state of New York (Blodgett and Worrall, 1992). Of thirty-four tree species examined, hardwoods were predominantly infected with *A. gallica*, *A. gemina* and *A. calvescens*; when oaks were separated from other hardwoods, *A. gallica* occurred on approximately ninety percent of infected trees (Blodgett and Worrall, 1992).

In addition to *Armillaria*, mortality following defoliation has been attributed to subsequent infestation by *Agrilus bilineatus* (Weber), the twolined chestnut borer (Dunbar and Stephens, 1975; Dunn et al., 1986). Both Nichols (1968) and Dunbar and Stephens (1975) reported the presence of *A. bilineatus* in a significant percentage of dead or dying oaks following defoliation. As with *Armillaria*, the level of dormant season carbohydrate storage has been linked to *A. bilineatus* infestation (Dunn et al., 1987; Dunn et al., 1990). Dunn et al. (1987) found that white oaks containing low levels of stored carbohydrates during the dormant season had greater incidence of borer attack. In addition, though borer attack was also observed in trees with higher starch levels, only those with low root starch levels suffered mortality.

While we have discussed the impacts of *Armillaria* and *A. bilineatus* separately, in many instances both organisms are involved, and the relative superiority of one over the other cannot be distinguished (Wargo, 1977). Currently, *Armillaria* and *A. bilineatus* are the most often mentioned mortality-causing agents following gypsy moth defoliation. As populations move further into the southern pine region of the southeastern United States however, interactions with other common organisms such as the southern pine beetle (*Dendroctonus frontalis* Zimmerman) and the black turpentine beetle (*Dendroctonus terebrans* Oliver) will probably become important (Gottschalk and Twery, 1989).

From the preceding discussion, it is obvious that tree death cannot be attributed to defoliation alone. The probability of mortality is dependent upon a complex interaction of many different factors, biotic and abiotic. This inherent variability makes the explanation of defoliation/mortality relationships and the accurate prediction of mortality extremely difficult.

RELATIONSHIPS BETWEEN DEFOLIATION AND TREE MORTALITY

The dynamics of gypsy moth defoliation and tree mortality have been studied in different forest communities, at different times and with wide variations in gypsy moth population levels throughout the years. As a result, a number of consistent relationships have been observed:

1) susceptible tree species are defoliated at higher rates and frequently suffer greater mortality than resistant species.
2) tree mortality increases as the intensity, duration, and frequency of defoliation increases.
3) trees in the lower canopy (those in the suppressed and intermediate crown classes) have a higher probability of being defoliated and dying, than trees in the upper canopy (dominants and codominants)
4) physiological condition prior to defoliation directly influences the probability of mortality of individual trees; those in good condition are less likely to die than those in poor condition.

Studies in New England utilizing the Melrose Highlands data[1] provided a first glimpse at the relationships between tree species, gypsy moth defoliation and tree mortality. Minott and Guild (1925) and Baker (1941) both observed that susceptible species were defoliated at a much higher rate than resistant species. These differential defoliation rates resulted in increased mortality among the susceptible species (Baker, 1941). Further analysis of the Melrose Highlands data verified these early observations and also confirmed the importance of crown class, physiological condition prior to defoliation, and the duration of defoliation episodes (Campbell and Sloan, 1977; Campbell, 1979). Mortality rates were highest among trees in the suppressed crown class and lowest among dominant trees (Table 3.2). Trees described as being in good condition prior to heavy defoliation had lower mortality rates than those classified in poor condition, and tree mortality increased with the duration of defoliation (Tables 3.2 and 3.3).

These relationships also have been observed in other regions and forest cover types subjected to gypsy moth defoliation. Crown class and crown condition were found to play a major role in defoliation-induced mortality in studies of forests in Pennsylvania, New Jersey and Rhode Island. Following two outbreaks in the Pocono Mountains of Pennsylvania, much of the observed tree mortality occurred in overstocked stands, and smaller lower quality oaks suffered the highest mortality rates (Gansner et al., 1983; Gansner et al., 1993). In mixed stands in Rhode Island more than 90 percent of all dead stems and 63 percent of the total basal area lost subsequent to defoliation was in the suppressed and intermediate crown classes (Brown et al., 1979). In oak dominated forests in New Jersey, Stalter and Serrao (1983) found that large, old trees and small suppressed trees died at the highest rates, results that were similar to those

[1] See Campbell and Valentine (1972) and Campbell and Sloan (1977) for descriptions of the original Melrose Highlands data set.

Table 3.2. Five year stem mortality rates for intermediate/suppressed and dominant trees in a composite mixed stand of oaks (*Quercus rubra*, *Q. velutina*, *Q. coccinea*, *Q. alba*) following a single heavy defoliation. From Campbell and Sloan (1977).

Crown Condition	Stem Mortality	
	Dominant	**Inter/Suppr.**
	---------------------------- % ----------------------------	
Good	3	12
Poor	22	41

Table 3.3. Crown condition and five year stem mortality rates for a composite mixed stand of oaks (*Quercus rubra*, *Q. velutina*, *Q. coccinea*, *Q. alba*) subjected to a single severe defoliation and two consecutive heavy defoliations. From Campbell and Sloan (1977).

Crown Condition	**Stem Mortality**		
	Baseline Mortality[a]	**One Defoliation**	**Two Defoliations**
	------------------------------ % ------------------------------		
Good	1	7	22
Fair	3	19	50
Poor	9	36	55

[a] Trees used for the baseline mortality estimate had not been severely defoliated for at least five years and rates were calculated at the end of an additional five year period.

observed by Kegg (1971). The duration of defoliation episodes influenced tree mortality in both a northern hardwood forest in New Jersey and southern Appalachian hardwood forests in Virginia (Kegg, 1971; Tigner, 1992). During the course of an outbreak in New Jersey, oak mortality increased with each successive defoliation, from 6 percent to 69 percent, over a four year period (Kegg, 1971). Similar results were observed by Tigner (1992) among individual stands that had experienced from zero to three defoliation episodes (Table 3.4).

