Tree Mortality in Mixed Pine–Hardwood Stands Defoliated by the European Gypsy Moth (*Lymantria dispar* L.)

Mark H. Eisenbies, Christopher Davidson, James Johnson, Ralph Amateis, and Kurt Gottschalk

Abstract: Defoliation by the European gypsy moth (*Lymantria dispar* L.) and subsequent tree mortality have been well documented in the northeastern United States. In this study we evaluate tree mortality after initial defoliation in mixed pine–hardwood stands in the southeastern United States as the range of European gypsy moth expands. In 1993, 46 mature pine–oak and pine–sweetgum stands were selected on the coastal plain in Maryland and Virginia along the advancing gypsy moth front. Initial stand conditions, defoliation, and tree mortality after a single defoliation outbreak were monitored for 4 years. Susceptible oaks and sweetgum were defoliated at the greatest intensities. After defoliation, mortality in attacked stands was 4.4 m^2/ha higher in pine–oak stands and 1.7 m^2/ha higher in pine–sweetgum stands, representing 13 and 3% of the total basal area, respectively. Mortality of pines was observed mainly among suppressed and intermediate trees. Logistic regressions were derived to correlate individual tree mortality to stand and tree factors associated with gypsy moth attack. On the basis of these models, susceptible understory species with degraded crowns in pine–oak stands were at the greatest risk of mortality. Dominant overstory pines in pine–hardwood stands appear to be at low risk. FOR. SCI. 53(6):683–691.

Keywords: vulnerability, pine–oak, stand dynamics, *Lepidoptera*, *Lymantriidae*, logistic regression

PHYTOPHAGOUS INSECTS are pervasive within forest ecosystems, and light to moderate defoliation of forest trees is a frequent occurrence. However, in the majority of situations their presence is often ignored, as the intensity of defoliation has no major effects on growth and mortality of the trees (Kulman 1971). Defoliation becomes a recognizable problem when insect populations become so large that extensive areas are involved, and large numbers of trees are completely defoliated. These conditions are associated with insect pests that are described as outbreak species, insects whose populations have the capability to experience sudden and rapid growth (Barbosa and Wagner 1989). One of the most destructive outbreak species in North America is an introduced member of the Lepidoptera, the European gypsy moth (*Lymantria dispar* L.).

Gypsy moth defoliation has numerous effects on forest stand dynamics. Defoliated trees experience reduced growth owing to the loss of their photosynthate-producing organs (Rafes 1970, Kozlowski et al. 1991). For forest managers, this growth loss means reductions in both quality of the desired product and increased rotation lengths. Conversely, during a defoliation outbreak, if only certain tree species are targeted, the undefoliated individuals may experience transient benefits as a result of increased light, water, and nutrients within the stand (Wickman 1980, Campbell and Garlow 1982, Schweingruber 1988). The targeting of certain species during a defoliation outbreak is characteristic of a number of defoliators, including the European gypsy moth. Although host preference can be described as a continuum, ranging from highly preferred species to species never consumed, forest scientists continue to categorize tree species into well-defined host preference classes. Currently a three-class system is favored, with trees being described as susceptible, resistant, or immune to defoliation (Montgomery 1991, Liebhold et al. 1995).

Reproductive failures of mast producing species, such as diminished acorn production by oak species (*Quercus* spp.), have also been associated with gypsy moth defoliation, with resultant effects on wildlife that depend on hard mast for food (Gottschalk 1990). Defoliation also weakens trees, making them less physiologically able to withstand the attacks of secondary action organisms such as *Armillaria* spp., resulting in tree mortality and potentially huge economic losses if the trees cannot be salvaged. Canopy gaps created by the mortality of overstory trees are frequently occupied by less desirable shade-tolerant species, such as

Mark H. Eisenbies, Department of Forestry, Virginia Tech, 228 Cheatham Hall, Blacksburg, VA 24061—Phone: (540) 231-8857; Fax (540) 231-3330; meisenbi@vt.edu. Christopher Davidson, International Paper—chris.davidson@ipaper.com. James Johnson, Oregon State University—Jim.Johnson@oregonstate.edu. Ralph Amateis, Virginia Tech—ralph@vt.edu. Kurt Gottschalk, US Forest Service—kgottschalk@fs.fed.us.

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red maple (*Acer rubrum* L.), reducing the ability of more desirable species such as oaks to move into dominant canopy positions (Fajvan and Wood 1996).

