CHAPTER 4

The European gypsy moth in Coastal Plain mixed pine-hardwood stands: defoliation patterns and prediction of stand susceptibility

INTRODUCTION

Within the last century, the European gypsy moth (*Lymantria dispar* L.), an introduced defoliator, has become endemic within forests of the northeastern United States. The gypsy moth is considered to be 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, large areas of forested land may suffer extensive defoliation and associated tree mortality.

During the last five decades, gypsy moth populations have continued to expand from their zone of original introduction within the northeastern United States. Currently, established populations may be found as far south as northern Virginia and the eastern shore of Maryland, and west into northern West Virginia and western Ohio (USDA, 1996). Though the total area defoliated by the gypsy moth has fallen within the last decade, outbreaks continue to occur along the leading edge and recent studies indicate there is considerable potential for continued defoliation in southern forests (Barbosa et al., 1983; Cook et al., 1994; USDA 1996).

The gypsy moth is a polyphagous herbivore and early studies described more than 400 tree and shrub species as potential hosts (Forbush and Fernald, 1896). Subsequent studies attempted to form classification schemes that would enable scientists and foresters to place tree species into readily identifiable host preference classes (Bess et al., 1947). These early studies categorized trees into four host preference classes; but the most recent and widely recognized grouping is the three class system proposed by Montgomery (1991) and utilized by Liebhold et al. (1995) in their summary of host suitability. In this system trees are classified as either susceptible, resistant, or immune to defoliation, based on the likelihood of defoliation. Susceptible tree species are described as those that are consumed by all larval stages. Resistant species are consumed by only some larval stages or when susceptible species are not available; while immune species are those that are rarely, if ever, consumed by any larval stage. Determining the susceptibility of forest stands to gypsy moth defoliation has been a goal of forest managers since the early days of the insects' introduction. Knowledge of the risk of defoliation allows forest managers to weigh their options prior to an outbreak, and assists them in the formulation of an effective management plan.

Field studies in northeastern hardwood stands have confirmed the susceptibility of the oak component within these forest types (Minott and Guild, 1925; Baker, 1941; Campbell and Sloan, 1977). However, as gypsy moth populations continue their advance into the southeastern United States, stands containing mixtures of southern oaks (*Quercus* spp.), sweetgum (*Liquidambar styraciflua* L.) and loblolly pine (*Pinus taeda* L.) are likely to be impacted (Cook et al., 1994; Gottschalk and Twery, 1989). Laboratory studies have identified sweetgum as a highly susceptible host; and though it is considered to be resistant, loblolly pine can be effectively utilized by larvae from the second instar onwards (Barbosa et al., 1983). Unfortunately, when attempting to formulate an effective forest management action plan, the results of laboratory studies cannot reliably be transferred to the field. Therefore a field study was designed with the following objectives: 1) to determine the relationship between species composition and gypsy moth defoliation in Coastal Plain mixed pine-hardwood stands; 2) to formulate a model to predict stand susceptibility to defoliation.

METHODS

Study Area and Site Selection

The study was established in the counties of Dorchester, Somerset, Wicomico and Worcester, MD, in the Atlantic Coastal Plain physiographic province (between latitude 38° 35' N and 38° 5' N, and longtitude 75° 56' W and 75° 25' W). This area is characterized by a humid continental climate (USDA, 1970, 1973). The average growing season ranges from 180 to 200 days, extending from the middle of April to the end of October (USDA, 1959, 1970, 1973). Precipitation averages from 102 to 152 cm annually and is well distributed throughout the year, with most of the variability in rainfall occurring as a result of summer showers and thunderstorms (USDA, 1970). Droughts are frequent and can have detrimental effects upon tree growth (Walker, 1994). The four counties are part of a low, eroded, plain where differences in elevation are generally slight; elevation ranges from sea-level to approximately 26 m above sea-level (USDA, 1970, 1973). Soils range from excessively drained to poorly drained, sands, loamy sands and sandy clay loams (USDA, 1959, 1970, 1973).They are sedimentary in origin and four soil orders are represented, Entisols, Inceptisols, Spodosols and Ultisols (USDA, 1959, 1970, 1973).

Research plots were established in sixteen mixed pine-hardwood stands in 1991, 1992 and 1993 (Figure 4.1, Table 4.1). Stands were selected that contained mixtures of loblolly pine and

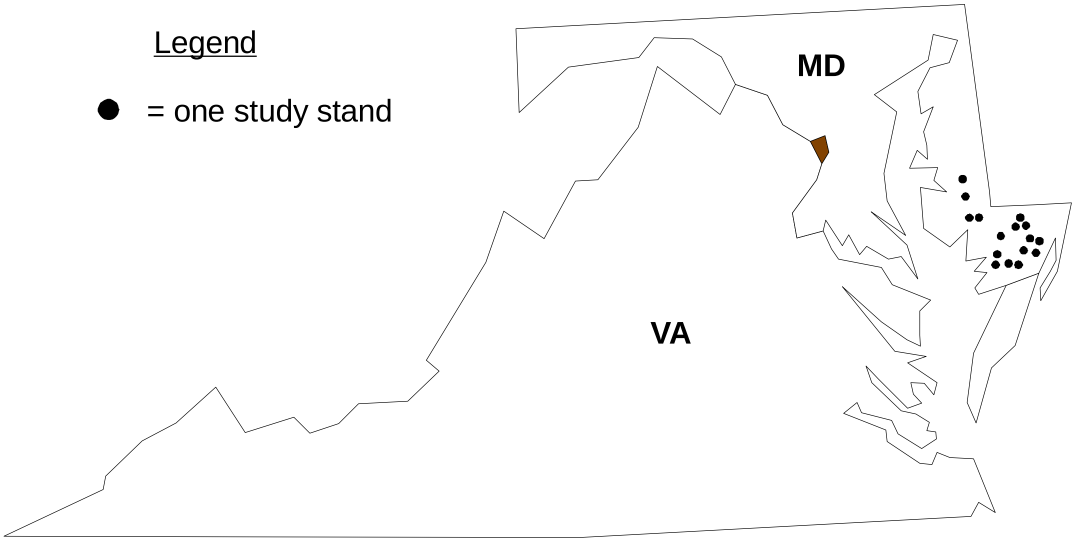

Figure 4.1. Map of Virginia and Maryland showing the location of study stands within the Atlantic Coastal Plain physiographic province.

Table 4.1: Year of study plot establishment, the number of years of vegetation measurements and the number of years of egg mass surveys of sixteen mixed pine-hardwood stands.

Stand No.	**Year of Plot Establishment**	**Vegetation Measurements**	**Egg Mass Surveys**
		------------------------ Yrs	------------------------
Pine-Oak			
1	1991	5	4
2	1992	5	4
3	1992	5	4
4	1993	4	3
5	1991	5	4
6	1992	5	4
7	1992	5	4
Pine-Sweetgum			
8	1993	4	3
9	1993	4	3
10	1992	5	4
11	1993	4	3
12	1992	5	4
13	1992	5	3
14	1992	5	4
15	1992	5	4
16	1992	5	4
	Total	76	59

oak, or loblolly pine and sweetgum. Selection was based on several criteria with the most important being stand composition; a range of species composition, from nearly pure hardwood to nearly pure pine was desired. Additionally stands were required to have a well-developed crown structure; to occur on medium quality forest sites, based on pine site index; to have minimal or no prior gypsy moth defoliation; and to occur on the "leading edge" of the gypsy moth infestation.

Plot Design and Vegetation Measurements

Within each of the sixteen stands, three 400 m^2 (0.04 ha) sample plots were randomly established with a minimum separating distance of 50 m. The following variables were measured at time of establishment and annually thereafter until 1996: tree species, total height, diameter at 1.37 m (dbh), and percent defoliation for all woody stems $\geq$ 5 cm dbh. 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%. 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 present within the stand. Three sample plots, 0.01 ha in size, were established at pre-determined locations within each 0.04 ha plot, and the number of egg masses within each plot was used to estimate population size. Within an individual stand both newly laid egg masses and those from previous generations may be present; differentiating between the two can be difficult unless the egg mass can be examined by hand. Therefore the method proposed by Liebhold et al. (1994)

was used to reduce the possibility of overestimating population sizes. Liebhold et al.'s method uses the proportion of new to old egg masses counted on the ground to adjust for the number counted in the tree crowns. However, because no distinction was made between old and new egg masses when the 1992 population survey was carried out, data for the number of egg masses in 1992 was adjusted using the proportion of new to old egg masses from the 1993 population survey. Increment cores were collected from overstory loblolly pines in mid-June 1997, and stand age was determined.

Plot center was permanently located on all 0.04 ha plots with steel rebar covered with a 3/4 inch pvc pipe. All trees $\geq$ 5cm dbh were individually numbered, and dbh was marked with a painted line to facilitate re-measurement at the same location every year. Annual measurements were taken during the summer months unless otherwise specified. Overstory measurements were collected through 1996; however, only tree diameters, defoliation and gypsy moth population size were measured in 1994, and height measurement was discontinued in 1995.

Statistical Analysis

Annual defoliation estimates for each stand were averaged over the three 0.04 ha sample plots. The midpoint of each defoliation class was used in all defoliation calculations. To account for differences in tree and crown size, the following formula was used to calculate weighted average defoliation for stands, individual species, and host preference classes (Herrick and Gansner, 1986):

$$\overline{DEF} = \frac{\sum_{i=1}^{n}(D_i^2 * DEF_i)}{\sum_{i=1}^{n} D_i^2} \qquad \textbf{(1)}$$

D_i = individual tree diameter (cm)

DEF_i = individual tree defoliation estimate (%)

Simple and multiple linear regression analysis was used to determine the relationship between total stand defoliation (dependent variable), and population size, initial species composition (basal area), stem density and the quadratic mean diameters (QMD) of pines, oaks, sweetgum and all susceptible species (independent variables). The number of egg masses present within a stand in the year prior to defoliation was used as an indicator of population size (Williams et al., 1991). The proportions of pines, oaks, sweetgum, and all susceptible species as a percentage of total basal area were used as indicators of initial species composition. The QMD's were used as a surrogate for the size of hardwoods and pines within the stand. The actual number of defoliation estimates available for use in defoliation prediction was 76 (Table 4.1). However, because egg mass density was utilized as a dependent variable, missing observations would have been generated for the years in which egg mass surveys were not available. Therefore, for stands in which egg mass density was available, the mean annual defoliation estimates from 1992 to 1996 were pooled (n=59), and these observations were used in the development of a prediction equation for mean total stand defoliation.

RESULTS AND DISCUSSION

Stand Characteristics

The sixteen stands were classified as either pine-oak or pine-sweetgum, based on whether oak or sweetgum was the dominant hardwood (on a percentage basal area basis) within the stand. Seven stands were classified as pine-oak, nine were classified as pine-sweetgum (Table 4.2). At the time of plot establishment, total stand basal area averaged 31.0 m^2/ha within pine-oak stands, and 45.7 m^2/ha within pine-sweetgum stands. Stand density ranged from 667 to 1483 stems/ha in pine oak stands, and from 800 to 2029 stems/ha in pine-sweetgum stands. Mean tree diameter was greater in pine-sweetgum stands (18.4 cm) than in pine-oak stands (16.2 cm. Mean stand age ranged from 30 to 88 years. The average age of pine-oak stands was 63 years, while pine-sweetgum stands averaged 54 years.

In both cover types, sweetgum and various species of oaks were the only susceptible tree species encountered. Though oaks were the dominant susceptible species in the pine-oak type, sweetgum was also a frequent stand component (Table 4.2). In the pine-sweetgum type, oaks were observed less frequently, occurring in only three of the nine stands (Table 4.2). Loblolly pine was the most frequently observed coniferous species, however, pitch pine (*P. rigida* Mill.), shortleaf pine (*P. echinata* Mill.), and Virginia pine (*P. virginiana* Mill.) were also found within both cover types (Table 4.3).

Table 4.2: Total stand basal area, stem density, mean diameter, age, and basal area of species and host preference classes of sixteen mixed pine-hardwood stands at the time of plot establishment.

Stand Type/ No.	**BA**	**Density**	**DBH**	**Age**	**Basal Area of Species and Host Preference Classes**						
					Oak	**Sweetgum**	**Pine**	**Other Hdwds.**	**Susc.**	**Resist.**	**Immune**
	-- m^2/ha --	- stems/ha -	---- cm ----	--- yrs ---	-- m^2/ha --						
Pine/Oak											
1	14.3	683	15.4	40	11.5	0.0	2.1	0.7	11.5	0.3	0.4
2	30.9	1092	15.8	55	13.5	3.2	11.0	3.2	16.7	2.5	0.7
3	27.9	992	16.4	68	9.4	0.5	15.8	2.2	9.9	0.2	2.1
4	34.4	667	20.4	73	10.0	1.5	16.4	6.5	11.5	5.7	0.9
5	37.1	1483	15.3	88	6.5	4.3	23.4	2.9	10.8	1.8	1.7
6	40.2	1358	16.6	62	4.6	1.4	30.4	3.8	6.0	2.6	1.3
7	32.0	1408	13.5	55	1.2	0.1	21.1	9.6	1.3	4.9	4.9
mean	31.0	1098	16.2	63	8.1	1.6	17.2	4.1	9.7	2.5	1.7
Pine/Sweetgum											
8	37.8	800	21.4	55	0.0	18.5	10.7	8.6	18.5	7.2	1.4
9	45.2	1167	18.1	65	0.0	15.0	24.4	5.8	15.0	3.6	2.0
10	52.8	1283	18.7	59	8.5	16.6	14.7	13.0	25.1	6.4	6.6
11	51.4	1425	17.9	49	0.0	14.3	27.3	9.8	14.3	9.3	0.5
12	50.4	1042	21.9	57	0.0	9.3	33.8	7.3	9.3	6.5	0.8
13	47.9	1142	19.2	54	0.0	7.7	33.0	7.2	7.7	6.7	0.5
14	40.0	1292	16.7	73	4.6	5.9	22.1	7.4	10.5	3.8	3.6
15	49.1	1308	18.4	46	0.0	7.2	34.4	7.5	7.2	7.2	0.3
16	36.8	2029	13.4	30	1.3	2.4	32.3	0.8	3.7	0.7	0.1
mean	45.7	1276	18.4	54	1.7	10.8	25.8	7.5	12.4	5.7	1.8

Table 4.3: Tree species, by host preference class, that were found in seven pine-oak and nine pine-sweetgum stands.