Initial Stand Composition

Although we continue to classify forest trees as either susceptible or resistant to defoliation, considerable variation has been observed in field situations. In addition, intraspecific variation is often such that individual trees of the same species may experience significantly higher rates of defoliation than their neighbors (Minott and Guild, 1925; Campbell and Sloan, 1977, Gansner et al., 1993). Nevertheless, it is well documented that forest stands containing large proportions of susceptible species suffer extensive defoliation in the event of a gypsy moth outbreak. But what part does the initial species composition play in the resultant mortality that is observed?

Based on subjective observations, some authors have concluded that stands containing a high proportion of resistant species would also be less vulnerable to mortality (Kegg, 1971; Campbell and Sloan, 1977; Stephens, 1988). There are several studies in which the authors have enumerated species differences and these appear to confirm this theory. The best example of differential defoliation and mortality due to species composition is given by Brown et al. (1979),

Table 3.4. The effect of duration of defoliation episodes on oak mortality in oak-hickory forests of Clarke County and the Lee Ranger District of the George Washington National Forest, Virginia. Comparisons were made between stands experiencing either zero, one, two, or three defoliations; mortality was based on the percentage of the original oak basal area that had been killed. From Tigner (1992).

Location	**Defoliation Episodes**			
	None	**One**	**Two**	**Three**
	------------------------------------- % -------------------------------------			
Clarke County	20	23	30	50
Lee Ranger District	8	24	32	37

who studied mixed oak, oak-pine, and mixed hardwood stands in Rhode Island. The stands were defoliated four times; two heavy defoliations (60-90 percent) in 1971 and 1972, followed by two years of defoliation below 60 percent. A significant reduction in overall tree mortality was observed as the proportion of oak declined within a stand and the number of resistant species increased (Table 3.5). Stands whose original basal area contained approximately 98 percent oak experienced mortality rates that were more than three times greater than stands which originally contained only 29 percent oak. Brown et al. (1988) observed similar trends in mixed stands in Rhode Island in the early 1980's. Stands containing a large percentage of oaks had more than double the mortality of those with a large percentage of eastern white pine (Table 3.5). The primary resistant species in both cases were conifers; however, this pattern of a reduction in mortality following a reduction in the proportion of susceptible species was also observed in both northern hardwood and southwestern Pennsylvania mixed hardwood stands where the resistant species encountered were other hardwoods (Campbell and Sloan, 1977; Fosbroke and Hicks, 1989). Campbell and Sloan's (1977) analysis of the Melrose Highlands data clearly showed that the greater the percentage of oak a stand contained initially, the less total basal area that stand contained at the conclusion of the study (Figure 3.1a). Fosbroke and Hicks (1989) found that stands with less than 60 percent of their basal area in oaks had losses that were comparable to undefoliated stands, while those with more than 60 percent exhibited a distinct increase in mortality (Figure 3.1b).

It is clear that total mortality following gypsy moth defoliation will rise as the percentage of oak basal area in the stand increases (Campbell and Sloan, 1977; Brown et al. 1979; Fosbroke

Table 3.5. Total mortality as a percentage of initial stand basal area, and oak mortality as a percentage of initial oak basal area, observed in stands with varying proportions of oak basal area prior to defoliation.

Stand Type	**Initial Oak BA**	**Mortality**		**Reference**
		Oak	**Total**	
	------------------------	%	------------------------	
Mixed oak	98	18	17	Brown et al., 1979
Oak-pine	60	9	7	
Mixed hardwood	29	5	5	
Oak-pine	60	6	17	Brown et al., 1988
Pine-oak	39	4	9	
Pine	3	--	7	