Individual tree mortality subsequent to defoliation is a function of a number of factors. The tree species, the frequency, intensity, and duration of defoliation, the physiological condition of the tree before defoliation, and the presence and efficiency of secondary-action organisms all play a potential role in determining postdefoliation tree mortality (Wargo and Houston 1974, Dunbar and Stephens 1975, Houston 1981, Parker 1981, Wargo 1981). Of these factors, tree species and physiological condition are the easiest to quantify, and previous researchers have attempted to use these characteristics in the prediction of tree mortality in hardwood stands (Crow and Hicks 1990).

The range of gypsy moth is expanding out of the northeast United States by 2–20 km/year and favoring a westerly expansion but also southerly (Whitmire and Tobin 2006). The movement of gypsy moth populations into the southeastern United States has raised some questions concerning the potential for defoliation within mixed pine–hardwood stands and loblolly pine (*Pinus taeda* L.) plantations and subsequent effects on tree growth and mortality. To what degree will these stands be defoliated? If they are defoliated, can tree mortality be expected? Therefore, the objectives of this study were to describe the initial stand conditions and subsequent tree mortality in mixed pine–hardwood stands on the Atlantic Coastal Plain as the range of gypsy moth expands southward and given well-established factors affecting defoliation and mortality in the northeastern United States, estimate the probability of individual tree mortality in mixed pine–oak stands on the basis of stand and tree characteristics.

Methods

Study Area and Site Selection

The study was established in the Atlantic Coastal Plain physiographic province of Maryland and Virginia (Figure 1). Between 1991 and 1993, 46 research stands were established in mature mixed pine–hardwood stands previously unaffected by gypsy moth. Qualifying mature, fully-stocked stands were selected on the basis of oak and sweetgum (*Liquidambar styraciflua* L.) basal area distributions, proximity to the leading edge of the gypsy moth range (Gottschalk 1993), the presence of no other apparent defoliating factors, and no schedule to be cut during the study period. Stand ownership included holdings from private industrial land, state forests, state parks, and military reservations. Loblolly pine site indices averaged 25 m and ranged from 18 to 30 m (base age 50 years). Median stand age was 56 years and ranged between 33 and 88 years. Primary stand compositions consisted of either mixtures of loblolly pine and oak (pine–oak) or loblolly pine and sweetgum (pine–sweetgum). In all cases oaks, sweetgum, and loblolly pine comprised the majority of stand basal area.

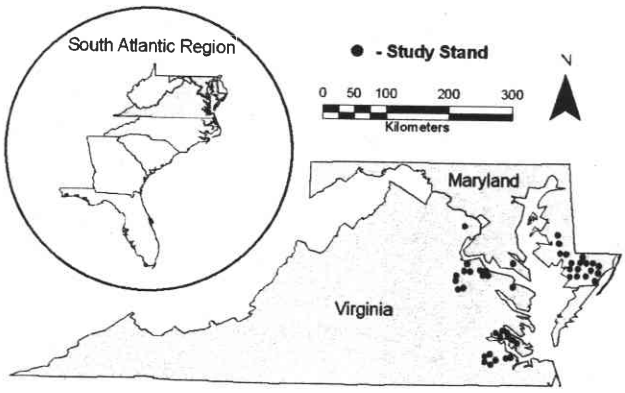

Figure 1. Map indicating the location of study stands on the coastal plain of Virginia and Maryland, U.S.A.

Plot Design and Vegetation Measurements

Within each stand three 400-m^2 (0.04-ha) sample plots were randomly established for all subsequent stand characterizations. Tree species, diameter at 1.37 m (dbh), crown class, crown condition, percent defoliation, and mortality were measured annually for all woody stems ≥5 cm dbh at the time of plot establishment (1992 and 1993) until 1996. Overstory trees were classified as the dominant and codominant trees in the main canopy, whereas understory trees were intermediate and suppressed trees. Host preference classes for tree and shrub species generally fall into three classes: susceptible, resistant, and immune (Davidson et al. 1999). For the purposes of this study, all oaks and sweetgum were categorized as susceptible and all other tree species were categorized as not susceptible. Overstory measurements were collected through 1996; however, only tree diameters, defoliation, and gypsy moth population size were measured in 1994.

Defoliation, crown condition, and mortality were monitored after gypsy moth infestations. Percent defoliation was measured using a visual estimate of individual tree defoliation at the time of peak defoliation within the stand. Trees were independently assessed and placed into one of five defoliation classes: none = 0–10%, light = 11–30%, moderate = 31–60%, heavy = 61–90%, and complete = 91–100%. Visual determinations of crown condition for individual trees was assessed during the mid- to late summer annually after the cessation of defoliation. Crown condition classes (Gottschalk and McFarlane 1993) were defined as follows: good = <25% of branches are dead; healthy foliage; few or no epicormic sprouts; fair = 25–49% of branches are dead; abnormal foliage coloration, density, and/or size; minor epicormic sprouting; poor = >50% of branches are dead; abnormal foliage coloration, density, and/or size; heavy epicormic sprouting. Mortality was calculated as both the total number and basal area of trees that died. Cumulative mortality was determined over the course of the study, from 1991 to 1996.

