
Tree Mortality Following Defoliation by the European Gypsy Moth (*Lymantria dispar* L.) in the United States: A Review

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ABSTRACT. This review presents information related to defoliation by the European gypsy moth (*Lymantria dispar* L.) and subsequent tree mortality in the eastern United States. The literature describing defoliation-induced tree mortality is extensive, yet questions still remain concerning (1) the association between initial stand composition and subsequent tree mortality, (2) the influence of site quality on tree mortality, and (3) observed differences between mortality rates in initial and subsequent outbreaks. Our review and analysis of the available literature indicates that initial species composition affects subsequent defoliation. Stands with predominantly susceptible host species have higher levels of species-specific and total mortality than mixed stands of susceptible, resistant, and immune host species. Differences in mortality on sites of varying productivity do not appear to be a direct result of site quality; rather, site quality indirectly influences mortality rates through its effect on species composition and therefore defoliation. Differences between initial and subsequent outbreaks appear to be due primarily to losses of vulnerable oaks and lower canopy species during the initial outbreak; oak mortality in initial outbreaks was found to be significantly greater ($P = 0.0727$) than oak mortality in subsequent outbreaks. *FOR. SCI.* 45(1):74–84.

Additional Key Words: Defoliation effects, vulnerability, stand dynamics, Lepidoptera, Lymantriidae.

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 north-central forests of North America. From its first introduction in 1869 to the early 1960s, defoliation episodes were concentrated in the northern hardwood and oak forests of New England and the Mid-Atlantic states. However, population expansion has continued to bring the insect into contact with stand types that have never been subjected to a gypsy moth outbreak. Like other defoliators, the primary effects of gypsy moth feeding on trees are reductions in tree growth, 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.

Defoliators are endemic within forest ecosystems; however, the gypsy moth is unique because of its exotic pest status, polyphagous habit, and the increased potential for extensive defoliation when compared to native defoliators (Crow and Hicks 1990, Liebhold et al. 1994). The gypsy moth is an outbreak species. Population densities are cyclical and are characterized by extended periods of low density, sudden, rapid increases to high densities which can be sustained over an extended period, followed by subsequent population crashes (Montgomery and Wallner 1988). During these periods of population expansion, extensive areas of forested land may experience defoliation and associated tree mortality.

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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. In reality, larval feeding preference is a continuum, dependent on 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 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 (Bess et al. 1947). Previous 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 (Campbell and Sloan 1977). 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, 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 reductions in the number of susceptible species also lowers stand vulnerability remains to be seen.

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

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 are also more vulnerable. 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 in rates of tree mortality have been observed between areas experiencing initial outbreaks as a result of new introductions, and those experiencing subsequent outbreaks from established populations. 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 (Kegg 1971, 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, our objective 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 United States.

Factors Influencing Tree Mortality Following Defoliation

The etiology of individual tree mortality subsequent to insect defoliation is extremely complex. Therefore, it is

prudent to review the relevant factors in detail before a discussion of the effects of gypsy moth defoliation. Whether a tree succumbs to mortality, or merely experiences a short-term reduction in growth increment following defoliation depends on 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 *Agilus 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 successive defoliations 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 depended on 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% defoliation (*light*), 30 to 60% defoliation (*moderate*), or greater than 60% (*heavy*) (Gottschalk 1993). Light defoliation generally results in minimal visual or physiological damage, while moderate and heavy defoliation may cause heavy damage. The duration of defoliation refers to the number of consecutive defoliation episodes that occur in a given time period, while 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 4 to 5 yr or every 10 to 12 yr). As the number of consecutive episodes increases, the probability of tree mortality rises (Campbell and Sloan 1977). Heavy defoliation frequently occurs as a single event during a gypsy moth defoliation outbreak; however, 2 or even 3 yr of heavy defoliation have been recorded (Kegg 1973, Tigner 1992, Davidson 1997). Following a single heavy defoliation in oak-hickory forests in Virginia, Tigner (1992) reported 23% oak mortality; two defoliation episodes increased this figure to 30%, and after three defoliation episodes, oak mortality averaged 50%.