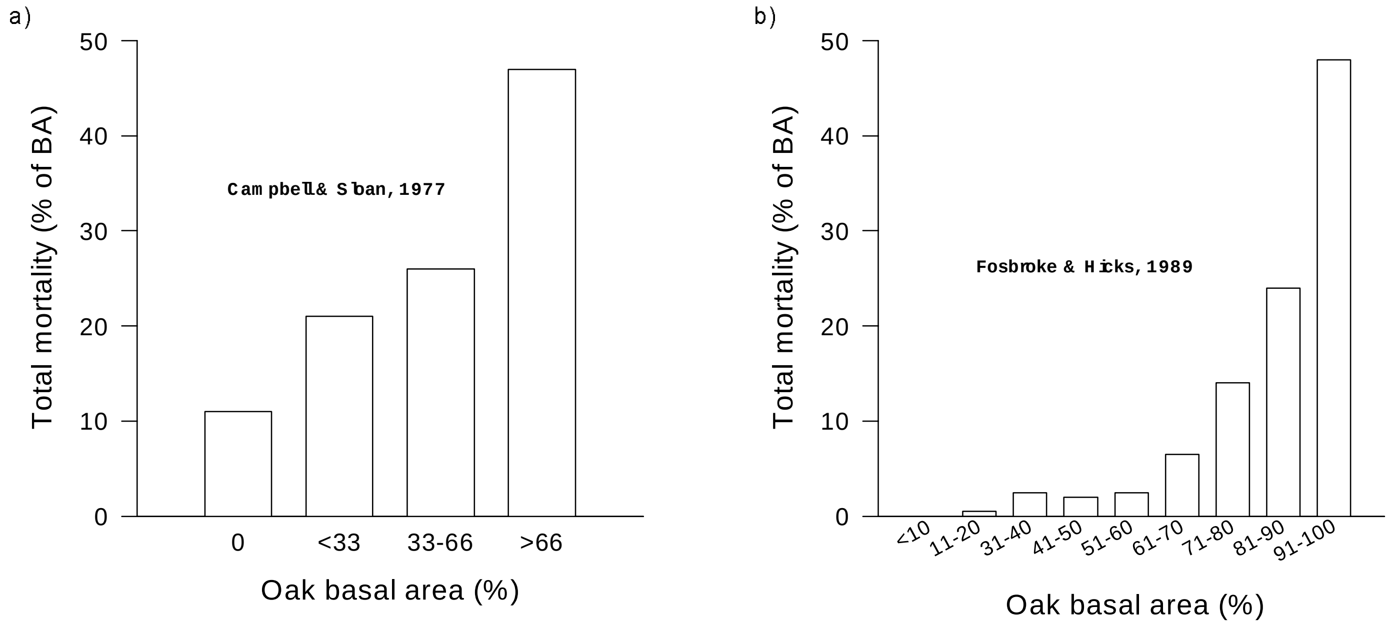

Figure 3.1: Influence of initial oak basal area on tree mortality subsequent to gypsy moth defoliation in a) forest stands in New England (Campbell and Sloan, 1977), and b) forest stands in southwestern Pennsylvania (Fosbroke and Hicks, 1989).

and Hicks, 1989). This indicates that there is an underlying relationship, and we can identify two plausible explanations (Figure 3.2). In the first case increased mortality may be attributed to changing proportions of susceptible species (i.e. the food base) affecting the dynamics of the larval population within the stand (Figure 3.2b). As the proportion of susceptible species within a stand increases there is a concomitant increase in the intensity, duration and frequency of defoliation. This in turn results in elevated species specific mortality rates and greater total mortality than would be expected based on the difference in composition. In the second case, species specific mortality rates are assumed to be independent of composition and the observed increase in mortality is simply a function of the proportion of susceptible species present as expected by the difference in composition, i.e. defoliation of a large number of susceptible species results in a large amount of mortality (Figure 3.2c). Are either of these explanations correct? Results from a number of studies, suggest that the observed differences are due to the former rather than the latter. Brown et al. (1979) found that stands comprised of 98 percent oak experienced significantly greater defoliation than stands with only 29 percent oak. Campbell and Sloan (1977) computed defoliation potentials for stands with varying proportions of oak and found a similar relationship; the greater the percentage of oak, the greater the defoliation potential. These differential defoliation rates contributed to the observed differential mortality exhibited within these stands. Brown et al. (1979) also found that in addition to differences in total mortality, species specific mortality rates also varied. Oak mortality was observed to increase as the total amount of oak increased within the stand (Table 3.5). These differences in species specific mortality rates were also observed by Brown et al. (1988), albeit on a smaller scale (Table 3.5). These results lend credence to the assertion that increased defoliation, associated with