Statistical Analyses

To evaluate initial stand conditions and tree mortality between attacked and unattacked stands, per objective 1, we used a completely randomized design and conducted an analysis of variance (ANOVA) (Hicks and Turner 1999), with two levels (attacked and unattacked) and two stand

types (pine–sweetgum and pine–oak) using the general linear model algorithm in SAS (SAS Institute, Inc., Cary, NC) at the $\alpha = 0.05$ level. Dependent variables tested included initial stand conditions (dbh, basal area, stem density, and species composition) and mortality (basal area mortality and stems per acre lost after infestation). The univariate procedure in SAS was used to validate the assumptions for ANOVA. Pine–oak stands and pine–sweetgum stands by definition generally lacked sweetgum and oak, respectively, and therefore did not satisfy normality assumptions. Proportions for oak and sweetgum were normalized using the $\arcsin(\pi^{1/2})$ transformation.

To estimate individual tree mortality (from all causes), per objective 2, two logistic models were constructed to evaluate factors affecting mortality over the 4-year period using individual tree and stand level data (Table 1). A baseline model used components that are not associated with a gypsy moth attack to assess factors associated with typical mortality in these mixed pine–hardwood stands. Tree mortality in both attacked and unattacked stands is described by

$$P = [1 + \mathrm{EXP}(-(\beta_0 + \beta_{1\text{-TYPE}} + (\beta_2 * \mathrm{BAHA}) + \beta_{3\text{-CANOPY}} + \beta_{4\text{-CRCOND}}))]^{-1}, \quad (1)$$

where P is the probability of individual tree mortality (event modeled), TYPE is pine–oak stand or pine–sweetgum cover type, BAHA is stand basal area (m^2/ha), CANOPY is understory or overstory, CRCOND is crown condition (good, fair, or poor), and β_0 to β_4 are the parameters to be estimated.

The baseline model was enhanced for the attacked stands by factors associated with gypsy moth defoliation. Because it was unclear whether mortality in two stands (3 and 16) could be attributed primarily to gypsy moth defoliation, they were removed from the model data set. The inclusion of predictor variables associated with gypsy moth defoliation resulted in an improved mortality:

$$P = \left[1 + \mathrm{EXP}\left(-\left(\begin{array}{l} \beta_0 + \beta_{1\text{-TYPE}} + (\beta_2 * \mathrm{BAHA}) \\ + \beta_{3\text{-CANOPY}} + \beta_{4\text{-CRCOND}} \\ + \beta_5 * \mathrm{SUSBA} \\ + (\beta_6 * \mathrm{YRSDEF}) + \beta_{1\text{-HOST}} \end{array} \right) \right) \right]^{-1} \quad (2)$$

where SUSBA is the proportion of the total stand basal area comprising the susceptible species (oaks and sweetgum), YRSDEF is the number of years over the 5-year period that defoliation was moderate or severe, HOST indicates susceptible or not susceptible, and β_0 to β_7 are the parameters to be estimated.

A nonautomatic variable selection strategy relying on evaluating each potentially important predictor variable one at a time and subsequently in combination (Collett 2003) was used for final model selection. Model colinearity was evaluated using variance inflation factors (Montgomory et al. 2001). Comparisons of model performance and fit were made using the likelihood ratio, Wald statistic (Montgomory et al. 2001), and Hosmer and Lemeshow (1989) goodness-of-fit test.

Results

Initial Stand Characteristics

Between 1992 and 1996, 16 of the 44 stands had gypsy moth defoliation outbreaks. There were no initial differences in dbh and stem density within the attacked and unattacked pine–oak stands (Table 2). The mean total stand basal area in pine oak stands was 33 m^2/ha and ranged

Table 1. Listing of the candidate variables used in the formulation of logistic regression equations

Discrete variables	Categories	Model designation	Model 1[a]	Model 2[a]
Individual tree				
Species (discrete)	24 species	SPECIES		
Crown class (discrete)	Suppressed Intermediate Codominant Dominant	CRCLASS		
Crown condition (discrete)	Good Fair Poor	CRCOND	*	*
Host preference class (discrete)	Susceptible Not susceptible	HOST		*
Canopy position (discrete)	Understory Overstory	CANOPY	*	*
Years of defoliation (continuous)	Years (range: 0–3)	YRSDEF		*
Stand level				
Cover type (discrete)	Pine–oak Pine–sweetgum	TYPE	*	*
Total basal area (continuous)	m^2/ha (range: 15–50)	BAHA	*	*
Basal area of susceptible species (continuous)	Proportion (range: 0.03–0.8)	SUSBA		*

*, included in model.