Stand type	**Susceptible species**	**Resistant species**	**Immune species**
Pine/Oak	*Liquidambar styraciflua*, sweetgum	*Acer rubrum*, red maple	*Ilex opaca*, American holly
	Quercus alba, white oak	*Carpinus caroliniana*, hornbeam	*Magnolia virginiana*, sweetbay
	Q. bicolor, swamp white oak	*Cornus florida*, flowering dogwood *	*Nyssa sylvatica*, blackgum
	Q. falcata, southern red oak	*Pinus echinata*, shortleaf pine	
	Q. michauxii, swamp chestnut oak	*P. rigida*, pitch pine	
	Q. nigra, water oak	*P. taeda*, loblolly pine	
	Q. phellos, willow oak	*P. virginiana*, Virginia pine *	
	Q. rubra, northern red oak	*Sassafras albidum*, sassafras	
	Q. stellata, post oak		
	Q. velutina, black oak *		
Pine/Sweetgum	*Liquidambar styraciflua*, sweetgum	*Acer rubrum*, red maple	*Ilex opaca*, American holly
	Quercus alba, white oak	*Carpinus caroliniana*, hornbeam	*Magnolia virginiana*, sweetbay
	Q. bicolor, swamp white oak	*Carya tomentosa*, mockernut hickory	*Nyssa sylvatica*, blackgum
	Q. falcata, southern red oak	*Fagus grandifolia*, American beech	
	Q. michauxii, swamp chestnut oak	*Pinus taeda*, loblolly pine	
	Q. nigra, water oak	*Prunus serotina*, black cherry *	
	Q. phellos, willow oak	*Sassafras albidum*, sassafras	
	Q. rubra, northern red oak		

* Species that were found in only one stand, all other species were widely distributed.

In pine-oak stands, pine basal area ranged from 2.1 to 30.4 m^2/ha; while oak basal area ranged from 1.1 to 13.5 m^2/ha (Table 4.2). The pine-sweetgum cover type tended to have greater pine basal areas, ranging from 10.7 to 34.4 m^2/ha. Basal area of sweetgum ranged from 2.4 to 18.5 m^2/ha (Table 4.2). Pine-sweetgum stands also contained a greater mean basal area of resistant species, while the mean basal area of immune species was approximately equal in both cover types (Table 4.2, 4.4).

Gypsy Moth Population Dynamics

When gypsy moth populations move into an area of forested land, defoliation episodes occur. A defoliation episode is defined as the gypsy moth defoliation that occurs within a forest stand during a single year, i.e. annual defoliation. A defoliation outbreak refers to a consecutive series of defoliation episodes. Table 4.5 lists the mean number of egg masses/ha calculated from annual surveys of the individual stands. During the study period, both pine-oak and pine-sweetgum stands were subjected to a single gypsy moth defoliation outbreak. Egg mass density was variable both between stands and among years (Table 4.5). However, each stand tended to experience an increase to some maximum level, followed by a decline. On an annual basis, the greatest mean population size occurred in 1993 in pine-oak stands, and 1994 in pine-sweetgum stands (Table 4.5). While maximum egg mass density of the individual stands did not always occur in the same year, in general there was little variability in the chronology of the outbreak. Of the seven pine-oak stands, five experienced their highest population levels in 1993; of the remaining two, one peaked in 1992, the other in 1994 (Table 4.5). Among the pine-sweetgum

Table 4.4: Basal area of pines, oaks, sweetgum, resistant and immune tree species as a percentage of total basal area in seven pine-oak and nine pine-sweetgum stands.

Cover Type		**Species / Host Preference Class**					
		Pine	Oak	Sweetgum	Susceptible	Resistant	Immune
		-- % --					
Pine/Oak							
1		15.0	80.3	0.0	80.3	17.3	2.4
2		35.6	43.8	10.4	54.2	43.6	2.1
3		56.4	33.6	2.0	35.5	56.9	7.5
4		47.5	29.1	4.3	33.5	63.9	2.6
5		63.0	17.6	11.7	29.2	66.2	4.6
6		75.5	11.5	3.4	14.9	81.9	3.2
7		65.7	3.6	0.1	3.7	81.0	15.3
	mean	51.2	31.3	4.6	35.9	58.7	5.4
	std. dev.	20.6	25.5	4.7	25.3	22.6	4.8
Pine/Sweetgum							
8		28.3	0.0	48.8	48.8	47.4	3.8
9		54.1	0.0	33.3	33.3	62.1	4.5
10		27.8	16.1	31.4	47.6	40.0	12.4
11		53.1	0.0	27.8	27.8	71.2	1.0
12		66.9	0.0	18.4	18.4	79.9	1.7
13		68.9	0.0	16.0	16.0	82.9	1.1
14		55.1	11.5	14.8	26.3	64.7	9.0
15		69.9	0.0	14.7	14.7	84.6	0.6
16		87.9	3.4	6.6	10.0	89.7	0.2
	mean	56.9	3.4	23.5	27.0	69.2	3.8
	std. dev.	19.6	6.1	12.9	14.0	17.2	4.2

Table 4.5: Annual gypsy moth population size, based on number of egg masses per hectare within seven pine-oak stands and nine pine-sweetgum stands.

Stand No.	**Years**			
	1992	**1993**	**1994**	**1995**
	---------------------------------- egg masses/ha ----------------------------------			
Pine/Oak				
1	8,463	6,478	7,166	1,083
2	851	8,099	5,542	5,138
3	2,337	7,806	932	1,566
4	---	3,291	8,773	1,369
5	7,653	21,073	1,672	1,431
6	2,343	14,959	3,300	1,221
7	1,195	3,742	2,837	920
mean	3,807	9,350	4,317	1,818
std. dev.	3,357	6,445	2,920	1,480
Pine/Sweetgum				
8	---	1,667	18,802	689
9	---	7,333	19,309	3,278
10	---	400	9,067	228
11	---	1,300	16,097	1,218
12	67	2,400	10,927	1,619
13	100	1,713	13,732	1,589
14	834	13,045	7,697	677
15	21	617	11,890	352
16	2140	12,293	4,133	619
mean	527	4,530	12,406	1,141
std. dev.	851	5,051	5,101	945

stands, the majority of the populations peaked in 1994; two stands reached maximum density in 1993 .

The maximum population size achieved by individual gypsy moth populations within these stands also was quite variable (Table 4.5). In pine-oak stands, the peak population size ranged from 3,742 to 21,073 egg masses/ha. In pine-sweetgum stands the largest mean number of egg masses/ha recorded was 19,309, while the lowest was 9,067. In both cover types, populations had dramatically declined by 1995, and the outbreak appeared to be completely over by 1996.

Trends in defoliation

Stands in both cover types were extensively defoliated during the outbreak period. Recent investigations of the relationship between egg mass density and defoliation have shown that peak defoliation occurs in the year prior to the maximum observed egg mass density (Williams et al., 1991). This was not found to be true within this study. Rather, in the majority of stands, peak defoliation occurred in the year subsequent to the maximum observed gypsy moth egg mass density (Figure 4.2). Only three stands out of sixteen departed from this trend; two experienced defoliation peaks in the year of peak egg mass density; in the third, defoliation peaked two years after the maximum observed egg mass density. In these three stands, localized outbreaks of the forest tent caterpillar (*Malacosoma disstria* Hübner) occurred in both 1994 and 1995, resulting in some additional defoliation.

The chronology of the outbreak in the two cover types is apparent in Figure 4.3. In pine-oak stands, mean egg mass levels were greatest in 1993 and this resulted in the greatest

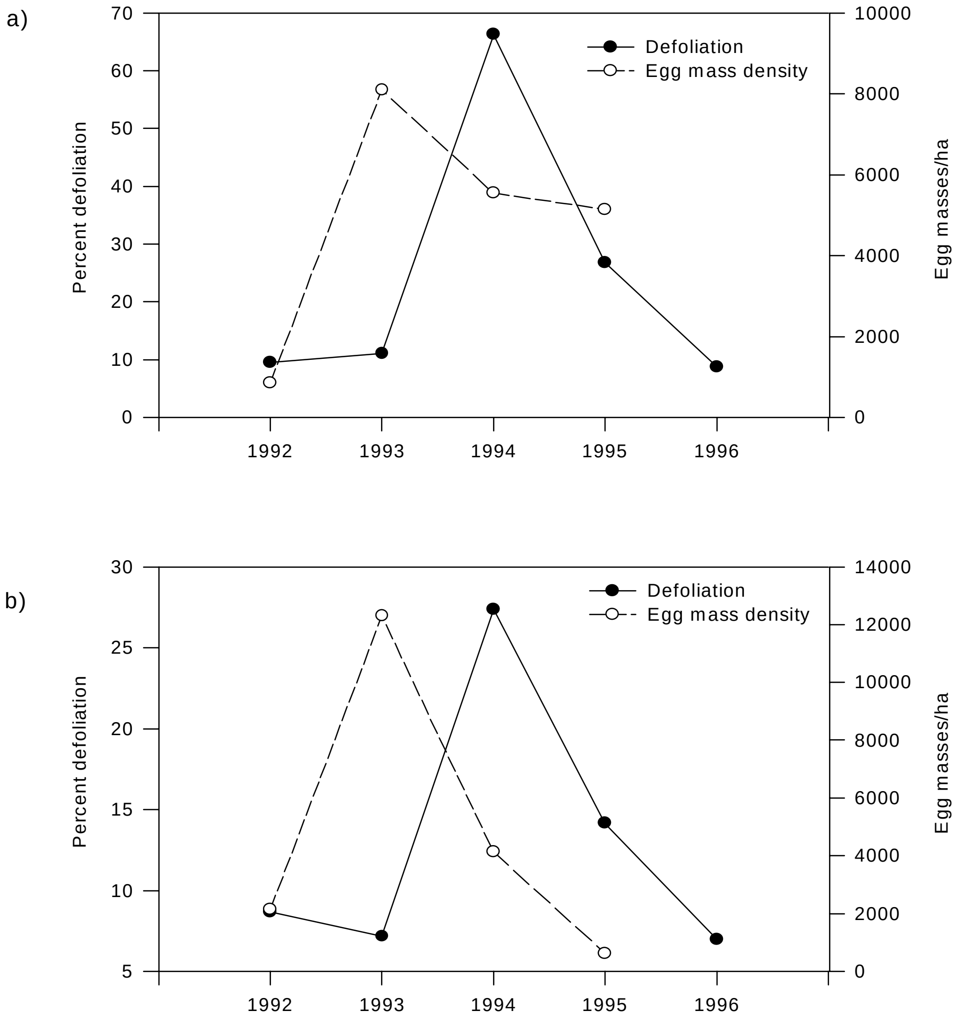

Figure 4.2: Relationships between years of maximum observed egg mass density and the occurrence of peak stand defoliation during the gypsy moth outbreak in two representative stands in a) the pine-oak and b) the pine-sweetgum types.

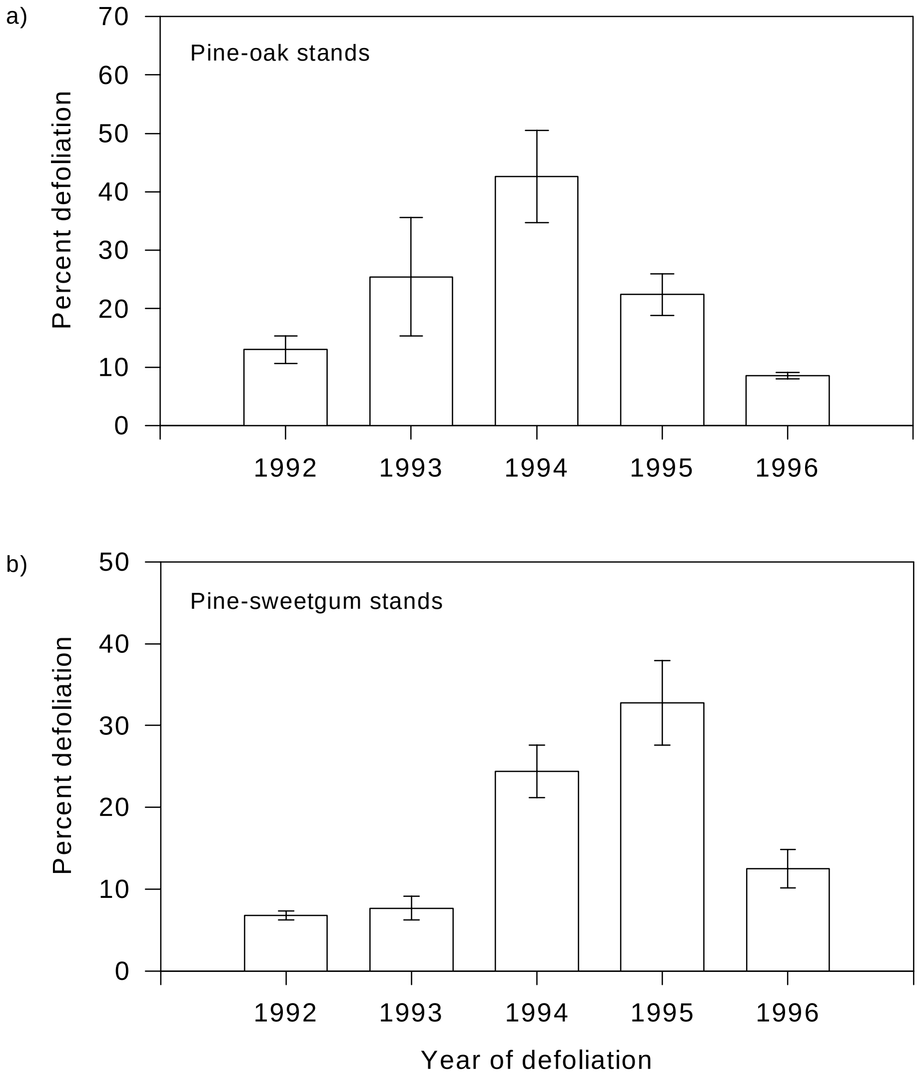

Figure 4.3: Mean stand defoliation between 1992 and 1996 in a) pine-oak stands and b) pine-sweetgum stands; error bars show the standard error of the mean.

defoliation intensities in 1994. Mean total stand defoliation in pine-oak stands in 1994 was 42.6 % (Figure 4.3a). In pine-sweetgum stands, mean egg mass levels were greatest in 1994, thus defoliation intensities did not peak within these stands until 1995, when mean total stand defoliation reached 32.8% (4.3b). The lower overall mean defoliation levels observed in the pine-sweetgum type may be due to the greater proportion of pine basal area within these stands in comparison to the proportion found in pine-oak stands.