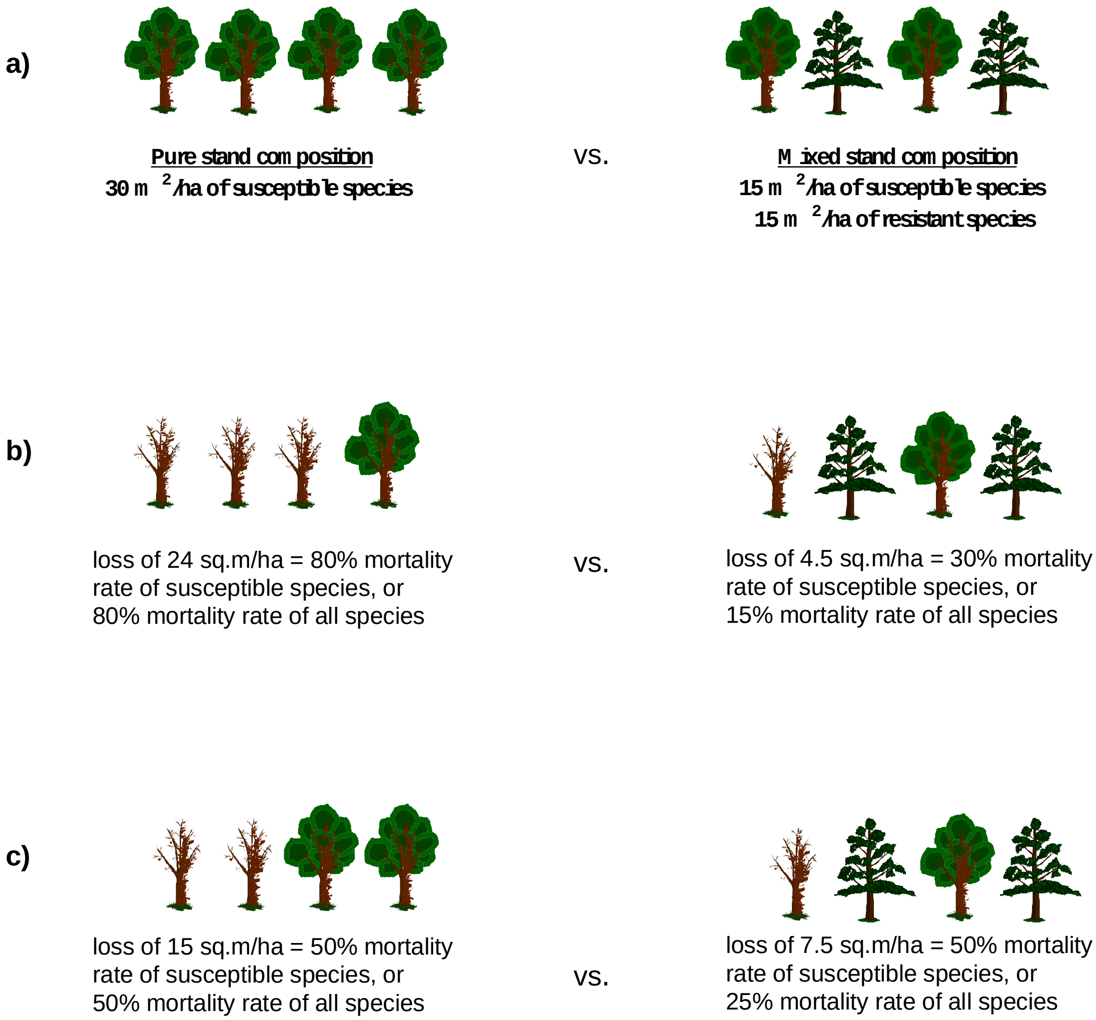

Figure 3.2: Diagram depicting the possible relationships between stand composition, defoliation and mortality rates, showing a) the original stand composition of hypothetical pure and mixed stands prior to defoliation; b) due to a greater proportion of susceptible species in the pure stand, defoliation intensity, duration and frequency increase, resulting in an elevated species specific mortality rate and total mortality greater than that expected based on difference in composition; i.e. total mortality (pure stand) = 2 x total mortality (mixed stand); c) following defoliation overall species specific mortality rates are the same in both stands, but due to a larger total initial basal area of susceptible species, the pure stand has a greater total amount of mortality; but this is expected based on the difference in composition.

greater amounts of susceptible species, results in elevated species specific mortality rates and thus greater total mortality (Figure 3.1b).

Effect Of Site Quality On Tree Mortality

Site quality has been postulated as a primary component of the complex that determines mortality rates following gypsy moth defoliation. Attributing significance to the individual factors that define site quality is difficult. This is due in part to the fact that references to possible relationships to tree mortality are often unclear; but it is also a result of correlation's between site conditions and resultant stand composition. Localized moisture limitations may result in some sites being dominated by xerophytic species that are susceptible to defoliation, such as chestnut oak (*Q. prinus* L.) and scarlet oak (*Q. coccinea* Muenchh.) (Smith, 1994). On some high quality sites, conifers may be excluded due to their limited ability to compete with hardwoods, resulting in susceptible species dominating the site. Determining whether mortality subsequent to defoliation can be attributed to pre-defoliation site conditions, or whether observed differences are simply an artifact of the influence of site on species composition is therefore difficult.

References to possible relationships between site condition and tree mortality can be found throughout the literature. However, in many cases a qualitative rather than a quantitative description of site quality was used. These descriptions of good and poor sites, though common, can be misleading; for instance, very dry and very wet sites are dramatically different, but they both may be described as poor. The use of site index to separate different sites provides us with a better tool to examine gypsy moth influence and facilitates comparisons between different studies.

The studies listed in Table 3.6 either provided site index measurements, or gave sufficient information for us to approximate site index.

Brown et al. (1979) used Bess et al.'s (1947) site descriptions to characterize the mixed stands they were studying as either susceptible or resistant to gypsy moth defoliation. Though they did not otherwise distinguish between sites in their article, the authors provided both the age and height of dominant and codominant oaks, which allowed for the estimation of site index for two of their study sites (Brown et al., 1979; Schnur, 1937). Their results showed that oak mortality and total mortality were greater on the poor quality site (SI 13.7-15.2) than on the good quality site (SI 15.2-16.8). This pattern was also observed by Fosbroke and Hicks (1989) in southwestern Pennsylvania, where the difference in total mortality between sites with SI <18.3 and those with SI >21.3 was 12 percent. Although no quantitative measure of site quality was given, Keggs' (1971, 1973) studies in New Jersey demonstrated a similar trend in mortality due to a gradient in site quality.

In apparent contradiction to the studies described above, some authors have observed greater mortality rates on high quality sites than on low quality sites. Gansner (1987) observed that on high (SI ≥ 22.9) and medium (SI 16.8-22.8) quality sites in central Pennsylvania, both total stand mortality and oak mortality were greater than on low quality sites (SI <16.8). Gansner proposed two explanations for his observations; the first was that trees on poor sites were physiologically better adapted to endure stresses such as defoliation. This is consistent with the results of Stalter and Serrao (1983), who compared mortality of northern red oak (*Q. rubra* L.)

Table 3.6. Mortality subsequent to gypsy moth defoliation observed within forest stands growing on sites of varying productivity; total mortality is expressed as a percentage of initial stand basal area (or stem density), oak mortality is expressed as a percentage of initial oak basal area (or stem density).

Site Index[a]	**Basis of Mortality Estimate**	**Mortality**		**Reference**
		Oak	**Total**	
-------- m --------		--------- % ---------		
13.7 - 15.2	BA	18	17	Brown et al., 1979
15.2 - 16.8	BA	9	7	
< 16.8	Stems	18	14	Gansner, 1987
16.8 - 22.8	Stems	26	21	
≥ 22.9	Stems	28	21	
< 16.8	BA	13	12	Gansner, 1987
16.8 - 22.8	BA	23	20	
≥ 22.9	BA	24	19	
< 18.3	Stems	--	26	Fosbroke & Hicks, 1989
18.3 - 21.3	Stems	--	16	
> 21.3	Stems	--	14	

[a] Site indices for Fosbroke and Hicks (1989) are based on equations from Wiant and Lamson (1983), all other site indices are based on equations from Schnur (1937).

on dry and mesic sites and observed lower mortality on the dry site. The second explanation was that secondary agents such as *Armillaria* and *Agrilus bilineatus* are less active on poor sites. However, there does not appear to be much evidence to support this theory. In fact, the opposite appears to be true, with pathogenicity of *Armillaria* increasing with reductions in site quality (Kile et al., 1991). Also, Dunbar and Stephens (1975) found that *A. bilineatus* played a major role in oak mortality on sites that were located on dry ridges, and upper slopes with thin rocky soils. A third possibility is the effect of an abnormal reduction in soil moisture. Pennsylvania experienced several years of below average rainfall during the early 1980's, the period during which the data analyzed by Gansner (1987) was collected (Quimby, 1991). The effects of this prolonged reduction in soil moisture were probably much greater on high quality mesic sites than on poor quality xeric sites. Consequently, defoliation on the high quality sites may have had a much greater than normal influence on subsequent tree mortality during this time period.