Table 2. Selected stand characteristics of attacked and unattacked stands for pine–oak and pine–sweetgum cover types at the time of plot establishment

Cover type	dbh (cm)	Basal area (m^2/ha)	Tree density (stems/ha)	Species basal area			
				Pine	Oak	Sweetgum	Other
				.....(%) of total.....			
Pine–oak							
Attacked	16.1a[1]	32.2b	1160ab	49a	30a[2]	4b[2]	17a
Not attacked	17.5a	34.1b	1000b	41a	35a	5b	19a
Pine–sweetgum							
Attacked	18.4a	46.2a	1290a	54a	4b	23a	19a
Not attacked	17.5a	38.7b	1130ab	41a	8b	27a	24a

[1] Letters indicate significant differences within columns at the $\alpha = 0.05$ level.
[2] Significant differences for percent basal area of oak and sweetgum were determined from the transformation $\arcsin(\pi^{1/2})$ to satisfy normality assumptions for ANOVA.

between 14 and 42 m^2/ha. Pine–sweetgum stands had a mean of 44 m^2/ha and ranged between 31 and 53 m^3/ha. Attacked pine–sweetgum sites had 8 m^2/ha greater initial basal area than their unattacked counterparts, but there were no differences in the amounts of pine or other hardwoods for the cover types.

The pattern of defoliation and subsequent mortality were similar in both cover types (Davidson et al. 2001b). During the outbreak period, annual defoliation episodes produced a range of defoliation intensities within individual stands. Defoliation levels ranged from none (0–10%) to heavy (61–90%) within both cover types. Oaks and sweetgum were the only susceptible species found within either cover type, and both genera were heavily defoliated between 1992 and 1996. Mortality in the attacked stands was approximately 2½ to 4½ times that of unattacked stands within 1–4 years (Table 3). Stem mortality (17% for basal area and 23% of stems) was greatest in pine–oak stands. Oaks made up 74% of the basal area mortality on the attacked pine–oak stands and 37% on the pine–sweetgum stands. Although sweetgum was susceptible, it did not show heavy mortality. Except on the attacked pine–oak stands, mortality of pines was 41–52% of the total basal area mortality. Mortality of other species was <16% of the total basal area mortality. On the attacked pine–sweetgum sites, >90% of the mortality of other hardwoods was red maple.

Models for Individual Tree Mortality

Model 1 adequately estimated individual tree mortality in the attacked and unattacked stands (Table 4). All parameter estimates were significant, and the likelihood ratio and Wald statistics were highly significant for the overall model. The Hosmer and Lemeshow test indicated consistent performance across groups for both the unattacked ($\chi^2 = 18.1$, $P = 0.0205$) and attacked ($\chi^2 = 30.1$, $P = 0.0002$) stands, which also indicates that the model adequately represents individual tree mortality events in these stands. The CRCOND "fair" was only significant for the unattacked stands. The added parameters, SUSBA, YRSDEF, and HOST, in model 2 increased the likelihood ratio and the Wald statistics by 45 and 23%, respectively, over model 1 (Table 5) and decreased the Hosmer and Lemeshow goodness-of-fit test by 30% ($\chi^2 = 21.2$, $P = 0.0066$); these statistics indicated improved model performance and precision. Variance inflation factors for all model parameters were <2.1 (threshold of 5) indicating that there was no significant colinearity between regressors for either model 1 or model 2.

Partial Regressions

Partial regressions of the reduced model 1 indicated that individual tree mortality on attacked stands was reduced in

Table 3. Basal area mortality and stem mortality for attacked and unattacked pine–oak and pine–sweetgum stands from 1992 to 1996

Cover type	Mortality	Total (%)	Pine	Oak	Sweetgum	Other
			.....(%) of total.....			
Basal Area Mortality (m^2/ha)						
Pine–oak						
Attacked	5.6a[1]	17	22	74	1	3
Not attacked	1.2b	4	46	32	7	16
Pine–sweetgum						
Attacked	2.9b	6	41	37	11	11[2]
Not attacked	1.2b	3	52	14	23	11
Stem Mortality (stems/ha)						
Pine–oak						
Attacked	270a	23	10	76	4	10
Not attacked	80b	7	20	22	22	37
Pine–sweetgum						
Attacked	120b	9	22	35	8	35[2]
Not attacked	50b	5	18	13	45	24

[1] Letters indicate significant differences within columns at the $\alpha = 0.05$ level.
[2] Large component of red maple (*Acer rubrum* L.).