Previous studies have shown that during the course of a gypsy moth outbreak, susceptible species are typically defoliated at the greatest intensities (Campbell and Sloan, 1977). The stands within this study exhibited similar patterns. Figure 4.4 shows the mean annual defoliation of the three major genera, pines, oaks, and sweetgum, in seven pine-oak stands. The susceptible oaks and sweetgum were defoliated during each of the outbreak years from 1992 to 1996. They were also consistently defoliated at much greater intensities than the pines, which were not subjected to intensive defoliation until 1994. An analysis of variance using the Ryan-Einot-Gabriel-Welsch multiple F test, revealed significant differences in mean defoliation levels in each of the outbreak years. Oak defoliation was significantly greater than that of pines throughout the defoliation outbreak. Defoliation of sweetgum however, did not significantly differ from pine defoliation until 1994. In 1994 mean defoliation levels of sweetgum also exceeded that of oak, however the difference was not significant. Figure 4.5 shows the mean annual defoliation of all pines, oaks, and sweetgum in nine pine-sweetgum stands. As previously described in pine-oak stands, susceptible species experienced the greatest defoliation intensities. Even though sweetgum was the dominant

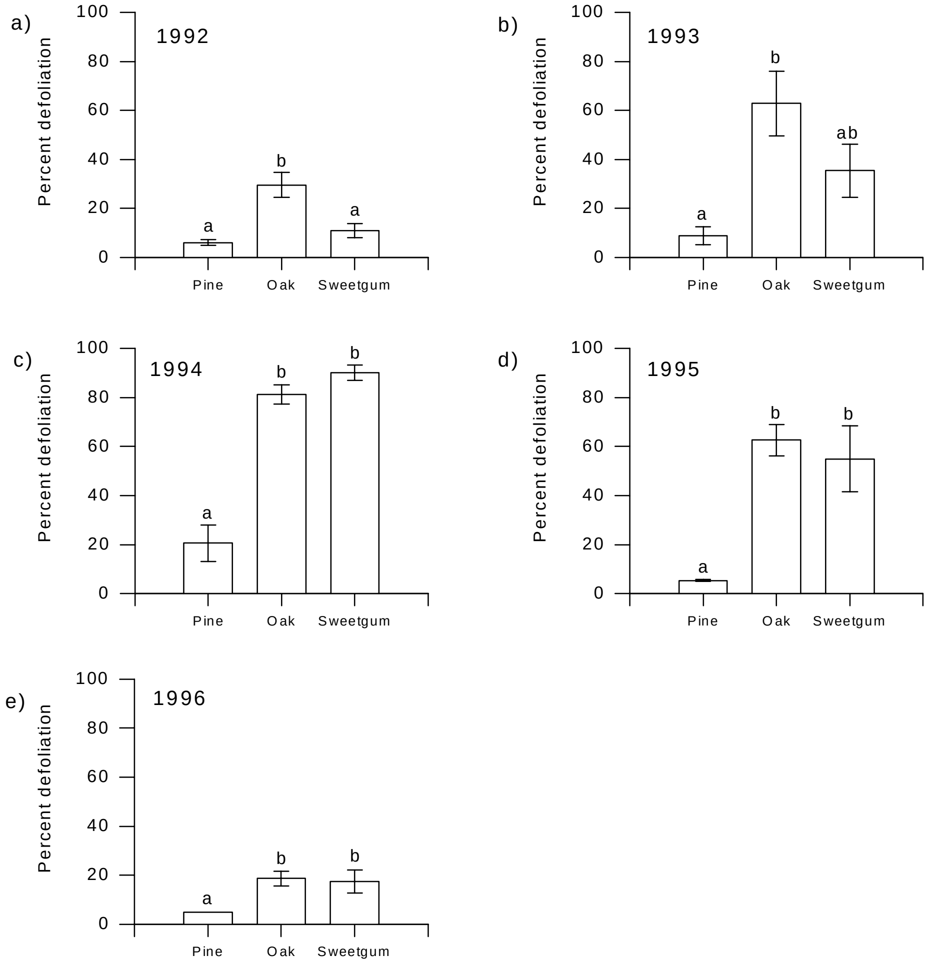

Figure 4.4: Mean annual defoliation of all pines, oaks, and sweetgum in pine-oak stands in the years 1992 to 1996; bars show the standard error of the mean, means with the same letter are not significantly different at the 0.05 alpha level.

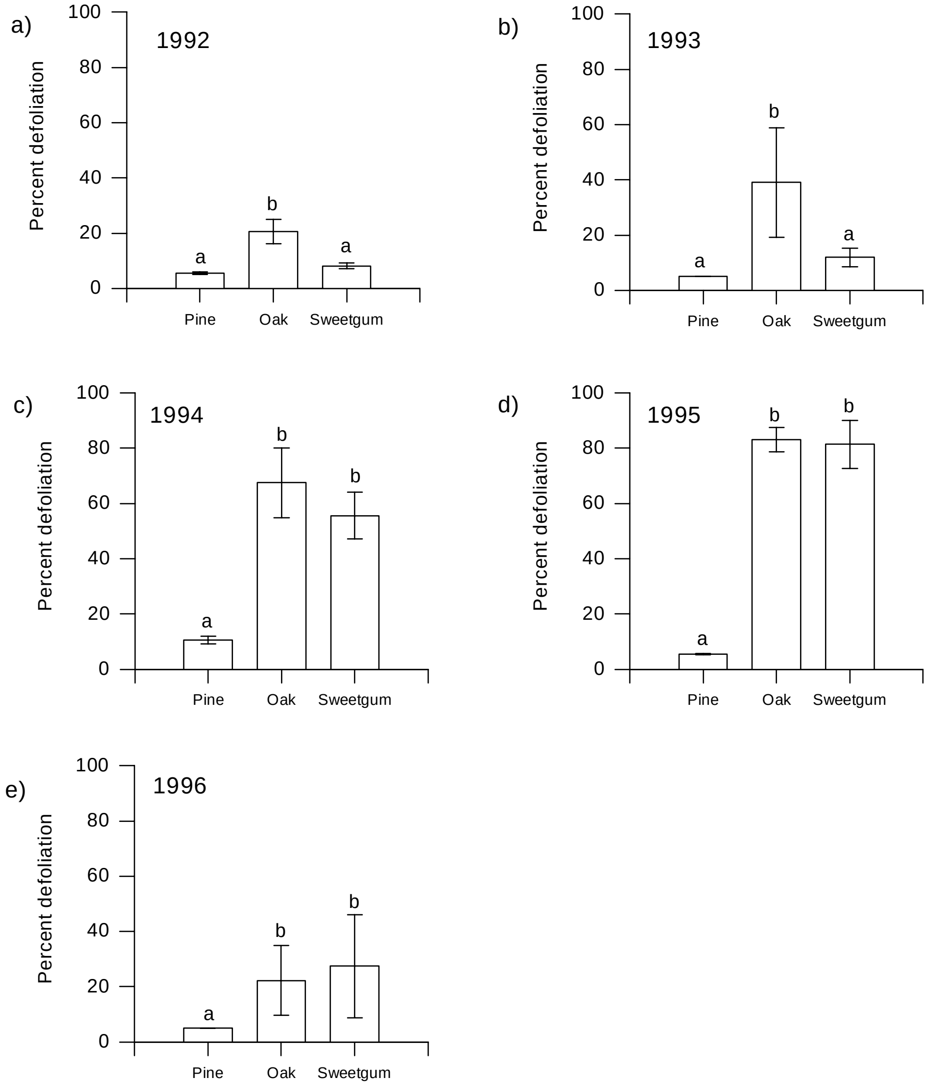

Figure 4.5: Mean annual defoliation of all pines, oaks and sweetgum in pine-sweetgum stands in the years 1992 to 1996; bars show the standard error of the mean, means with the same letter are not significantly different at the 0.05 alpha level.

susceptible species in these stands, the trend in defoliation first observed in pine-oak stands was also observed here. Oak defoliation was significantly greater than both pine and sweetgum defoliation during the early years of the outbreak, while sweetgum defoliation did not differ significantly from pine defoliation (Figure 4.5). In 1994, mean defoliation of sweetgum increased, and significant differences between sweetgum and pine defoliation were observed throughout the remainder of the outbreak.

Further examination of species defoliation on an individual stand basis revealed some interesting trends. In 1994 mean defoliation of pines increased in pine-oak stands (Figure 4.4). This increase was due primarily to intensive defoliation within three of the seven pine-oak stands where a few overstory pines suffered moderate to heavy defoliation. In each case, the susceptible species were completely defoliated and larvae probably switched to the more resistant pines when the supply of susceptible host foliage was depleted (Gottschalk and Twery, 1989). Within these stands the mean pine defoliation levels rose to 17, 34 and 59%. Figure 4.6a illustrates that this increase in pine defoliation appears to be related to a threshold level of oak defoliation. When oak defoliation exceeded 80% the intensity of pine defoliation increased dramatically. This relationship was not as well defined within pine-sweetgum stands (Figure 4.6b), and defoliation of pines never exceeded 20%, though the basal area of susceptible species and defoliation intensities were similar to those of pine-oak stands.

These results illustrate the variation in species and individual tree defoliation that is commonly found in areas subjected to gypsy moth outbreaks. It is often extremely difficult to attribute these observed differences to a specific causal factor because so many have been

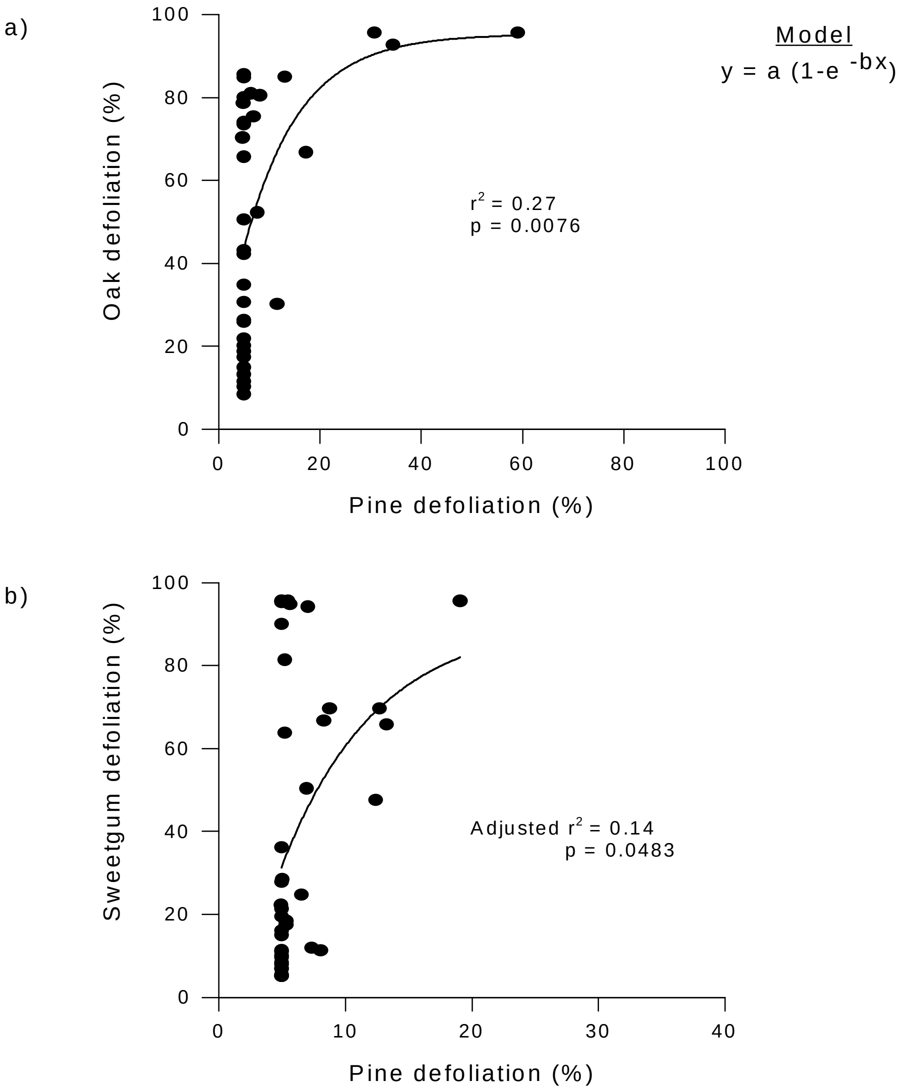

Figure 4.6: Relationships between a) defoliation of pines and oaks in pine-oak stands, and b) defoliation of pines and sweetgum in pine-sweetgum stands, between 1992 and 1996.

identified throughout the years, and because they are frequently correlated. Climate, site factors, inter- and intraspecific susceptibility to defoliation, and the dynamics of predator and prey populations have all been cited as possible contributors to differential defoliation rates in previous studies (Byington et al., 1994; Campbell and Sloan, 1977; McManus, 1987). Some investigators have speculated that pine stands with an understory of susceptible hardwoods may be at risk of severe defoliation. Based on these results, even in areas of intense gypsy moth activity, it would be premature to expect widespread pine defoliation. However, moderate to heavy defoliation of individual trees or within small, localized areas may be possible.