While site differences often appear to result in differential mortality rates, they do not follow a consistent pattern and involve a complex system of interacting factors. Intuitively it seems probable that trees on sites with a low site index would suffer greater mortality than those trees growing on high quality sites. As noted in the literature, however, the opposite is sometimes true. Much of this inconsistency has been ascribed to differences in species composition and physiological condition (Gansner, 1987). Though trees growing on sites with low site index may not initially be as vigorous as those growing on better sites, some authors believe that because they are adapted to adverse conditions they may be better able to tolerate defoliation-induced stress (Stalter and Serrao, 1983). Thus, when trees on high quality sites are subjected to drought, frost, or some other perturbation, and are subsequently defoliated, these individuals suffer higher rates of mortality. Other authors have concluded that their results were due more to site factors influencing stand composition rather than a direct site/mortality relationship. Fosbroke and Hicks (1989) attributed their results to the fact that the oak component was greatest on poor sites. Brown et al. (1988) demonstrated that, in three mixed stands in Rhode Island, mortality appeared to be independent of site and wholly dependent on species composition. The authors stated that the three stand types occurred on similar sites (SI < 18.3 for oaks), but both oak mortality and total mortality were observed to increase with increased oak basal area.

Tree Mortality in Initial and Subsequent Outbreaks

A distinction is often made between areas that are on the leading edge of the gypsy moth infestation, and those that are in what is commonly called the generally infested area. While outbreaks occur in both situations, the effects of the outbreaks have been observed to differ; the implication being that initial outbreaks associated with the leading edge are more devastating than subsequent outbreaks (Campbell, 1979).

Because it is an introduced insect, the dearth of natural predators and parasites of the gypsy moth has been forwarded as one reason that sustained outbreaks are more prevalent and more destructive along the leading edge than within the generally infested area (McManus, 1987). Others attribute these differences to shifts in species composition due to inter- and intraspecific susceptibility to defoliation (Brown and Sheals, 1944; Campbell and Sloan, 1977). The latter theory is bolstered by the results of recent studies which have demonstrated both local adaptation to generalized herbivory (in the form of resistance), and within-population variation (family differences) in red oak seedling response to gypsy moth defoliation (Sork et al., 1993; Byington et al., 1994). Based on previous observations, another logical explanation is shifts in composition due to differences in vulnerability (Campbell and Sloan, 1977). During an initial outbreak, defoliation results in mortality of the most vulnerable trees within a stand; these are frequently suppressed and intermediate individuals of susceptible species, and those upper canopy trees that are in poor condition or have previously experienced some other form of stress (Kegg, 1971; Campbell and Sloan, 1977; Stalter and Serrao, 1983). During subsequent outbreaks total stand mortality is reduced because these highly vulnerable trees have already been removed and less vulnerable individuals remain (Kegg, 1971; Brown et al, 1988).

The previous observations are borne out by the results of an examination of two groups of defoliated stands (Table 3.7). Several established studies were separated into two groups of predominantly oak stands, those that could be considered initial outbreaks and those that fell into the category of subsequent outbreaks. When the individual studies within each group were combined, oak mortality in initial outbreaks averaged 20 percent, while in subsequent outbreaks oak mortality averaged only 7 percent. When tested using a two-sample t-test (SAS, 1992) this difference proved to be significant (p=0.0727). This provides strong evidence that differences between the two situations are due to the loss of susceptible oaks in initial outbreaks. A visual examination of total mortality rates indicated that the initial outbreaks also experienced greater mean total basal area mortality than the subsequent outbreaks (Table 3.7). However, in this case the null hypothesis that the means of the two groups were equal could not be rejected (p=0.3027).

Table 3.7. Total mortality in predominantly oak stands following an initial gypsy moth outbreak, and following subsequent outbreaks; total mortality is expressed as a percentage of initial stand basal area (or stem density), oak mortality is expressed as a percentage of initial oak basal area (or stem density).

Stand or Forest Type(s)	Basis of Mortality Estimate	Mortality		Reference
		Oak	Total	
Initial Outbreaks		-------- % --------		
Oak	Stems	--	43	Kegg, 1973, 1974
Oak	BA	--	12	Gansner et al., 1993
MIxed oak	BA	35	47	Campbell & Sloan, 1977
Mixed oak	BA	18	17	Brown et al.,1979
Oak-pine	BA	9	7	Brown et al., 1979
Mixed hardwood	BA	17	24	Stephens & Ward, 1992
	mean	20	21	
	std. dev.	10.9	15.6	
Subsequent Outbreaks				
Oak	Stems	--	13	Gansner et al., 1983
Oak	BA	13	10	Gansner et al., 1993
Mixed hardwood	BA	6	15	Stephens & Ward, 1992
Mixed hardwood	BA	3	10	Stephens & Ward, 1992
Oak-white pine	BA	6	17	Brown et al., 1988
	mean	7	13	
	std. dev.	4.2	3.6	

Though differences in total mortality were not statistically significant, the results from a number of studies indicate that differences between the two situations can be quantified. The situation described by Gansner et al. (1993) in the Pocono mountain region of Pennsylvania is one example. This area experienced two gypsy moth outbreaks between 1970 and 1990. The first episode (1972 to 1976) resulted in a cumulative mortality loss of 12 percent of the 1972 stand volume. Following the second outbreak (1978-89), 10 percent of the 1978 stand volume had been killed. Similar results were noted in Connecticut forests by Stephens and Ward (1992) who observed a 9 percent reduction in total mortality between the first and second gypsy moth outbreaks, and a 5 percent reduction between the second and third outbreaks. Gypsy moth damage appraisal surveys of the state of Pennsylvania provided an opportunity to examine these trends on a regional basis. Surveys were carried out in 1984, 1987, and 1990, and included areas that had suffered an outbreak in the preceding three year period (Quimby, 1991). As shown in Figure 3.3, the total area affected by defoliation varied considerably between surveys. However, the portion of the defoliated area that was actually affected by moderate or heavy tree mortality has steadily fallen. Quimby (1991) attributed these differences to above-average rainfall during 1989 and 1990. However, this does not adequately explain the reduction in mortality that was observed between 1984 and 1987, and it is likely that loss of vulnerable species in the initial outbreak is the most probable cause.