Table 4. Logistic regression parameter estimates and fit statistics for model 1 applied to tree mortality data in mixed pine–hardwood stands that were unattacked and attacked by gypsy moth

Parameter	Unattacked stands (N = 2,442)				Attacked stands (N = 2,308)			
	Estimate	SE	Wald χ^2	Pr > χ^2	Estimate	SE	Wald χ^2	Pr > χ^2e
β_0	−4.5232	0.5873	59.312	<0.0001	0.2511	0.4105	0.3740	0.5408
$\beta_{1\text{-TYPE}}$								
Pine–sweetgum	0	n/a	n/a	n/a	0	n/a	n/a	n/a
Pine–oak	0.3932	0.1097	12.853	0.0003	0.4038	0.0925	19.077	<0.0001
β_2	0.0703	0.0155	20.674	<0.0001	−0.0263	0.0097	7.3307	0.0068
$\beta_{3\text{-CANOPY}}$								
Overstory	0	n/a	n/a	n/a	0	n/a	n/a	n/a
Understory	0.2641	0.1039	6.4639	0.0110	0.5110	0.0980	27.175	<0.0001
$\beta_{4\text{-CRCOND}}$								
Poor	0	n/a	n/a	n/a	0	n/a	n/a	n/a
Fair	−0.3017	0.1262	5.7128	0.0168	−0.0503	0.1638	0.0941	0.7590
Good	−1.4456	0.1203	144.40	<0.0001	−1.8145	0.1466	153.19	<0.0001
χ^2 (Pr > χ^2) fit statistics								
Likelihood		237.4 (<0.0001)				291.5 (<0.0001)		
Wald		233.4 (<0.0001)				223.1 (<0.0001)		

n/a, not applicable.

Table 5. Logistic regression parameter estimates and fit statistics for Model (2) applied to tree mortality data in attacked mixed pine–hardwood stands.

Parameter	Attacked Stands (N = 2,308)			
	Estimate	SE	Wald χ^2	Pr > χ^2
β_0	3.1692	0.6382	24.6566	<0.0001
$\beta_{1\text{-TYPE}}$				
Pine–sweetgum	0	n/a	n/a	n/a
Pine–oak	0.4499	0.0970	21.5303	<0.0001
β_2	−0.0560	0.0129	18.8733	<0.0001
$\beta_{3\text{-CANOPY}}$				
Overstory	0	n/a	n/a	n/a
Understory	0.5497	0.1033	28.3283	<0.0001
$\beta_{4\text{-CRCOND}}$				
Poor	0	n/a	n/a	n/a
Fair	0.1158	0.1756	0.4346	0.5098
Good	−2.0852	0.1615	166.747	<0.0001
β_5	−2.6334	0.5016	27.5610	<0.0001
β_6	−0.5830	0.0851	47.013	<0.0001
$\beta_{7\text{-HOST}}$				
Not susceptible	0	n/a	n/a	n/a
Susceptible	1.0460	0.1048	99.575	<0.0001
χ^2 (Pr > χ^2) fit statistics				
Likelihood		425.5 (<0.0001)		
Wald		274.5 (<0.0001)		

n/a, not applicable.

stands with higher total basal areas (Figure 2). There was a negative correlation (P = 0.0088) between SUSBA and BAHA indicating that resistant species (primarily pines) comprised a greater proportion of the total stand basal area in stands with high total basal area. There was also a positive correlation (P = 0.0145) between the SUSBA and the proportion of the basal area comprising the largest individuals in pine–oak stands. Partial regressions of our expanded model 2 indicated that mortality is most likely for trees with poor crown condition, susceptible species (oaks and sweetgum), and understory trees (Figure 3). Finally, partial regressions showed that individual tree mortality decreased with multiple years of defoliation (Figure 4).

Discussion

Certain trends in mortality that have been described in mixed hardwood stands in the northeastern United States and Pennsylvania were also observed in selected mixed pine–hardwood stands of the Atlantic Coastal Plain. Susceptible species displayed greater mortality and lost nearly one-third of their basal area. Overall, mortality on these pine–oak (17% of basal area) and pine–sweetgum (6% of basal area) sites was light. On these sites, the average peak egg mass densities were 12,400 and 2,700 masses/ha in the post peak year (Davidson et al. 2001b). Initial outbreaks can result in relatively little total mortality (Davidson et al. 1999). Brown et al. (1979) observed mortality owing to