Numerous studies have confirmed the importance of species composition in determining stand susceptibility and subsequent defoliation in mixed hardwood stands (Campbell and Sloan, 1977; Herrick and Gansner, 1986; Houston and Valentine, 1985). Because both of the cover types within this study contained varying levels of susceptible species, examination of defoliation trends on an individual stand basis provides a better feel for the relationships between species composition, stand susceptibility, and defoliation intensity (Table 4.6). While the factors described above are important, the principal determinant of defoliation intensity is larval presence and the size of the larval population. Both cover types were examined during the course of an outbreak, thus defoliation intensities were quite variable within the five year measurement period (Table 4.6). However, an obvious relationship between species composition and subsequent gypsy moth defoliation in both pine-oak and pine-sweetgum stands was observed. In both cover types, pine basal area displayed a negative relationship with mean total stand defoliation (Figures 4.7a and 4.8a); while the relationship between mean total stand defoliation and oak, sweetgum and

Table 4.6: Mean stand defoliation from 1992 to 1996 in seven pine-oak stands and nine pine-sweetgum stands.

Stand No.		Years				
		1992	1993	1994	1995	1996
		--- % ---				
Pine/Oak						
1		18.4	83.0	60.5	35.7	9.0
2		9.6	11.0	66.2	26.8	8.7
3		20.6	28.7	31.4	8.6	5.7
4		---	6.1	65.9	22.5	8.5
5		14.8	25.1	32.3	30.6	10.5
6		8.6	15.7	18.6	16.4	8.5
7		6.1	8.7	23.1	16.3	8.8
	mean	13.0	25.5	42.6	22.4	8.6
	std. dev.	5.8	26.7	20.9	9.4	1.4
Pine/Sweetgum						
8		---	7.0	40.3	61.8	17.9
9		---	7.7	32.6	42.7	11.4
10		6.2	5.6	14.4	37.9	10.1
11		---	5.6	30.0	36.8	28.8
12		6.1	6.4	20.2	27.2	9.4
13		6.3	5.4	17.5	30.6	9.9
14		8.1	18.9	26.9	34.0	12.0
15		5.4	5.0	10.1	9.6	5.8
16		8.7	7.2	27.4	14.1	7.0
	mean	6.8	7.6	24.4	32.8	12.5
	std. dev.	1.3	4.3	9.6	15.4	7.0

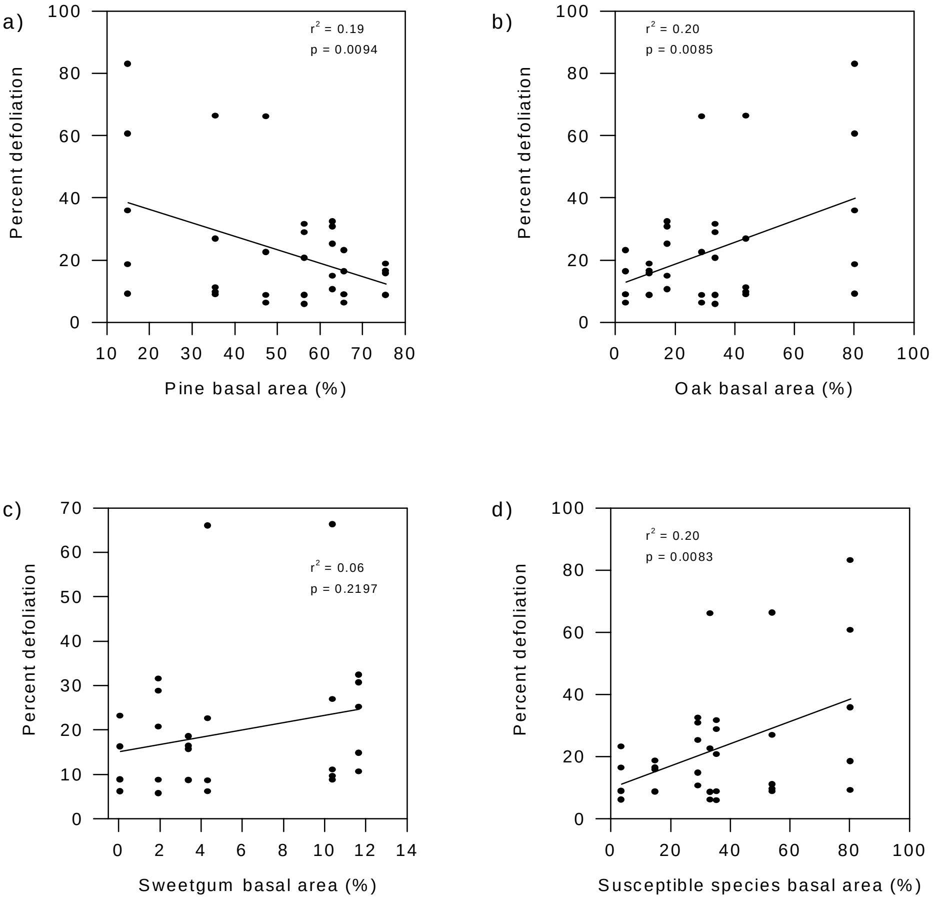

Figure 4.7: The relationship between mean stand defoliation and the proportion of a) pine, b) oak, c) sweetgum, and d) all susceptible species in pine-oak stands; species composition was determined as a percentage of total initial basal area.

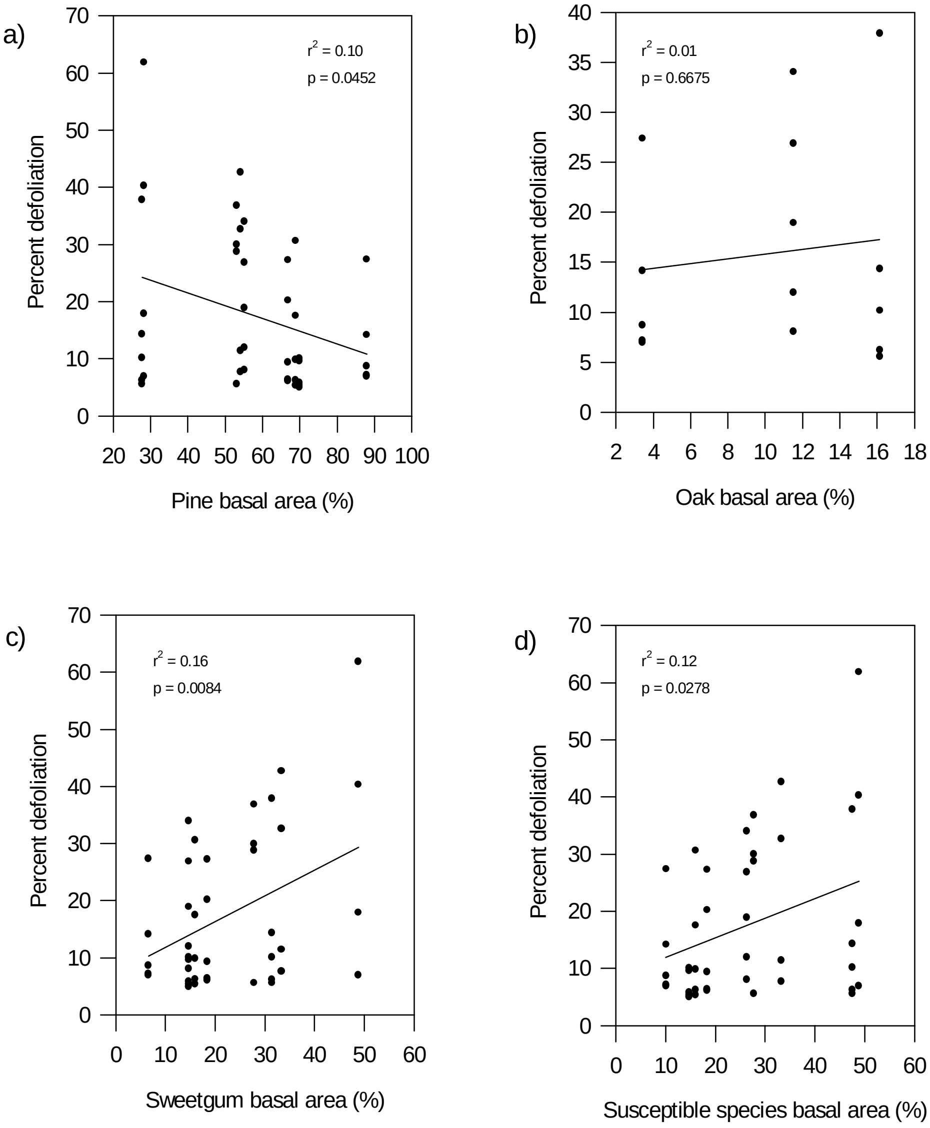

Figure 4.8: The relationship between mean stand defoliation and the proportion of a) pine, b) oak, c) sweetgum, and d) all susceptible species in pine-sweetgum stands; species composition was determined as a percentage of total initial basal area.

susceptible species basal areas was positive (Figures 4.7b-d and 4.8b-d). In pine-oak stands, simple linear regression analysis confirmed the significance of three of these relationships. Initial basal areas of pine, oak, and susceptible species were all significant at the 0.05 probability level, only sweetgum basal area proved to be non-significant (Table 4.7). Pine basal area explained 19% of the variation in mean defoliation, while oak and susceptible species basal area explained 20% of the variability. In pine-sweetgum stands, these variables exhibited the same general relationships; the initial basal areas of pine, sweetgum and susceptible species were significant at the 0.05 level, but oak basal area was non-significant (Figure 4.8b, Table 4.7). The amount of variability explained by each independent variable in this stand type was lower than in pine-oak stands (Table 4.7). In both stand types the species that comprised the minor proportion of the susceptible hardwood component did not significantly influence defoliation intensity.

Previous investigators have successfully utilized the QMD of susceptible species in the determination of stand susceptibility (Houston and Valentine, 1985). In this study, relationships between the QMD's of the various species and species group, and mean total stand defoliation were not as clear. While scatter plots of the data appeared to indicate possible relationships, simple linear regression analysis found no significant influence of QMD on defoliation (Table 4.7). None of the regression models were significant at the 0.05 probability level and r^2 values were very low (Table 4.7).

Egg mass density has shown considerable promise in the prediction of defoliation in mixed hardwood stands in Pennsylvania and the New Jersey (Gansner et al., 1985; Liebhold et al., 1993; Williams et al., 1991). Scatter plots of egg mass density showed a strong relationship between this

Table 4.7: Results of simple linear regressions of mean total stand defoliation (%) on the percentage basal area and quadratic mean diameter of pine, oak, sweetgum and susceptible species (combined oak and sweetgum).

Cover Type	**Variable**	**Measurement Units**	**r^2**	**Standard Error**	***t* value**	***p* value**
Pine/Oak						
	Pine BA	%	0.19	0.1570	-2.76	0.0094
	Oak BA	%	0.20	0.1260	2.80	0.0085
	Sweetgum BA	%	0.06	0.6510	1.26	0.2197
	Susceptible BA	%	0.20	0.1272	2.81	0.0083
	QMD - pine	cm	0.11	0.4771	-1.95	0.0596
	QMD - oak	cm	0.02	0.7150	0.78	0.4432
	QMD - sweetgum	cm	0.08	0.4219	1.54	0.1354
	QMD - susceptible	cm	0.04	0.6671	1.19	0.2443
	Egg mass density	#/ha	0.15	8.07×10^{-6}	2.09	0.0471
	Stem density	stems/ha	0.16	1.21×10^{-4}	-2.22	0.0361
Pine/Sweetgum						
	Pine BA	%	0.10	0.1083	-2.07	0.0452
	Oak BA	%	0.01	0.5399	0.44	0.6675
	Sweetgum BA	%	0.16	0.1632	2.77	0.0084
	Susceptible BA	%	0.12	0.1504	2.28	0.0278
	QMD - pine	cm	0.03	0.2785	1.16	0.2541
	QMD - oak	cm	0.02	0.2986	0.53	0.6021
	QMD - sweetgum	cm	0.02	0.2701	0.90	0.3732
	QMD - susceptible	cm	0.03	0.2979	1.18	0.2444
	Egg mass density	#/ha	0.53	2.86×10^{-6}	5.77	0.0001
	Stem density	stems/ha	0.08	7.38×10^{-5}	-1.63	0.1141

variable and mean total stand defoliation in pine-sweetgum stands ($r^2 = 0.53$, p = 0.0001); in pine-oak stands the relationship was weaker ($r^2 = 0.15$, p= 0.0471), but this may be due to a limited range of data points (Figure 4.9).

Though both oak and sweetgum basal area were significant factors within their respective cover types, when present as a minor stand component they contributed very little to the understanding of the defoliation/species composition relationship. Therefore, combined susceptible species basal area was chosen as an independent variable in further regression models. This choice was bolstered by the fact that both oaks and sweetgum are widely recognized as susceptible hosts (Barbosa et al., 1983; Houston and Valentine, 1985; Liebhold et al., 1995). Also, in addition to these species co-occurring within this study, the southern oaks and sweetgum are also sympatric throughout much of the Atlantic Coastal Plain (Harlow et al., 1991; Liebhold et al., 1997). Finally, using only oak basal area ignored the contribution of sweetgum to overall defoliation in pine-oak stands and using only sweetgum basal area ignored the contribution of oak in pine-sweetgum stands.