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 (Schowalter et al. 1986). Baker (1941) found that when eastern white pine (*Pinus strobus* L.) defoliation exceeded 80%, tree mortality was nearly three times greater than that of trees defoliated less than 80%. Possible mechanisms for the differing responses to defoliation observed in

hardwoods and conifers have focused on patterns of carbon storage and foliage loss and replacement. While deciduous species tend to store the majority of their carbon in woody tissues, evergreen conifers also utilize their needles for carbon storage (Kulman 1971, Krause and Raffa 1996). Therefore defoliation of evergreen conifers results in a greater loss of stored energy and a higher probability of mortality following defoliation (Kulman 1971, Krause and Raffa 1996, Schowalter et al. 1986). In addition, unlike deciduous hardwoods, conifers are not adapted to rapid leaf turnover and this may contribute to their inability to withstand complete or consecutive defoliation episodes (Schowalter et al. 1986).

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% of living trees and 96% of dead or dying trees (Wargo 1977). In addition, recent studies in Michigan have revealed that *Armillaria* plays a key role in the mortality of quaking aspen (*Populus tremuloides* Michx.) following gypsy moth defoliation (Hart 1990). Historically, many authors

have described the species responsible for oak mortality as *Armillaria mellea* (Vahl, Quel.), but 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 34 tree species examined, hardwoods were predominantly infected with *A. gallica*, *A. gemina* Bérubé & Dessureault, and *A. calvescens* Bérubé & Dessureault; when oaks were separated from other hardwoods, *A. gallica* occurred on approximately 90% 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 importance of one over the other cannot be distinguished (Wargo 1977).

From the preceding discussion it is obvious that tree death cannot be attributed to defoliation alone. The probability of mortality depends on 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

In the eastern United States, 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 [see Campbell and Valentine (1972) and Campbell and Sloan (1977) for descriptions of the original Melrose Highlands data set] 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 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 2 and 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% of all dead stems and 63% of the total basal area lost subsequent to defoliation were 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 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% to 69%, over a 4 yr period (Kegg 1971).

Initial Stand Composition

Although we continue to classify forest trees as either susceptible or resistant to defoliation, considerable variation

Table 2. Five-year stem mortality rates, following a single heavy defoliation, of dominant and intermediate/suppressed trees in a composite mixed stand of mature oaks (*Quercus rubra*, *Q. velutina*, *Q. coccinea*, *Q. alba*) in eastern New England.¹ From Campbell and Sloan (1977).

Crown condition	Stem mortality (%)	
	Dominant	Intermediate/suppressed
Good	3	12
Poor	22	41

¹ The composite mixed oak stand consisted of data that was summarized from 122 plots that were measured between 1911 and 1921.

Table 3. Crown condition and 5 yr stem mortality rates following a single severe defoliation and two consecutive heavy defoliations in a composite mixed stand of mature oaks (*Quercus rubra*, *Q. velutina*, *Q. coccinea*, *Q. alba*) in eastern New England.¹ From Campbell and Sloan (1977).

Crown condition	Stem mortality (%)		
	Baseline mortality ²	One defoliation	Two defoliations
Good	1	7	22
Fair	3	19	50
Poor	9	36	55

¹ The composite mixed oak stand consisted of data that was summarized from 122 plots that were measured between 1911 and 1921.

² Trees used for the baseline mortality estimate had not been severely defoliated for at least 5 yr, and rates were calculated at the end of an additional 5 yr period.

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), who studied mixed oak, oak-pine, and mixed hardwood stands in Rhode Island. The stands were defoliated four times; two heavy defoliations (60–90%) in 1971 and 1972, followed by 2 yr of defoliation below 60%. 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 4). Stands whose original basal area contained approximately 98% oak experienced mortality rates that were more than three times greater than stands which originally contained only 29% oak. Brown et al. (1988) observed similar trends in mixed stands in Rhode Island in the early 1980s. Stands containing a large percentage of oaks had more than double the mortality of those with a large percentage of eastern white pine (Table 4). 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 between 1911 and 1921 clearly showed that reductions in the proportion of susceptible oaks within a stand reduced total mortality (Figure 1a). Fosbroke and Hicks (1989) found that stands with less than 60% of their basal area

Table 4. Total mortality as a percentage of initial stand basal area, and oak mortality as a percentage of initial oak basal area, observed in Rhode Island forest stands with varying proportions of oak basal area prior to defoliation.