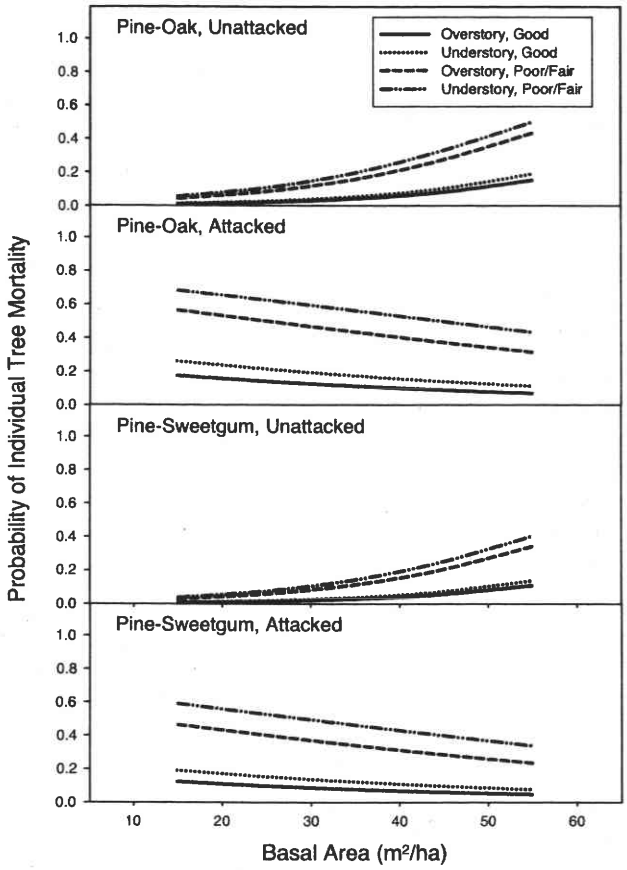

Figure 2. The probability of individual tree mortality on attacked and unattacked stands given total stand basal area (BAHA) for overstory and understory trees with good and poor/fair crown conditions for pine–oak and pine–sweetgum cover types shown by partial regressions of model 1.

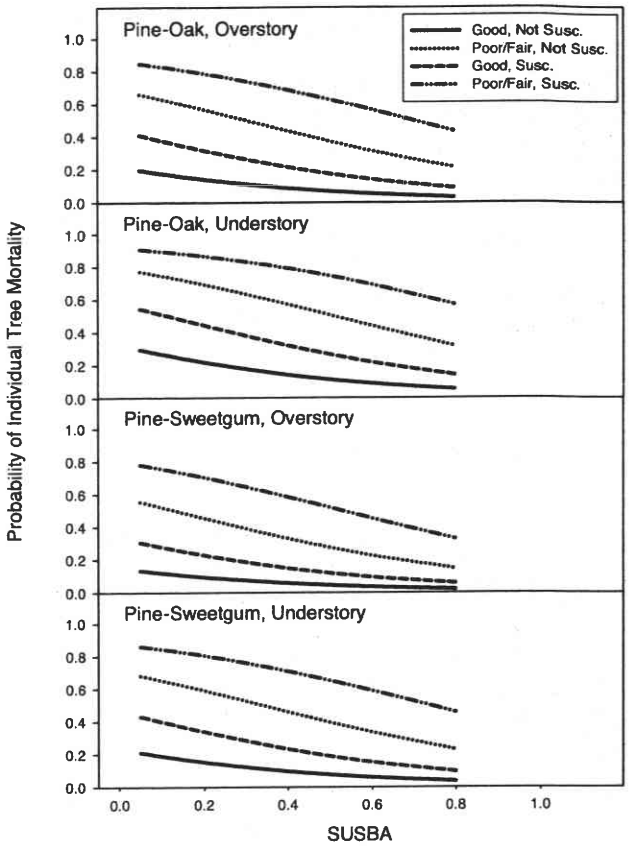

Figure 3. The probability of individual tree mortality of overstory and understory trees given the proportion of susceptible basal area (SUSBA) for susceptible and nonsusceptible species with good and poor/fair crown conditions on pine–oak and pine–sweetgum cover types shown by partial regressions of model 2.

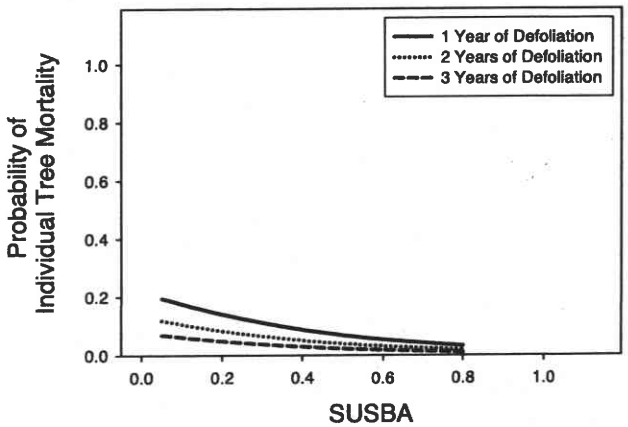

Figure 4. The probability of individual tree mortality for nonsusceptible, overstory trees with good crown condition on pine–oak stands (basal area 40 m²/ha) given the proportion of susceptible basal area (SUSBA) for 1–3 years of defoliation shown by partial regressions of model 2.