In addition to combining oak and sweetgum basal area to form susceptible species basal area, determining whether the two cover types could be considered as separate significant factors in stand susceptibility was also of interest. This hypothesis was tested by combining the two data sets (pine-oak and pine-sweetgum stands), and using multiple linear regression with a dummy variable for cover type to test for significance. The results of this analysis revealed cover type to be non-significant (F value=0.15, p=0.7045). Gypsy moth larvae seek out suitable foliage when feeding; laboratory studies have classified both species as suitable hosts, therefore, whether oaks

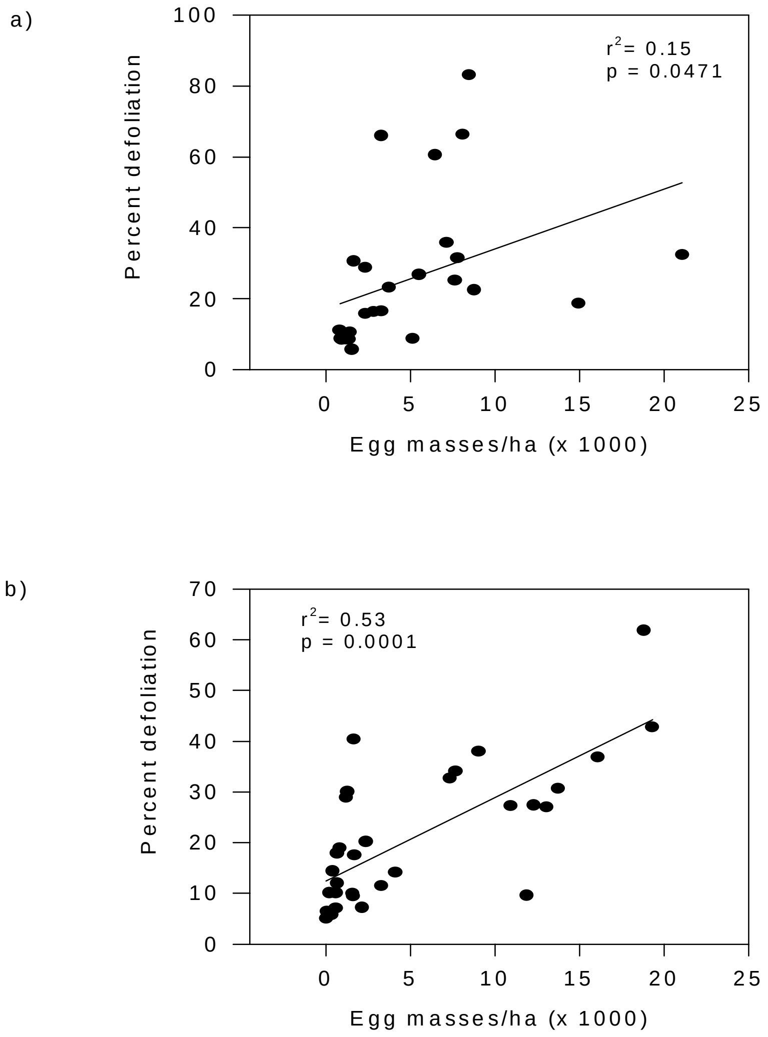

Figure 4.9: The relationship between mean stand defoliation and gypsy moth population density in the year prior to defoliation in a) seven pine-oak stands and b) nine pine-sweetgum stands.

or sweetgum are a dominant or minor stand component is irrelevant. The more important question in the determination of stand susceptibility is whether they (or other susceptible species) are present.

Because the relationships between stand composition and defoliation are so complex, it seems probable that the interactions between variables would affect susceptibility more than any single variable. Therefore, three-dimensional scatter plots were utilized to search for interactions among the variables that appeared to have the most promise in predicting defoliation. The interactions between gypsy moth population density, species basal area and mean total stand defoliation in pine-oak and pine-sweetgum stands are shown in Figures 4.10 and 4.11. Both figures show a distinct response surface relating these three variables. In the pine-oak type, stands with approximately the same gypsy moth population size exhibited reduced defoliation as the amount of pine basal area increased (Figure 4.10a). Reductions in pine basal area and population size combined to produce an overall reduction in mean total stand defoliation. A near mirror-image of this relationship is produced when susceptible species basal area is substituted for pine basal area (Figure 4.10b). The above relationships are also true in pine-sweetgum stands, and they can be clearly seen in Figure 4.11. A simple linear regression analysis of the relationship between mean stand defoliation and the interaction between susceptible species basal area and egg mass density found the interaction term to be significant within both pine-oak ($r^2 = 0.49$, $p = 0.0001$) and pine sweetgum stands ($r^2 = 0.68$, $p = 0.0001$). The interaction between pine basal area and egg mass density was significant in pine-sweetgum stands ($r^2 = 0.28$, $p = 0.0015$), but was not significant in pine-oak stands ($r^2 = 0.008$, $p = 0.6606$).

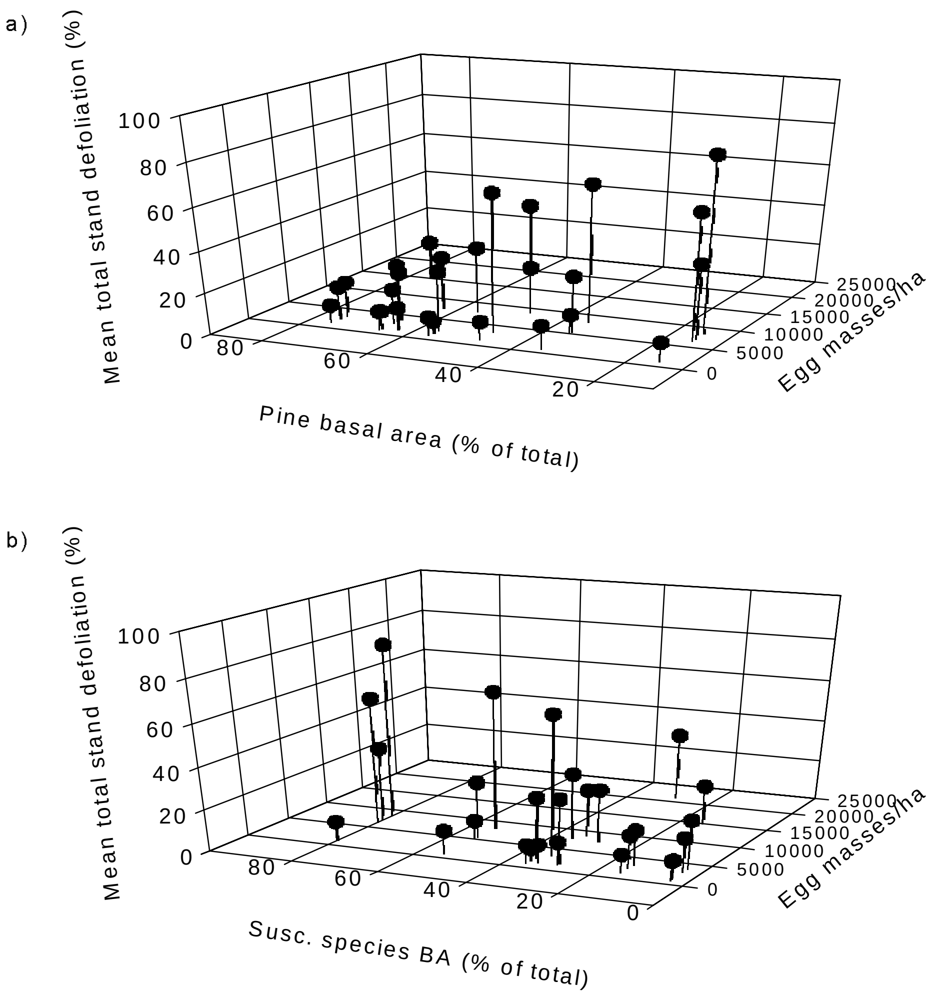

Figure 4.10: The effect of a) initial pine basal area and population density (egg masses/ha) on mean stand defoliation, and b) initial susceptible species basal area and population density on mean stand defoliation in pine-oak stands.

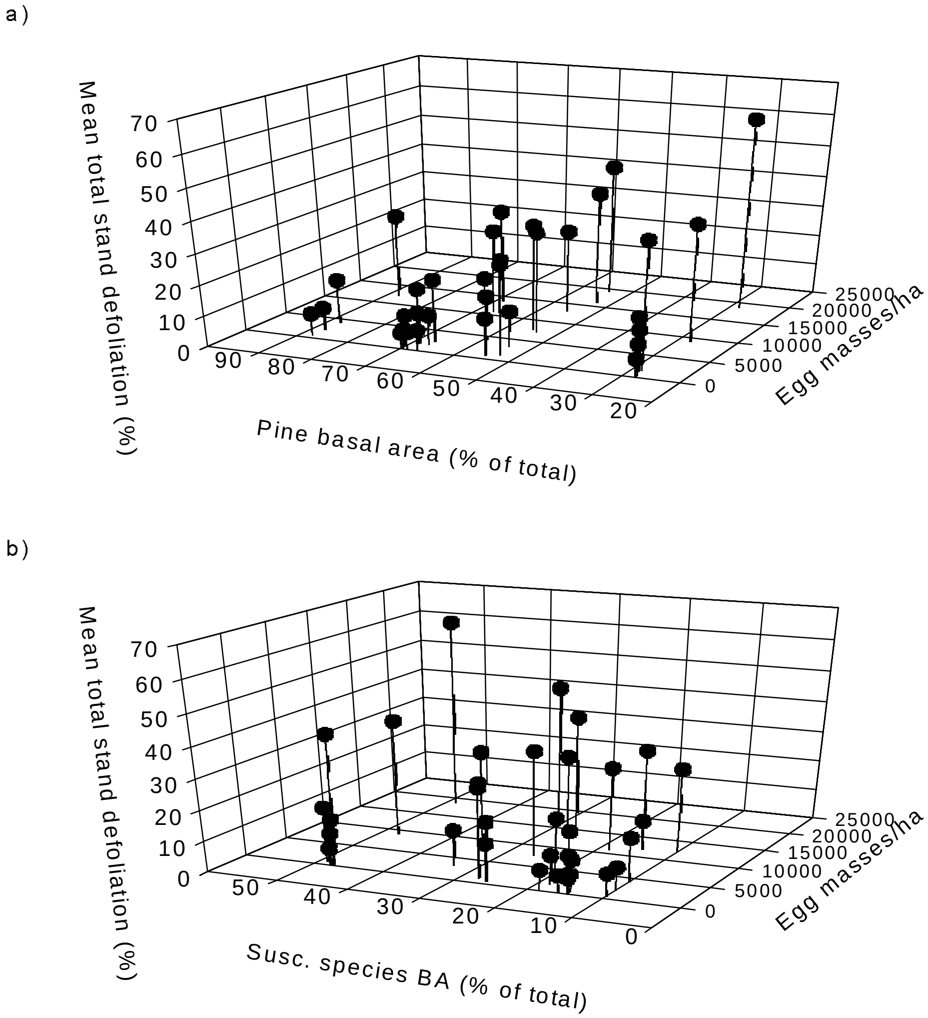

Figure 4.11: The effect of a) initial pine basal area and population density (egg masses/ha) on mean stand defoliation, and b) initial susceptible species basal area and population density on mean stand defoliation in pine-sweetgum stands.

Modeling Defoliation Relationships

Prior to conducting a multiple linear regression analysis, correlation analysis was used to test for multicollinearity. Multicollinearity creates redundancies, blurs the relationships among variables, and reduces the overall effectiveness of the regression model (Rawlings, 1988). Because of the underlying relationships between some of the variables in this study, collinearity was a valid concern. Table 4.8 shows the results of a correlation analysis between egg mass density, pine basal area, susceptible species basal area, the QMD's of pines and susceptible species and stem density, using Pearson correlation coefficients (SAS, 1992). Not surprisingly, pine basal area and susceptible species basal area show significant collinearity ($r = -0.92$, $p = 0.0001$). Therefore, these two variables were not included in the same model in subsequent regressions.

The all possible regressions method was used to assist in the selection of an appropriate prediction model. This procedure fits all the possible regression models, then pre-determined criteria are used to assess model adequacy (Draper and Smith, 1981). Mallows' Cp statistic was used as a model discriminator (SAS, 1992). With this method, regression equations with a Cp value that is less than p, the number of variables within the equation including the intercept, are all possible candidates. The theoretically "best" model is one where Cp is approximately equal to p (Draper and Smith, 1981). Sixty-four regression equations were examined; the analysis identified 33 possible candidates for further analysis. Simple and multiple regression analysis, in conjunction with regression diagnostics to identify potential problems within each equation were then used to reduce the number of potential models to four (Table 4.9). In addition to linear regression analysis, non-linear logistic and Weibull functions were also tested. However, these did not

Table 4.8: Pearson correlation coefficients of six independent variables; the values in parentheses are the *p* values for *r* under H_o: *Rho* = 0.

	Egg mass density	**Pine BA**	**Susc. BA**	**Susc. QMD**	**Pine QMD**	**Stem Density**
Egg mass density (#/ha)	1.0000 (0.0)	-0.0402 (0.7604)	0.0895 (0.4966)	-0.0283 (0.8298)	0.0291 (0.8253)	-0.0113 (0.9317)
Pine BA (%)		1.0000 (0.0)	-0.9244 (0.0001)	-0.6818 (0.0001)	0.0233 (0.8596)	0.6926 (0.0001)
Susc. BA (%)			1.0000 (0.0)	0.4440 (0.0004)	-0.2519 (0.0521)	0.6336 (0.0001)
Susc. QMD (cm)				1.0000 (0.0)	0.5771 (0.0001)	-0.4919 (0.0001)
Pine QMD (cm)					1.0000 (0.0)	-0.1692 (0.1962)
Stem Density (#/ha)						1.0000 (0.0)

provide an adequate fit and were discarded.