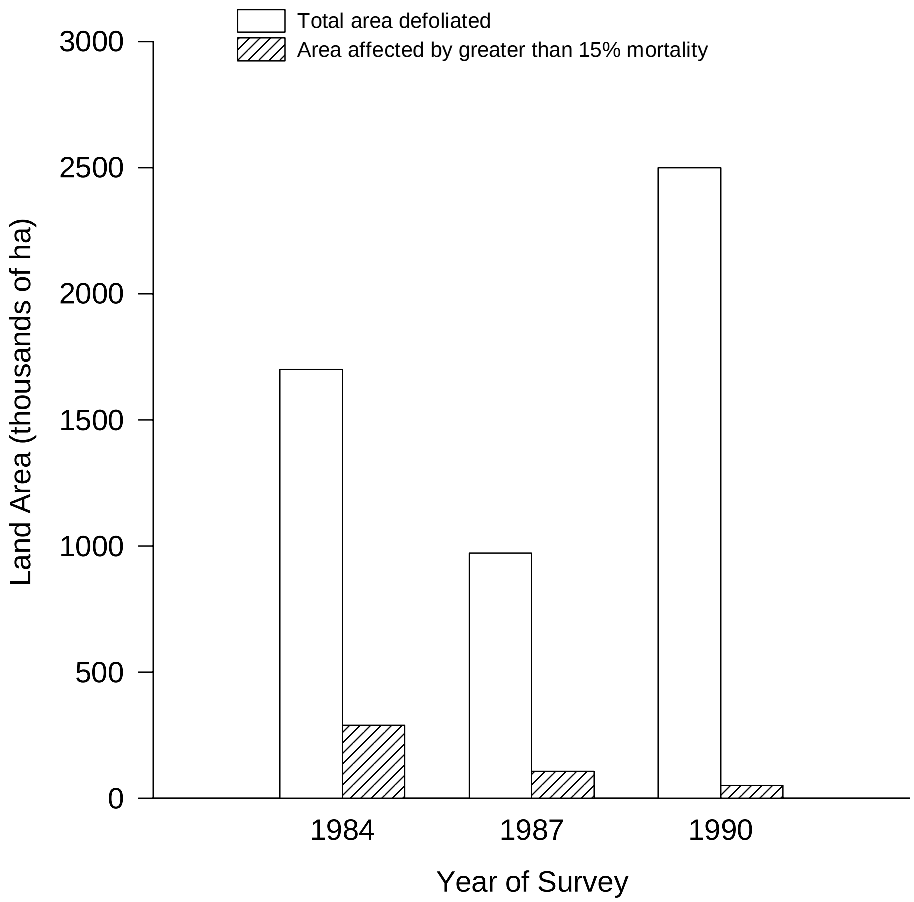

Figure 3.3: Total area defoliated and area sustaining more than 15 percent tree mortality in Pennsylvania; surveys were carried out in 1984, 1987, and 1990, and included the year of the survey and the two preceding years. From Quimby (1991).

SUMMARY

In conclusion, the effect of gypsy moth defoliation on tree growth and mortality continues to be of great interest to both foresters and entomologists. Though numerous studies have been carried out, many questions remain. There can be no doubt that the dynamics of defoliation in mixed stands of susceptible and resistant species is different from that of pure stands of susceptible species; and it appears that there is a direct relationship between the proportion of susceptible species within a stand and subsequent tree mortality. Increasing proportions of susceptible species result in greater intensity, frequency and duration of defoliation episodes, and thus greater total and species specific mortality. In reference to site quality, although the studies that were examined clearly demonstrated that total mortality rates are not the same across all sites, the observed differences have not been consistent. Differences in mortality do not appear to be a direct result of site quality; there is however, a strong probability that site quality indirectly influences mortality rates through its effect on species composition and therefore defoliation. Observed differences between initial and subsequent outbreaks appear to be primarily influenced by the previously described relationship between stand composition and tree mortality. Losses of large numbers of vulnerable oaks and lower canopy species during the initial outbreak increased stand resistance, resulting in reduced mortality rates during subsequent outbreaks. In addition the possibility that selection effects are also present cannot be discounted. While the studies that were reviewed described different regions, and may have experienced different defoliation patterns, the average species specific mortality rate of those categorized as initial outbreaks was consistently greater than those experiencing subsequent outbreaks. This review points out the need for the establishment of long-term replicated studies in order to adequately test some of the questions raised here.

LITERATURE CITED

Baker, W.L. 1941. Effect of gypsy moth defoliation on certain forest trees. J. For. 39:1017-1022.

Baker, W.L., and A.C. Cline. 1936. A study of the gypsy moth in the town of Petersham, Mass., in 1935. J. For. 34:759-765.

Bess, H.A., S.H. Spurr, and E.W. Littlefield. 1947. Forest site conditions and the gypsy moth. Bull. No.22. Petersham, MA: Harvard Forest. 56 p.

Blodgett, J.T., and J.J. Worrall. 1992. Distributions and hosts of Armillaria species in New York. Plant Disease. 76 (2):166-170.

Brown, J.H., D.B. Halliwell, and W.P. Gould. 1979. Gypsy moth defoliation: impact in Rhode Island forests. J. For. 77:30-32.

Brown, J.H., V.B. Cruickshank, W.P. Gould, and T.P. Husband. 1988. Impact of gypsy moth defoliation in stands containing white pine. North. J. Appl. For. 5:108-111.