gypsy moth attack to be as low as 7% in oak-pine stands in Rhode Island. Further outbreaks can seem erratic; pine–oak stands on xeric sites may experience periodicities of 5 years, whereas periodicities for less-susceptible stands can be up to 10 years (Liebhold et al. 2000, Johnson et al. 2006).

Partial regressions of the reduced model 1 showed that attacked stands did not adhere to the expected rules for stand self-thinning because of density-induced mortality (Monserud et al. 2005, Pretzsch and Biber 2005), and individual tree mortality was reduced in stands with higher total basal areas. This relationship may be explained by two factors. The first possibility is the negative correlation between SUSBA and BAHA. The expansion of the gypsy moth's range and the persistence of vanguard colonies are not necessarily influenced by the abundance of preferred species, land use, or geography (Whitmire and Tobin 2006). However, if the vanguard population of these outbreaks represents a relatively fixed level of disturbance to the total foliage available, moths may concentrate their attack on fewer individual trees, resulting in higher individual mortality. Davidson et al. (2001b) found that gypsy moth foraging on these sites was concentrated on susceptible species. Pine defoliation did not exceed 10% except where defoliation levels >60% were observed for susceptible species and did not exceed 20% until defoliation levels were >90% for susceptible species. The second possibility is the negative correlation of the proportion of basal area occupied by large trees in pine–oak stands. Large overstory trees, with good vigor and ample reserves of carbohydrates, are inherently less likely to show individual mortality even after multiple defoliations.

In mixed-oak stands, individual stem mortality increased with basal area in newly infested mixed-oak stands in Pennsylvania, and mortality responses varied by oak species (Amrhein, 1988). Mortality due to defoliation within pure stands seems to be driven by stocking (Amrhein 1988, Gottschalk et al. 1998, Yang et al. 2003, Pothier and Mailly 2006). However, mixed stands with SUSBA values <0.6 can have mortality rates that are comparable to undefoliated stands (Campbell and Sloan 1977, Fosbroke and Hicks 1989). Mean values for SUSBA on our sites were 0.3 in both pine–oak stands (ranging between 0.03 and 0.8) and pine–sweetgum stands (ranging between 0.1 and 0.5).

Mortality models in mixed hardwoods stands in the Northeast have identified species susceptibility, defoliation class, crown condition, crown position, stand basal area, stem density, and topographic position as factors affecting individual tree mortality (Amrhein 1988, Gottschalk et al. 1998). Likewise, the partial regressions of the expanded model 2 indicated that mortality is most likely for trees with poor crown condition, susceptible species (oaks and sweetgum), and understory trees. Crown condition (CRCOND) appears to have the strongest effect, followed by host susceptibility (HOST), cover type (TYPE), and crown position (CANOPY). The probability of individual tree mortality was lower in stands with higher proportions of susceptible species (SUSBA). Similar to the reasoning used with mortality and BAHA, if there is no superabundance of caterpillars in a vanguard attack, the total defoliation distributed over a higher leaf area may reduce the likelihood that individual trees die.

Increased defoliation intensity of susceptible species has been observed in a number of prior studies and is cited as the primary factor in elevated mortality rates (Baker 1941, Kegg 1971, Campbell and Sloan 1977, Herrick and Gansner 1987, Fosbroke and Hicks 1989, Davidson et al. 2001a, 2001b). Oak defoliation was greater than that of both sweetgum and pines in the early years of the defoliation outbreak, but there was no observed difference between sweetgum and pines (Davidson et al. 2001a). As the outbreak progressed, sweetgum defoliation increased and for the remainder of the outbreak both oak and sweetgum defoliations were significantly greater than pine defoliation. However, sweetgum appeared to weather these events, and pine mortality was not much different than that on unattacked stands (Table 3). Red maple also had high stem mortality in the pine–sweetgum stands, but they were mostly understory trees. All "other hardwoods" comprised less than one-quarter of the total basal area, and no more than 16% of the basal area mortality.