Stand type	Oak BA (%)	Mortality (%)		Reference
		Oak	Total	
Mixed oak	98	18	17	Brown et al. 1979 ¹
Oak-pine	60	9	7	
Mixed hardwood	29	5	5	
Oak-pine	60	6	17	Brown et al. 1988 ²
Pine-oak	39	4	9	
Pine	3	—	7	

¹ Number of study plots was not given; study period was 1971 to 1975.

² n = 18 plots; study period was 1981 to 1983.

in oaks had losses that were comparable to undefoliated stands, while those with more than 60% exhibited a distinct increase in mortality (Figure 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 and Hicks 1989). This indicates that there is an underlying relationship, and we can identify two plausible explanations (Figure 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 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 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% oak experienced significantly greater defoliation than stands with only 29% 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 4). These differences in species specific mortality rates were also observed by Brown et al. (1988), albeit on a smaller scale (Table 4). Brown et al. (1988) also noted that the mortality of resistant white pine was greatest in stands with a large percentage of oaks, where the pine occurred as an understory species. Increasing mortality of resistant species as a result of

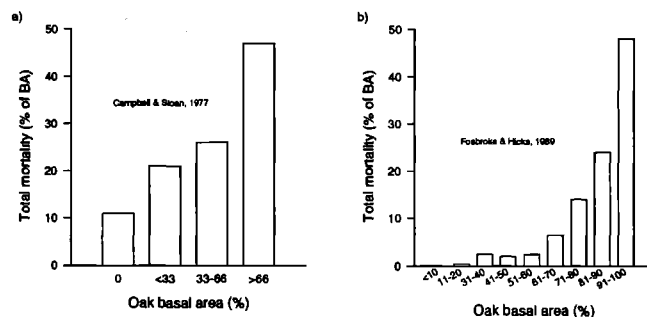


Figure 1. Influence of initial oak basal area on tree mortality subsequent to gypsy moth defoliation in (a) mixed oak stands in New England, data was obtained from 122 plots (Campbell and Sloan 1977); and (b) mixed hardwood stands in southwestern Pennsylvania, data was obtained from 237 plots (Fosbroke and Hicks 1989).

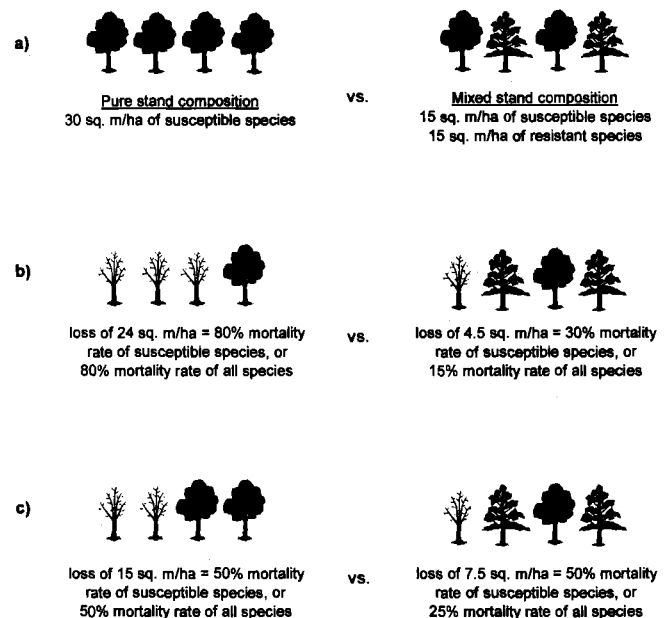


Figure 2. Diagram depicting the possible relationships between stand composition, defoliation, and mortality rates, showing (a) the original stand composition of hypothetical pure and mixed stands prior to defoliation; (b) due to a greater proportion of susceptible species in the pure stand, defoliation intensity, duration and frequency increase, resulting in elevated species specific mortality rate and total mortality greater than that expected based on difference in composition; i.e., total mortality (pure stand) = 2 × 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 amount of total mortality; an expected result based on the difference in composition.