Brown, R.C., and R.A. Sheals. 1944. The present outlook on the gypsy moth problem. J. For. 42:393-407.

Byington, T.S., K.W. Gottschalk, and J.B. McGraw. 1994. Within-population variation in response of red-oak seedlings to herbivory by gypsy moth larvae. Am. Midl. Nat. 132:328-339.

Campbell, R.W. 1979. Gypsy moth: forest influence. USDA Agric. Inf. Bull. 423. 44 p.

Campbell, R.W., and R.J. Sloan. 1977. Forest stand responses to defoliation by the gypsy moth. For. Sci. Monogr. 19. 34 p.

Campbell, R.W., and H.T. Valentine. 1972. Tree condition and mortality following defoliation by the gypsy moth. USDA For. Serv. Res. Pap. NE-236. 331 p.

Clement, G.E., and W. Munro. 1917. Control of the gypsy moth by forest management. USDA Agric. Inf. Bull. 484. 54 p.

Dunbar, D.M., and G.R. Stephens. 1975. Association of twolined chestnut borer and shoestring fungus with mortality of defoliated oak in Connecticut. For. Sci. 21:169-174.

Dunn, J.P., T.W. Kimmerer, and G.L. Nordin. 1986. Attraction of the twolined chestnut borer, *Agrilus bilineatus* (Weber) (Coleoptera: Buprestidae), and associated borers to volatiles of stressed white oak. Can. Entom. 118(6):503-509.

Dunn, J.P., T.W. Kimmerer, and D.A. Potter. 1987. Winter starch reserves of white oak as a predictor of attack by the twolined chestnut borer, *Agrilus bilineatus* (Weber) (Coleoptera: Buprestidae). Oecologia. 74:352-355.

Dunn, J.P., D.A. Potter, and T.W.Kimmerer. 1990. Carbohydrate reserves, radial growth, and mechanisms of resistance of oak trees to phloem-boring insects. Oecologia. 83:458-468.

Forbush, E.H., and C.H. Fernald. 1896. The gypsy moth. Wright & Potter, Boston. 495 p.

Fosbroke, D.A., and R.R. Hicks, Jr. 1989. Tree mortality following gypsy moth defoliation in southwestern Pennsylvania. P. 74-80 *in* Proc. 7th Central Hardwood Forest Conf., Rink,G., and C.A. Budelsky (eds.). USDA For. Serv. Gen. Tech. Rep. NC-132.

Gansner, D.A. 1987. Site productivity and tree mortality on new frontiers of gypsy moth infestation. USDA For. Serv. Res. Note. NE-340. 3 p.

Gansner, D.A., O.W. Herrick, P.S. DeBald, and R.E. Acciavatti. 1983. Changes in forest condition associated with gypsy moth. J. For. 81(3):155-157.

Gansner, D.A., S.L. Arner, R.H. Widmann, and C.L. Alerich. 1993. After two decades of gypsy moth, is there any oak left? North. J. Appl. For. 10(4):184-186.

Gottschalk, K.W. 1993. Silvicultural guidelines for forest stands threatened by the gypsy moth. USDA For. Serv. Gen. Tech. Rep. NE-171. 50 p.

Gottschalk, K.W., and M.J. Twery. 1989. Gypsy moth impacts in pine-hardwood mixtures. P. 50-58 *in* Proc. Pine-Hardwood Mixtures: A Symp. on Management and Ecology of the Type, Waldrop, T.A. (ed.). USDA For. Serv. Gen. Tech. Rep. SE-58.

Houston, D.R. 1981. Mortality and factors affecting disease development. P. 281-293 *in* The gypsy moth: Research toward integrated pest management, Doane, C.C., and M.L. Mcmanus (eds.). USDA For. Serv. Tech. Bull. 1584. 757 p.

Houston, D.R., and H.T. Valentine. 1977. Comparing and predicting forest stand susceptibility to gypsy moth. Can. J. For. Res. 7:447-461.

Houston, D.R., and H.T. Valentine. 1985. Classifying forest susceptibility to gypsy moth defoliation. USDA Agric. Handbook 542. 19 p.

Kegg, J.D. 1971. The impact of gypsy moth: Repeated defoliation of oak in New Jersey. J. For. 69:852-854.

Kegg, J.D. 1973. Oak mortality caused by repeated gypsy moth defoliations in New Jersey. J. Econ. Entomol. 66(3):639-641.

Kegg, J.D. 1974. Quantitative classification of forest stands as related to their vulnerability to loss following initial outbreak of the gypsy moth, *Porthetria dispar* (L.), with equations for forecasting basal area losses. M.S. Thesis, Rutgers University. 36 p.

Kile, G.A., G.I. McDonald, and J.W. Byler. 1991. Ecology and disease in natural forests. P. 102-121 *in* Armillaria root disease, Shaw, C.G. III., and G.A. Kile (eds.). USDA For. Serv. Agric. Handbook 691. 233 p.

Korstian, C.F., and A.G. Ruggles. 1941. Report of findings and recommendations with reference to the gypsy moth project of the Bureau of Entomology and Plant Quarantine. J. For. 39:973-979.

Kozlowski, T.T., P.J. Kramer, and S.G. Pallardy. 1991. The physiological ecology of woody plants. Academic Press Inc., Harcourt Brace Jovanovich, San Diego. 657 p.

Kulman, H.M. 1971. Effects of insect defoliation on growth and mortality of trees. Ann. Rev. Entom. 16:289-324.

Liebhold, A.M., K.W. Gottschalk, R.M. Muzika, M.E. Montgomery, R. Young, K. O'Day, and B. Kelley. 1995. Suitability of North American tree species to the gypsy moth: a summary of field and laboratory tests. USDA For. Serv. Gen. Tech. Rep. NE-211. 45 p.