Individual tree mortality decreased with multiple years of defoliation, which is possibly due to low-vigor trees succumbing immediately after the first year. Individual pines or suppressed hardwoods, for instance, may succumb after any significant defoliation within their crown. Pines are considered to be resistant to defoliation and are only consumed once gypsy moth larvae have reached the second instar (Montgomory 1991, Liebhold et al. 1995). However, during a defoliation outbreak there may be significant interspecific variation in tree response so that gypsy moth preference does not directly translate into individual mortality (McGraw et al. 1990, Davidson et al. 1999). Thus, mortality can result for individuals classified as resistant after a single defoliation, whereas susceptible individuals may tolerate multiple defoliation episodes (Campbell and Sloan 1977, Twery 1991). Additionally, it is possible for the vigor of subcanopy trees to improve if light conditions improve after defoliation of the overstory (Fajvan and Wood 1996, Jedlicka et al. 2004).

Although loblolly pine mortality was observed, it was difficult to isolate the source and thereby determine whether gypsy moth defoliation was a primary causal factor. Because of the low number of stands attacked, we were also unable to test interactions between model terms. However, the results from this study seem to imply that that the potential for extensive overstory pine mortality in mixed pine–hardwood stands after initial defoliation by the gypsy moth is low.

Planning and Silvicultural Options

Realistically, we are unlikely to ever fully control or eliminate the gypsy moth. Currently, one-quarter of the potential range of gypsy moth has been colonized, with speculation that it may take over 100 years for full colonization to occur (Sharov et al. 2002, Morin et al. 2005). The present strategy for regionally managing gypsy moth has three components: eradication in uninfested regions use of pesticides (e.g., *Bacillus thuringiensis*, nucleopolyhedrosis virus, or diflubenzuron), suppression in infested regions (e.g., barrier bands or pheromone traps), and slowing the expansion of the range (Sharov et al. 2002, Tobin and Whitmire 2005). Such larger-scale programs have successfully reduced the rate of spread by half.

At the stand level, silviculturists have limited options to indirectly affect future gypsy moth populations (Muzika and Liebhold 2000). Strategies may entail maintenance or restoration stand structure, enhancing tree vigor, regeneration of healthy and resistant trees or tree species, and timber extraction (Waring and O'Hara 2005). Silvicultural practices such as thinning can remove vulnerable trees or reduce overstocking, but the dilemma is removing host species before it is economically desirable (Muzika and Liebhold 2000). There appears to be little evidence that thinning has an effect on the vulnerability of stands to gypsy moth attack (Liebhold et al. 1998, Davidson et al. 1999). Stands generally need a relatively high proportion of resistant species (>70% of basal area) to be considered less vulnerable (Davidson, 1999).

Foster and Orwig (2006) cautioned that care must be taken when using treatments that may introduce more severe impacts than the threat and further argued that in some cases allowing nature to take its course may be a better alternative from the standpoint of ecosystem function if the threat is inevitable. However, the approach of doing nothing may be difficult to accept in areas not yet threatened by exotic pests or when such a decision may adversely affect neighboring landowners. The dynamic interactions of factors affecting cyclic gypsy moth populations are complex

(e.g., population density, predation, reproduction, defoliation history, mast cycles, and regional weather); thus, predictions are difficult from year to year (Liebhold et al. 2000, Wilder 2001). Muzika and Liebhold (2000) ultimately conceded that it is very difficult to predict the repercussions of an attack; therefore, it is difficult to formulate silvicultural treatments that will have consistent results.

Conclusions

Mortality in mixed pine–hardwood stands on the coastal plain of Virginia and Maryland was 17% (basal area) on pine–oak stands and 6% on pine sweetgum stands. Loblolly pine appears to be at low risk for widespread mortality in the overstory from vanguard gypsy moth attack. Despite being susceptible to gypsy moth defoliation, sweetgum also appeared to be at low risk for mortality. Oaks generally comprised the largest proportion of basal area mortality.

Logistic regression was a useful tool for predicting individual tree mortality subsequent to gypsy moth attack in Coastal Plain pine–hardwood stands. Cover type, crown condition, host preference class, canopy position, years of defoliation, total basal area, and basal area of susceptible species before the outbreak were significantly correlated to tree mortality after the defoliation of attacked stands. On the basis of this model, individual trees in pine–oak stands had the greater vulnerability. Susceptible species, understory trees, and trees with degraded crown condition were the most vulnerable.

Because of the relatively light outbreak, defoliation and mortality were heaviest in stands with smaller proportions of susceptible species. Overall, the probability that a susceptible overstory tree (oak or sweetgum) with good crown condition will die was approximately 1 in 3 in an average stand. Thinning may improve the vigor of individual susceptible trees, but according to these models it is unlikely to prevent individual tree mortality within the stand. The role of additional stress factors was beyond the scope of this study; however, fire stress, drought stress, and attacks by southern pine beetle may also influence mortality.

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