The top four models listed in Table 4.9 contain two independent variables that are intuitively the most appropriate within the situation under study. Egg mass density provides a direct estimation of the population size, a known component of stand susceptibility. The basal area of susceptible species provides an estimate of the proportion of available foliage that prior studies have shown are preferred by larvae. The importance of the interaction of these two variables was described previously. Stem density has not been cited as a significant contributor to stand susceptibility in prior studies. It was included here because of its variability among the stands under study.

All four regression models were significant ($p = 0.0001$). An analysis of the residuals, influence statistics and collinearity estimates did not indicate any serious departures from the assumptions of multiple linear regression (Figure 4.12). However, of the individual parameter estimates within each model, only the interaction between egg mass density and the basal area of susceptible species was significant. Though the other terms contributed to the overall prediction of defoliation, their parameter estimates were not significant.

Model 3 which uses the interaction of egg mass density and susceptible species basal area, is the most suitable of the four equations for the prediction of mean total stand defoliation. It has a low mean square error (0.01352), plots of the studentized residuals are normal, and defoliation predictions are reasonable. In contrast, Models 1, 2, and 4 all exhibit traits that removed them from further consideration. Addition of another variable to the regression model did not significantly reduce the mean square error; the greatest reduction was for Model 1, where addition

Table 4.9: Regression statistics for the top four models identified by all possible regressions using Mallows' Cp statistic (SAS, 1992).

Model No.	r^2	Adj. r^2	Independent Variables[1]	t value	p value
1	0.57	0.56	EM	-1.589	0.1177
			(EM x Susc. BA)	6.294	0.0001
2	0.57	0.56	Stem density	-1.486	0.1427
			(EM x Susc. BA)	7.635	0.0001
3	0.55	0.55	(EM x Susc. BA)	8.486	0.0001
4	0.24	0.23	Susc. BA	4.295	0.0001

[1] EM = egg mass density in number of egg masses per hectare; Susc. BA = basal area of susceptible species as a percentage of the total initial basal area; Stem density = initial stem density in number of stems per hectare.

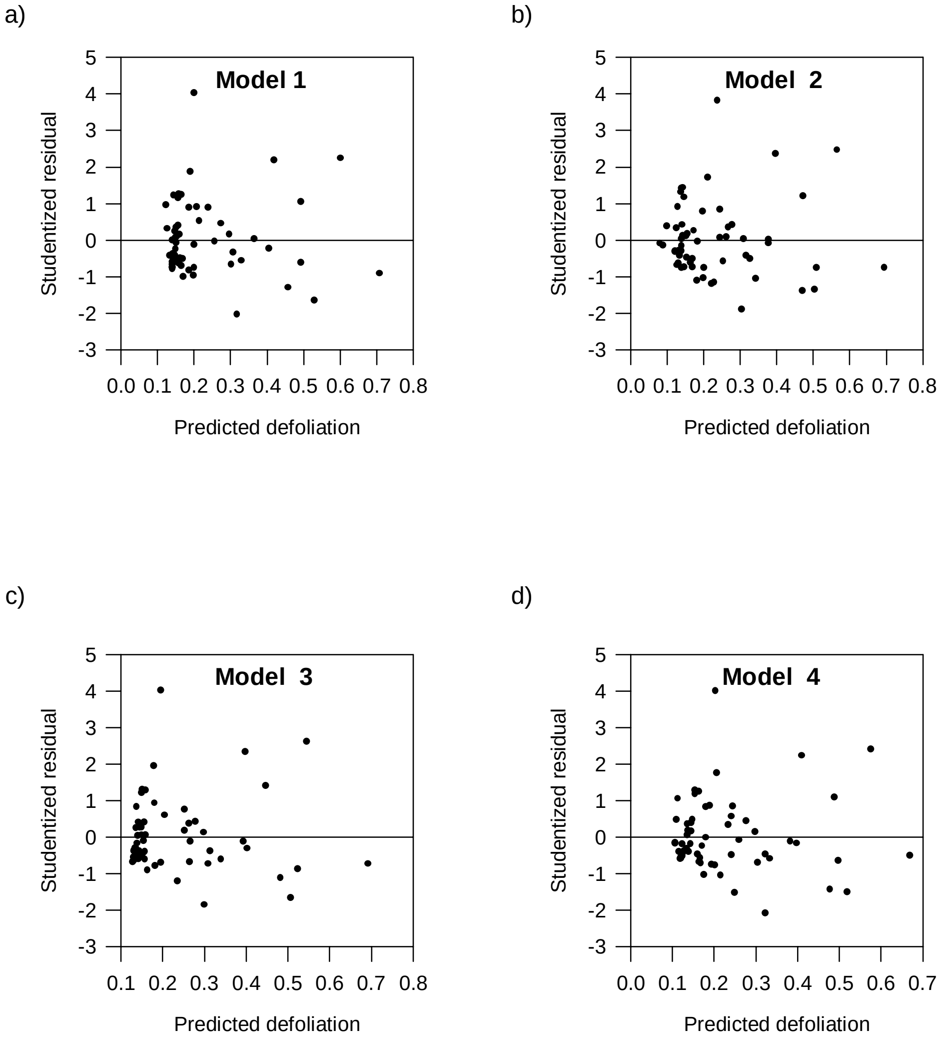

Figure 4.12: Residual plots of the studentized residuals vs. predicted defoliation for a) Model 1, b) Model 2, c) Model 3, and d) Model 4.

of egg mass density resulted in a mean square error of 0.1317. However, the parameter estimate for this variable was not significant and more importantly the sign on the estimate was now incorrect. Instead of a positive relationship, egg mass density was negative. Model 2 displayed similar problems with the parameter estimate of stem density. Collinearity diagnostics also indicated some problems with the addition of this variable to the regression model. In model 4, though the parameter estimate was significant and collinearity was no longer a concern, the lack of a significant reduction in mean square error and a significant reduction in predictive ability ($r^2=0.24$) resulted in it's elimination.

Therefore, Model 3 as outlined below appeared to be the most appropriate model for use in the prediction of mean total stand defoliation in mixed pine hardwood stands.

<u>Model 3:</u>

percent defoliation = 0.12896 + 0.0000614 (egg mass density x susceptible species BA)

where the percent defoliation value predicted is the mean total stand defoliation (%), egg mass density is the number of egg masses per hectare, and susceptible species basal area is the proportion of susceptible species as a percentage of total basal area within the stand.

Model Validation

A prediction model is only useful if future estimates of the variable of interest can be made with confidence. This confidence is often achieved through validation of the model using an independent data set. The creation of this data set can be accomplished by either splitting the original development data set and using a portion for model development and the remainder for validation, or by collection of another set of data for the specific purpose of model validation. Both methods have their advantages and disadvantages. In the former case, whenever a data set is reduced there is the possibility that important predictive information will be lost. In the latter, both the length of time required and the cost of additional data collection is often prohibitive. In this study the original data set was relatively small (n=59), thus all of the original observations were used in model development. Model validation was achieved through selection of a random sample of 20 observations from the 59 original observations to create a validation data set, and subsequent defoliation prediction using Model 3. Results of this prediction are shown in Table 4.10. The model appeared to perform adequately; the mean difference between actual and predicted defoliation was –3.15 (standard deviation = 10.68). If the model performed perfectly, then the expected mean difference would be zero, thus values that are close to zero are desirable. The negative sign associated with the mean difference indicates that on average the model tends to over-predict the actual defoliation.

Figure 4.13 shows partial regression curves that were produced using Model 3 and a range of possible values for the number of egg masses per hectare and susceptible species basal area.These curves can be used in place of the equation to predict the average defoliation for a mixed pine-hardwood stand if the basal area of susceptible species, and the gypsy moth population size is known. In areas that do not currently have gypsy moth populations, but where the basal area of susceptible species can be estimated, the curves can be utilized to predict the

Table 4.10: Actual defoliation values and corresponding predicited values using Model 3 for a random sample (n=20 observations) of the development data set.

Actual Stand Defoliation	**Predicted Stand Defoliation**	**Difference**
-------------------------- % --------------------------		
9	14	-6
9	13	-4
9	30	-21
9	18	-9
9	15	-5
11	16	-5
14	14	0
16	14	3
16	16	0
19	27	-8
23	31	-8
27	25	2
29	18	11
31	16	15
33	28	5
36	48	-13
38	39	-1
61	45	16
62	69	-7
83	55	28

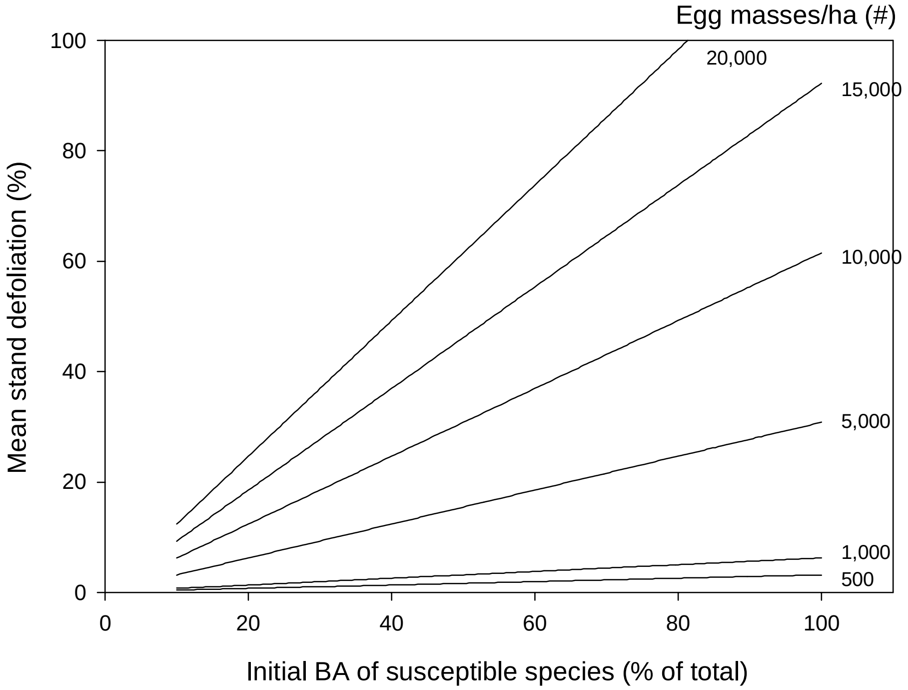

Figure 4.13: Partial regression curves for use in the prediction of mean stand defoliation in mixed pine-hardwood stands; in the diagram each curve represents a particular density of gypsy moth egg masses, by using the initial basal area of susceptible species (% of total basal area) on the X axis and the number of gypsy moth egg masses per hectare in the stand, the estimated mean stand defoliation (%) can be found on the Y axis.

worst case scenario for a particular stand. In addition to its’ predictive ability this model has some advantages over other prediction models. Both egg mass density and susceptible species basal area, the variables that comprise the interaction term, are relatively easy to collect. Through forest inventory, many forest managers may already know the proportion of susceptible species basal area within their management units. Collection of data on egg mass density through the use of fixed plots is relatively simple (Liebhold et al., 1994); and the incorporation of egg mass surveys into existing management plans should be relatively painless. Though variables such as egg mass length, and tree structural features may increase the accuracy of prediction, as suggested by previous researchers, they are much more time consuming and difficult to estimate (Houston and Valentine, 1977; Liebhold et al., 1993). When selecting models for use in forest management it is important to remember that for the most part, ease of use largely determines whether a procedure is accepted and adopted.

CONCLUSIONS

The continued advance of gypsy moth populations into the southeastern United States is inevitable. A favorable climate and an abundance of susceptible hosts only increases the likelihood that southern forests will at some point experience gypsy moth defoliation (Liebhold et al., 1997). Mixed pine-hardwood stands and pine plantations with a hardwood understory comprise a significant proportion of the forest types within the southeast. Therefore a tool that would allow forest managers to predict the susceptibility of these stand types would be a welcome addition.

In this paper the factors that affect the susceptibility of Coastal Plain mixed pine-hardwood stands have been examined. Gypsy moth defoliation was observed in both pine-oak and pine-sweetgum cover types. Stand composition was significantly related to defoliation intensity; stands with a greater proportion of susceptible species experienced greater defoliation. Among individual species, the susceptible oaks and sweetgum were defoliated at the greatest intensities. Pines were not heavily defoliated in either cover type. Therefore, the probability of widespread gypsy moth defoliation in pine plantations appears to be low. However, in three stands within the pine-oak type, defoliation intensities did increase and they appeared to be related to a threshold level of oak defoliation. These results indicate these relationships are dynamic and require further study.

A multiple linear regression model for the prediction of mean total stand defoliation within these stands is also presented. While the model performs adequately, it must be remembered that gypsy moth defoliation is dependent upon a complex of interacting and often interrelated factors. Accurate prediction of defoliation is therefore difficult. Thus use and interpretation of this model outside the range of the measurements used its formulation is inadvisable.

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CHAPTER 5

The European gypsy moth in Coastal Plain mixed pine-hardwood stands: patterns of tree mortality and prediction of individual tree mortality

INTRODUCTION

Phytophagous insects are pervasive within forest ecosystems, and defoliation of forest trees is a frequent occurrence. However, in the majority of situations their presence is overlooked as the intensity of defoliation is relatively negligible. 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 often has numerous effects on forest stand dynamics. Defoliated trees experience reduced growth due to the loss of their photosynthate producing organs (Rafes, 1970, Kozlowski et al., 1991). This growth reduction may result in both a reduction in quality of the desired product and increased rotation lengths for forest managers. Conversely, during a defoliation outbreak, if only certain tree species are targeted, the undefoliated individuals may experience temporary benefits as a result of increased water, nutrients and light within the stand

(Wickman, 1980; Campbell and Garlo, 1982, Schweingruber, 1988). Targeting of certain species during a defoliation outbreak is characteristic of a number of defoliators, including the European gypsy moth. Though in actuality 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, such as aborted acorns, or a complete lack of acorn production, 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 red maple (*Acer rubrum* L.), reducing the ability of more desirable species such as oaks (*Quercus* spp.) to move into dominant canopy positions (Fajvan and Wood, 1996).