McManus, M.L. 1987. The gypsy moth problem: history, biology, spread. P. 1-10 *in* Proc. Coping with the gypsy moth in the new frontier: a workshop for forest managers. Fosbroke, S., and R.R. Hicks (eds.). West Virginia Univ. Books, Morgantown. 153 p.

Minott, C.W., and I.T. Guild. 1925. Some results of the defoliation of trees. J. Econ. Entomol. 18:345-348.

Montgomery, M.E. 1991. Variation in the suitability of tree species for the gypsy moth. P. 1-13 *in* Proc. U.S. Department of Agriculture Interagency Gypsy Moth Research Review 1990. Gottschalk, K.W., M.J. Twery, and S.I. Smith (eds.). USDA For. Serv. Gen. Tech. Rep. NE-146. 152 p.

Mosher, F.H. 1915. Food plants of the gypsy moth in America. USDA Agric. Inf. Bull. 250. 39 p.

Nichols, J.O. 1968. Oak mortality in Pennsylvania. J. For. 66:681-694.

Parker, J. 1981. Effects of defoliation on oak chemistry. P. 219-225 *in* The gypsy moth: Research toward integrated pest management, Doane, C.C., and M.L. Mcmanus (eds.). USDA For. Serv. Tech. Bull. 1584. 757 p.

Parker, J., and D.R. Houston. 1971. Effects of repeated defoliation on root and root collar extractives of sugar maple trees. For. Sci. 17(1):91-95.

Quimby, J.W. 1987. Impact of gypsy moth defoliation on forest stands. P. 21-29 *in* Proc. Coping with the gypsy moth in the new frontier: a workshop for forest managers. Fosbroke, S., and R.R. Hicks (eds.). West Virginia Univ. Books, Morgantown. 153 p.

Quimby, J.W. 1991. Tree mortality following gypsy moth epidemics - 1990. Pennsylvania Bureau of Forestry, Division of Forest Pest Management Report. 50 p.

SAS Institute. 1992. SAS/STAT[7] Users Guide Volume 2, GLM-VARCOMP, Version 6, Fourth edition. SAS Institute, Cary, NC. p.891-996.

Schnur, G.L. 1937. Yield, stand, and volume tables for even-aged upland oak forests. USDA Tech. Bull. 560. 87 p.

Smith, D.W. 1994. The southern Appalachian hardwood region. P. 173-225, *in* Regional Silviculture of the United States, 3rd ed. Barrett. J.W. (ed). John Wiley and Sons, New York.

Sork, V.L., K.A. Stowe, and C. Hochwender. 1993. Evidence for local adaption in closely adjacent subpopulations of northern red oak (*Quercus rubra* L.) expressed as resistance to leaf herbivores. Am. Nat. 142(6):928-936.

Staley, J.M. 1965. Decline and mortality of red and scarlet oaks. For. Sci. 11(1):2-17.

Stalter, R., and J. Serrao. 1983. The impact of defoliation by gypsy moths on the oak forest at Greenbrook Sanctuary, New Jersey. Bull. Torrey Bot. Club. 110(4):526-529.

Stephens, G.R. 1988. Mortality, dieback and growth of defoliated hemlock and white pine. North. J. Appl. For. 5:93-96.

Stephens, G.R., and J.S. Ward. 1992. Sixty years of natural change in unmanaged mixed hardwood forests. Conn. Agric. Exp. Stn. Bull. 902. 63 p.

Tigner, T. 1992. Gypsy moth impact on Virginia's hardwood forests and forest industry. Virginia Dept. of Forestry, Charlottesville, VA. 36 p.

Turner, N. 1963. Effect of defoliation by the gypsy moth. Conn. Agric. Exp. Stn. Bull. 658. 30 p.

Twery, M.J. 1991. Effects of defoliation by gypsy moth. P.27-39 *in* Proc. U.S. Department of Agriculture Interagency Gypsy Moth Research Review 1990. Gottschalk, K.W., M.J. Twery, and S.I. Smith (eds.). USDA For. Serv. Gen. Tech. Rep. NE-146. 152 p.

Twery, M.J., G.N. Mason, P.M. Wargo, and K.W. Gottschalk. 1990. Abundance and distribution of rhizomorphs of *Armillaria* spp. in defoliated mixed oak stands in western Maryland. Can. J. For. Res. 20:674-678.

Wargo, P.M. 1972. Defoliation-induced chemical changes in sugar maple roots stimulate growth of *Armillaria mellea*. Phytopathology. 62:1278-1283.

Wargo, P.M. 1977. *Armillariella mellea* and *Agrilus bilineatus* and mortality of defoliated oak trees. For. Sci. 23(4):485-492.

Wargo, P.M. 1981a. Defoliation and secondary-action organism attack: with emphasis on *Armillaria mellea*. J. Arbor. 7(3):64-69.

Wargo, P.M. 1981b. Defoliation and tree growth. P. 225-240 *in* The gypsy moth: Research toward integrated pest management, Doane, C.C., and M.L. Mcmanus (eds.). USDA For. Serv. Tech. Bull. 1584. 757 p.

Wargo, P.M. and D.R. Houston. 1974. Infection of defoliated sugar maple trees by *Armillaria mellea*. Phytopathology 64:817-822.

Wargo, P.M. and T.C. Harrington. 1991. Host stress and susceptibility. P. 88-101 *in* Armillaria root disease, Shaw, C.G. III., and G.A. Kile (eds.). USDA For. Serv. Agric. Handbook 691. 233 p.

Watling, R., G.A. Kile, and H.H. Burdsall, Jr. 1991. Nomenclature, taxonomy, and identification. P 1-9 *in* Armillaria root disease, Shaw, C.G. III., and G.A. Kile (eds.). USDA For. Serv. Agric. Handbook 691. 233 p.

Wiant, H.V. Jr., and N.I. Lamson. 1983. Site index equations for even-aged oak stands in northwestern West Virginia. West Virginia For. Notes. 10:11-12.