an association with large numbers of susceptible species has also been observed in other situations (Campbell and Sloan 1977). The results described above lend credence to our assertion that increased defoliation associated with greater amounts of susceptible species results in elevated species specific mortality rates and thus greater total mortality (Figure 2b).

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 correlations 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 predefoliation 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 5 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 us to estimate 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 m) than on the good quality site (SI 15.2–16.8 m). 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 m and those with SI > 21.3 m was 12%. 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 m) and medium (SI 16.8–22.8 m) quality sites in central Pennsylvania, both total stand mortality and oak mortality were greater than on low quality sites (SI < 16.8 m). Gansner proposed two explanations for his observations; the first was that on poor sites trees 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

Table 5. 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 ¹ (m)	Basis of mortality estimate	Mortality (%)		Reference
		Oak	Total	
13.7–15.2	BA	18	17	Brown et al. 1979 ²
15.2–16.8	BA	9	7	
< 16.8	Stems	18	14	Gansner 1987 ³
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 ⁴
18.3–21.3	Stems	—	16	
> 21.3	Stems	—	14	

¹ 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).

² Rhode Island forests, number of study plots was not given, study period was 1971 to 1975.

³ n = 574 plots in Pennsylvania, study period was 1979 to 1985.

⁴ n = 237 plots in Pennsylvania, study period was 1985 to 1988.

(*Q. rubra* L.) 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 1980s, the period during which the data analyzed by Gansner (1987) was collected (Quimby, 1991). Trees growing on poor quality xeric sites have adapted to conditions of low moisture and can tolerate periods of drought that would seriously impede the growth of trees adapted to growth on high quality mesic sites (Oliver and Larson 1990, Kozlowski et al. 1991). Thus, the effects of this prolonged reduction in soil moisture were probably much greater on the mesic sites than on the 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 we saw from 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 proposed 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 variation in 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, in part, by the results of our examination of two groups of defoliated stands (Table 6). We took several established studies and separated them 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%, while in subsequent outbreaks oak mortality averaged only 7%. When we tested this difference using a two-sample t-test (SAS 1992) it proved to be significant ($P = 0.0727$, $t = 2.1740$, $df = 6$). 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 6). However, in this case we were unable to reject the null hypothesis that the means of the two groups were equal ($P = 0.3027$, $t = 1.1646$, $df = 4.5$). 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% of the 1972 stand volume. Following the second outbreak (1978-89), 10% of the 1978 stand volume had been killed. Cumulative volume losses were estimated from 143 plots for the first outbreak and 235 plots for the second. 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,

Table 6. 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 ¹	20	21	
	SD	10.93	15.63	
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	
	SD	4.24	3.56	

¹ Mean and SD are calculated for BA estimates only.

1987, and 1990, and included areas that had suffered an outbreak in the preceding 3 yr period (Quimby 1991). The total area affected by defoliation varied considerably between surveys, from 972,000 to 2.5 million ha. However, the portion of the defoliated area that was actually affected by moderate or heavy tree mortality has steadily fallen, from 17% in 1984 to 11% in 1987, and finally to 2% in 1990. Quimby (1991) attributed these differences to above-average rainfall during 1989 and 1990. There is also the possibility that a drought during the early 1980s increased mortality during this period. As a result, while the data strongly supports differences in species-specific (oak) mortality, the relationship between total mortality in initial and subsequent outbreaks is not definitive.

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 we 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 possibly increased stand resistance and reduced mortality rates during subsequent outbreaks. We cannot discount the possibility that selection effects are present as well. While the studies that we reviewed were from 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. Our review points out the need for the establishment of long-term replicated studies in order to adequately test some of the questions raised here.

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