Individual tree mortality subsequent to defoliation is a function of a number of interrelated factors. The tree species, the frequency, intensity and duration of defoliation, the physiological condition of the tree prior to defoliation, and the presence and efficiency of secondary-action organisms all play a role in determining post-defoliation tree response (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 studies have attempted to utilize these characteristics in the prediction of tree mortality in hardwood stands (Crow and Hicks, 1990).

The movement of gypsy moth populations into the southeastern United States has raised some interesting 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. Will these stands be defoliated? If they are defoliated can tree mortality be expected, and if so at what scale, and which species are likely to be affected? Therefore, the objectives of this study were 1) to examine the relationships between initial stand conditions, gypsy moth defoliation and subsequent tree mortality in mixed pine-hardwood stands of the Atlantic Coastal Plain; and 2) to predict the probability of tree mortality within these stands.

METHODS

Study Area and Site Selection

The study was established in the counties of Dorchester, Somerset, Wicomico and Worcester, MD, in the Atlantic Coastal Plain physiographic province (between latitude 38° 35' N and 38° 5' N, and longtitude 75° 56' W and 75° 25' W). This area is characterized by a humid continental climate (USDA, 1970, 1973). The average growing season ranges from 180 to 200 days, extending from the middle of April to the end of October (USDA, 1959, 1970, 1973). Precipitation averages from 102 to 152 cm annually and is well distributed throughout the year, with most of the variability in rainfall occurring as a result of summer showers and thunderstorms

(USDA, 1970; Walker, 1994). Droughts are frequent and may negatively influence tree growth (Walker, 1994). The four counties are part of a low, eroded, plain where differences in elevation are generally slight; elevation ranges from sea-level to approximately 26 m above sea-level (USDA, 1970, 1973). Soils range from excessively drained to poorly drained, sands, loamy sands and sandy clay loams (USDA, 1959, 1970, 1973). They are sedimentary in origin and four soil orders are represented, Entisols, Inceptisols, Spodosols and Ultisols (USDA, 1959, 1970, 1973).

Research plots were established in sixteen mixed pine-hardwood stands in 1991, 1992 and 1993 (Figure 5.1). Stands were selected that contained mixtures of loblolly pine and oak, or loblolly pine and sweetgum (*Liquidambar styraciflua* L.). Selection was based on several criteria with the most important being stand composition; a range of species composition, from nearly pure hardwood to nearly pure pine was desired. Additionally stands were required to have a well-developed crown structure; to occur on medium quality forest sites, based on pine site index; to have minimal or no prior gypsy moth defoliation; and to occur on the "leading edge" of the gypsy moth infestation.

Plot Design and Vegetation Measurements

Three 400 m^2 (0.04 ha) sample plots were randomly established within each of the sixteen stands. All plots were located with a minimum separating distance of 50 m. The following variables were measured at time of establishment and annually thereafter until 1996: tree species, total height, diameter at 1.37 m (dbh), and percent defoliation for all woody stems ≥ 5 cm dbh.

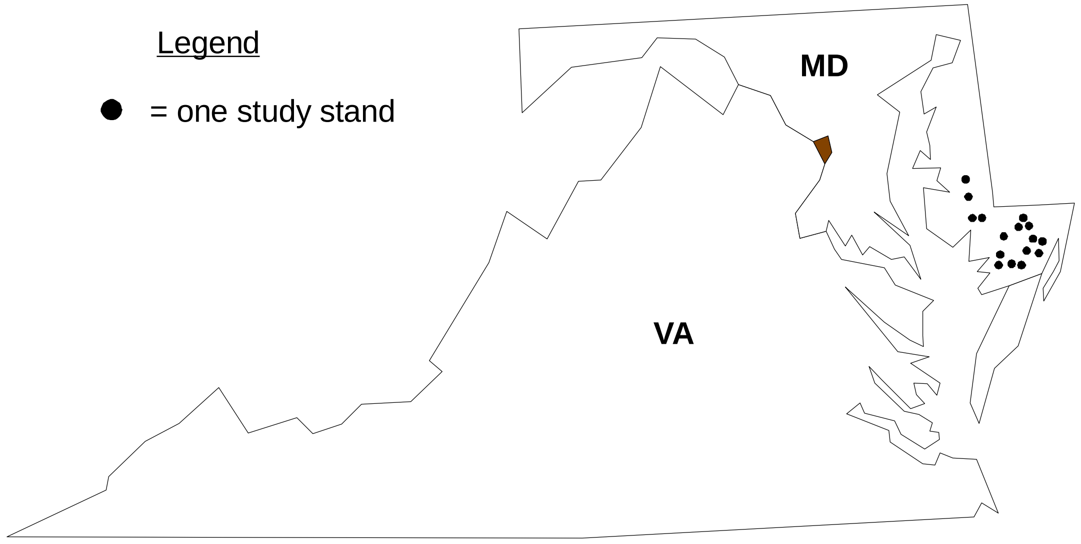

Figure 5.1. Map of Virginia and Maryland showing the location of study stands within the Atlantic Coastal Plain physiographic province.

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%. 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 present within the stand. Three sample plots, 0.01 ha in size, were established at pre-determined locations within each 0.04 ha plot, and the number of egg masses within each plot was used to estimate population size. Within an individual stand both newly laid egg masses and those from previous generations may be present; differentiating between the two can be difficult unless the egg mass can be examined by hand. Therefore the method proposed by Liebhold et al. (1994) was used to reduce the possibility of overestimating population sizes. Liebhold et al.'s method uses the proportion of new to old egg masses counted on the ground to adjust for the number counted in the tree crowns. However, because no distinction was made between old and new egg masses when the 1992 population survey was carried out, data for the number of egg masses in 1992 was adjusted using the proportion of new to old egg masses from the 1993 population survey.

Plot center was permanently located on all 0.04 ha plots with steel rebar covered with a 3/4 inch pvc pipe. All trees ≥ 5cm dbh were individually numbered, and dbh was marked with a painted line to facilitate re-measurement at the same location every year. Annual measurements were taken during the summer months unless otherwise specified. Overstory measurements were collected through 1996; however, only tree diameters, defoliation and gypsy moth population size were measured in 1994, and height measurement was discontinued in 1995. Tree mortality was assessed every year, from time of plot establishment (1992 or 1993) until 1996. Mortality was calculated as both the total number, and basal area, of trees that died.

Stand Characteristics and Defoliation History

Two cover types were examined; stands containing mixtures of loblolly pines and oaks, hereafter referred to as the pine-oak type; and stands containing mixtures of loblolly pines and sweetgum, the pine-sweetgum type (Table 5.1). In both cover types, various species of oaks, pines and sweetgum comprised the largest percentage of total basal area.

Both cover types were subjected to a single defoliation outbreak encompassing the years between 1992 and 1996. During the outbreak period, annual defoliation episodes produced a range of defoliation intensities within individual stands. Stand defoliation levels ranged from none (0-10%) to heavy (62-90%) within both the pine-oak and the pine-sweetgum types. The pattern of defoliation was similar in both cover types; stands with a high percentage of susceptible species experienced the greatest defoliation intensities.

Oaks, sweetgum, and pine were the three major genera observed within both pine-oak and pine-sweetgum cover types. Oaks and sweetgum are considered susceptible to gypsy moth defoliation, that is, they are eaten by all larval stages of the gypsy moth (Montgomery, 1991; Liebhold et al., 1995). Both genera were heavily defoliated between 1992 and 1996. Pines are considered resistant to defoliation, and are only consumed once gypsy moth larvae have reached the second instar (Montgomery, 1991; Liebhold et al., 1995). In both cover types, oak defoliation

Table 5.1: Stand characteristics of sixteen mixed pine-hardwood stands at the time of plot establishment.

Cover Type and Stand #	**Stand BA**	**Density**	**Mean DBH (cm)**	**Stand Age (yrs)**	**Species Basal Area (% of total)**			
					Oak	Sweetgum	Pine	Other Hdwds
	--- m^2/ha ---	- stems/ha -	-- cm --	--- yrs ---	-------------------------------- % of total --------------------------------			
Pine/Oak								
1	14.3	683	15.4	40	80.3	0.0	15.0	4.7
2	30.9	1092	15.8	55	43.8	10.4	35.6	10.1
3	27.9	992	16.4	68	33.6	2.0	56.4	8.0
4	34.4	667	20.4	73	29.1	4.3	47.5	19.0
5	37.1	1483	15.3	88	17.6	11.7	63.0	7.8
6	40.2	1358	16.6	62	11.5	3.4	75.5	7.6
7	32.0	1408	13.5	55	3.6	0.1	65.7	30.6
Pine/Sweetgum								
8	37.8	800	21.4	55	0.0	48.8	28.3	22.9
9	45.2	1167	18.1	65	0.0	33.3	54.1	12.5
10	52.8	1283	18.7	59	16.1	31.4	27.8	24.6
11	51.4	1425	17.9	49	0.0	27.8	53.1	19.1
12	50.4	1042	21.9	57	0.0	18.4	66.9	14.7
13	47.9	1142	19.2	54	0.0	16.0	68.9	15.1
14	40.0	1292	16.7	73	11.5	14.8	55.1	18.6
15	49.1	1308	18.4	46	0.0	14.7	69.9	15.3
16	36.8	2029	13.4	30	3.4	6.6	87.9	2.0

was significantly greater than that of both sweetgum and pines in the early years of the defoliation outbreak; but there was no significant difference between sweetgum and pines (Figures 4.4, 4.5). As the outbreak progressed, sweetgum defoliation increased and for the remainder of the outbreak both oak and sweetgum defoliation were significantly greater than pine defoliation. Within individual stands, the susceptible species were also defoliated at much greater intensities. These patterns of defoliation among susceptible species have been observed in a number of prior studies (Baker, 1941; Kegg, 1971; Campbell and Sloan, 1977; Fosbroke and Hicks, 1989). As a result, the greater defoliation intensity among susceptible species has been cited as a primary factor in the elevated mortality rates that have been observed in this group (Herrick and Gansner, 1987) .

Statistical Analysis

Logistic regression was used to determine the relationship between individual tree mortality, and initial stand and individual tree characteristics. Logistic regression is a technique that can be used to describe the functional relationship between a dichotomous (or polychotomous) dependent variable, and several discrete or continuous independent variables (Anderson et al., 1980; Trexler and Travis, 1993). Previous studies have utilized discriminant analysis in the prediction of tree mortality (Monserud, 1976). Discriminant analysis, however, requires that the independent variables have a multivariate normal distribution (Monserud, 1976; Hassler et al., 1986). In cases where discrete independent variables are utilized this requirement is not satisfied and the use of logistic regression has been suggested (Press and Wilson, 1978). The logistic regression function is

$$\pi(x) = [\ 1 + e\ (-\ (\ \beta_0 + \beta_1 X_1 + \ldots + \ \beta_n X_n\ )\ )\ ]^{-1} \qquad \textbf{(1)}$$

where,

$\pi(x)$ = probability of tree mortality (0 to 1)

e = the base of natural logarithms

β_0 = intercept

$\beta_1 \ldots \beta_n$ = regression coefficients

$X_1 \ldots X_n$ = independent variables

In this study the individual trees were classified as either 0 (dead) or 1 (alive) at the end of the gypsy moth outbreak. The method of maximum likelihood (SAS, 1992) was used to fit linear logistic regression models using six discrete and four continuous independent variables. These discrete variables are listed in Table 5.2. The continuous variables included the initial basal area of susceptible species within the stand, as a percentage of the total basal area (SUSCBA); the stem density (DENSITY); the maximum mean total stand defoliation observed during the outbreak (MAXDEF); and the number of years of defoliation greater than 60% (YRSOFDEF). Among the discrete variables, both HOST and CANOPY were created with a specific purpose, to reduce the number of levels within the original variables SPECIES and CRCLASS, and thereby aid in the prediction of mortality. The use of HOST enabled trees to be classified as either susceptible or

Table 5.2: Listing of the discrete variables used in the formulation of logistic regression equations, the coded value refers to the descriptive term used for the variable in the logistic regression equations.

Discrete Variables	Categories	Coded Value
Cover type	pine-oak pine-sweetgum	COVER
Species	24 species	SPECIES
Crown Class	suppressed intermediate codominant dominant	CRCLASS
Crown condition	good fair poor	CRCOND
Host preference class	susceptible non-susceptible	HOST
Canopy position	understory overstory	CANOPY

non-susceptible, reducing the levels used in prediction from 24 to 2. The use of CANOPY allowed trees to be classified as understory or overstory, rather than one of the four defined crown classes.

Model development

There are two schools of thought regarding the correct techniques to be used in model development. The first is that for adequate development of predictive equations the original data should be split into two data sets, one for model development, the other for validation of the derived prediction equations. This method is used to eliminate the inherent bias that results when the same data used to develop an equation is then used to judge its predictive ability. The second school of thought is based on the knowledge that using a large amount of data in model development results in an equation with enhanced predictive ability. In addition, by incorporating all of the available data, a wider spectrum of possible values for the variables under study are included. When data is split for any reason, there is a possibility that some information may be lost. When applying this method, all of the original data is included in model development and the predictive ability of the resulting equation is determined using jacknifing or bootstrapping techniques.

A preliminary multiple linear regression analysis revealed that cover type had a significant effect on the probability of tree mortality. This was supported by the previous results of an analysis of the relationships between species composition and stand susceptibility (Chapter 4). These results justified separation of the data and development of individual logistic equations by cover type. The original data for each cover type were then split into two data sets, one of which was used for model development, the other for model validation. The original data covered a wide range of stand conditions from nearly pure hardwoods to pine plantations. To account for this variation in species composition, individual tree observations from each of the seven pine-oak, and nine pine-sweetgum stands were included in the respective development and validation data sets. The development data set for the pine-oak cover type contained 547 observations, while the validation data set contained 256 observations. The development data set for the pine-sweetgum type consisted of 796 observations, and the validation data set contained 451 observations. Two of the sixteen stands were not included in the model development process due to the presence of confounding factors that indicated the observed mortality was not the result of gypsy moth defoliation alone. Stepwise logistic regression was then used to identify the “best” models for predicting the probability of tree mortality within each cover type based on the development data sets (SAS, 1992).

RESULTS AND DISCUSSION

Tree Mortality Subsequent to Defoliation

Variation in initial basal area and initial stem density was greater in pine-oak stands than in pine-sweetgum stands (Table 5.1), and this pattern was also evident in tree mortality subsequent to the outbreak. Mortality was observed in both cover types and in all of the defoliated stands that were examined (Table 5.3). Pine-oak stands lost an average of 5.0 m^2/ha of basal area, and 221 stems/ha. Basal area mortality in pine-sweetgum stands averaged 2.6 m^2/ha, while mean stem mortality was 119 stems/ha.

Table 5.3: Cumulative basal area mortality in m^2/ha and as a percentage of the initial basal area, and cumulative stem mortality in stems/ha and as a percentage of the initial number of stems in pine-oak and pine sweetgum stands.

Cover type and Stand #	**BA Mortality**		**Stem Mortality**	
	--- m^2/ha ---	-------- % -------	- stems/ha - -	------- % -------
Pine-oak				
1	0.5	3.3	50	7.3
2	4.6	14.8	150	13.7
3	11.0	39.6	575	58.0
4	8.1	23.5	116	17.5
5	4.8	13.0	325	21.9
6	5.1	12.6	283	20.8
7	0.6	1.8	50	3.6
Mean	5.0	15.5	221	20.4
Std. deviation	3.8	12.9	189	17.9
Pine-sweetgum				
8	0.9	2.5	50	6.2
9	0.8	1.8	75	6.4
10	1.2	2.3	50	3.9
11	1.2	2.4	116	8.3
12	0.7	1.4	66	6.4
13	8.3	17.3	175	15.3
14	4.9	12.3	158	12.2
15	1.6	3.2	150	11.5
16	3.6	9.7	233	11.2
Mean	2.6	5.8	119	9.0
Std. deviation	2.6	5.8	64	3.7

Influence of species composition

It is well known that gypsy moth larvae exhibit preferences for certain tree species, preferentially defoliating susceptible species, while avoiding resistant and immune species. As a result, during a defoliation outbreak there may be significant inter- and intraspecific variation in tree response (Mcgraw et al., 1990). This translates into the death of some species following a single defoliation, while others may tolerate multiple defoliation episodes (Campbell and Sloan, 1977; Twery, 1991). Also, trees of the same species may exhibit differences in vulnerability. Figure 5.2 shows mortality of individual species as a proportion of the total stem mortality within each cover type; Figure 5.3 shows how this mortality was distributed among host preference classes. Oaks and sweetgum were the only susceptible species found within either cover type. In the pine-oak type, susceptible species comprised 78% of total stem mortality. Of this amount, 94% were oaks and 6% were sweetgum. Resistant species (primarily pines) and immune species (primarily American holly, *Ilex opaca* L.) made up the remainder of the observed mortality, contributing 12.9% and 9.1% respectively. Within individual stands, susceptible species lost an average of 37.6 % of their original basal area and 38.6% of the original number of stems (Table 5.4). Mortality of resistant species averaged 7.2% of the original basal area while stem mortality averaged 7.9%. Heavy oak mortality has been characteristic of many of the recorded defoliation outbreaks in the northeastern U.S. and Pennsylvania (Baker, 1941; Campbell and Sloan, 1977; Gansner et al. 1993). While laboratory studies have shown southern oaks to be as susceptible to defoliation as their northern counterparts, the vulnerability of these species was only speculative (Barbosa et al., 1983). The response of oak species to defoliation in pine-oak stands is shown in Table 5.5. Some of the listed species, such as southern red (*Q. falcata* Michx.), water (*Q. nigra* L.), and willow oak (*Q. phellos* L.), are characteristic of Coastal Plain sites while others such as white (*Q. alba* L.), northern red (*Q. rubra* L.), and black oak (*Q. velutina* Lam.), are more widely

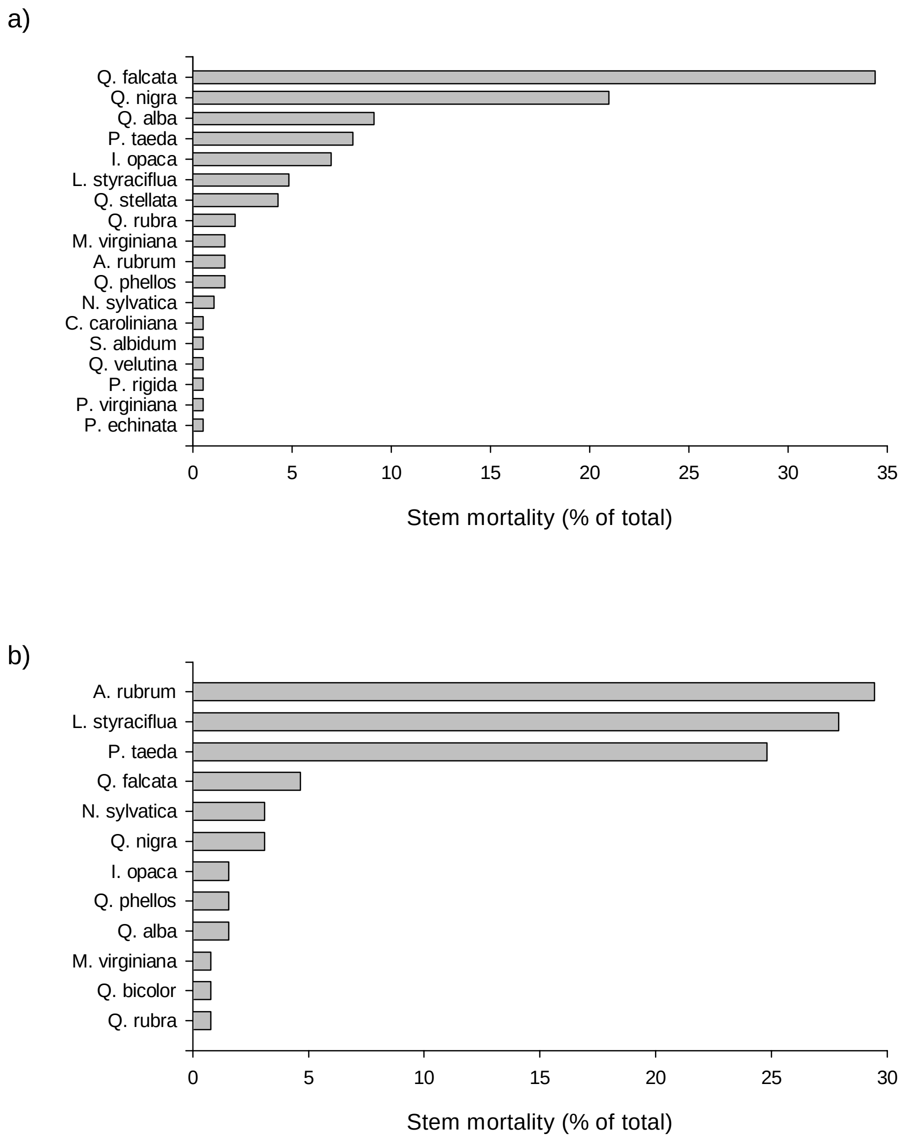

Figure 5.2: Mortality of individual tree species between 1992 and 1996 as a percentage of the total tree mortality within a) seven pine-oak stands and b) nine pine-sweetgum stands.

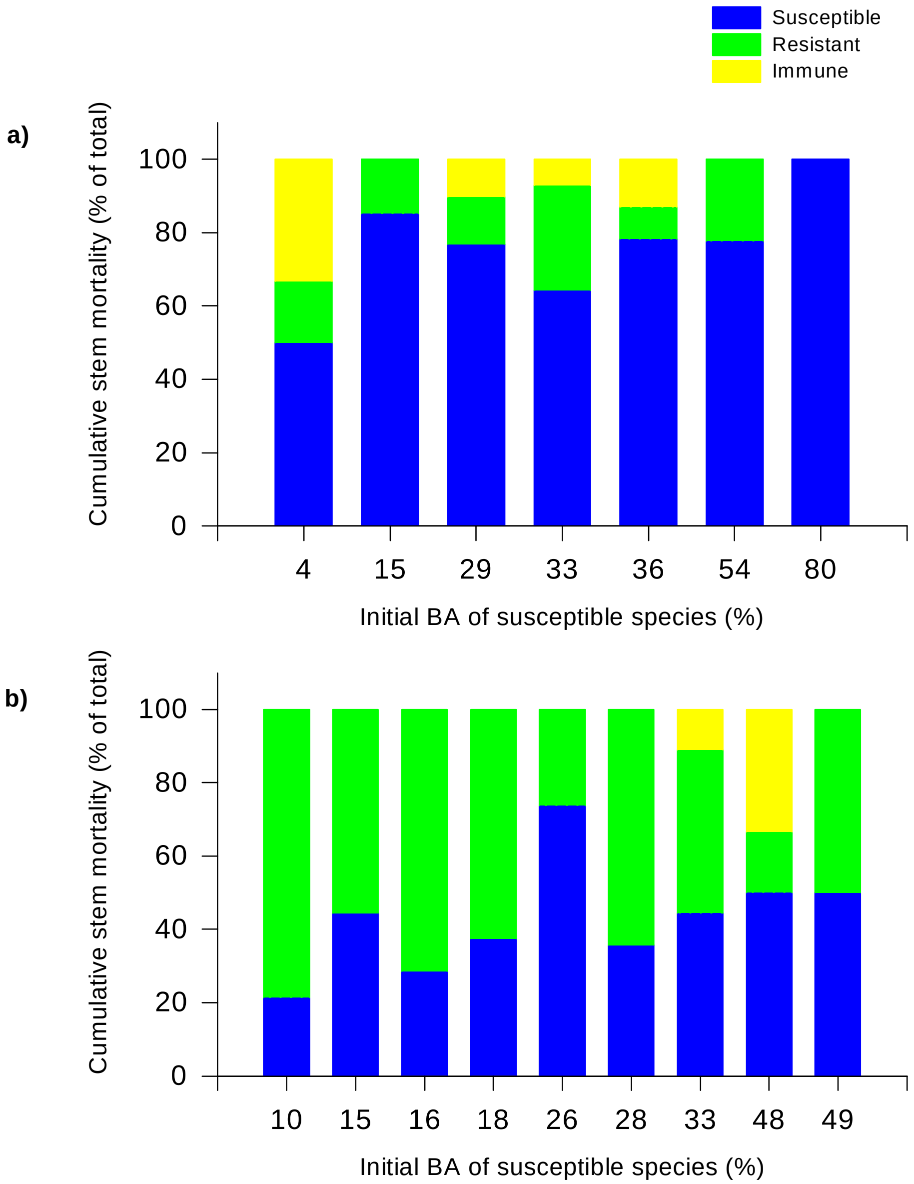

Figure 5.3: Distribution of total stem mortality among host preference classes in a) seven pine-oak stands and b) nine pine-sweetgum stands.

Table 5.4: Cumulative basal area and stem mortality separated by host preference class in pine-oak and pine-sweetgum stands; basal area mortality and stem mortality are measured as percentages of the initial basal area and initial number of stems.

Stand No.	**BA Mortality By Host Preference Class**			**Stem Mortality By Host Preference Class**		
	Susceptible	**Resistant**	**Immune**	**Susceptible**	**Resistant**	**Immune**
	%					
Pine-oak						
1	4.3	0	0	10.5	0.0	0.0
2	24.5	3.7	0	25.0	6.9	0.0
3	89.9	9.4	28.6	84.4	19.4	37.5
4	62.1	11.8	11.1	40.9	9.5	6.2
5	11.6	17.0	6.2	30.3	10.0	14.0
6	40.0	8.2	0	42.0	7.9	0.0
7	30.8	0.1	2.0	37.5	1.4	2.2
mean	37.6	7.2	6.8	38.6	7.9	8.6
std. dev.	29.8	6.3	10.5	22.9	6.4	13.7
Pine-sweetgum						
8	4.3	0.6	0	7.5	8.6	0.0
9	2.7	1.4	5.0	7.4	6.8	3.7
10	4.4	0.1	1.5	8.8	2.3	2.6
11	2.8	2.2	0	10.6	7.8	0.0
12	3.2	1.0	0	8.6	6.6	0.0
13	3.9	20.1	0	17.1	15.6	0.0
14	35.2	4.6	0	29.2	8.5	0.0
15	5.5	2.6	0	17.8	9.4	0.0
16	2.7	10.6	0	6.5	14.3	0.0
mean	7.2	4.8	0.7	12.6	8.9	0.7
std. dev.	10.5	6.6	1.7	7.5	4.0	1.4

Table 5.5: Cumulative stem mortality as a percentage of the initial number of stems of different oak species within pine-oak stands of the Atlantic Coastal Plain; numbers in parentheses are the initial number of stems sampled within each stand.

Stand #	Stem Mortality								
	Q. alba	***Q. bicolor***	***Q. falcata***	***Q. michauxii***	***Q. nigra***	***Q. phellos***	***Q. rubra***	***Q. stellata***	***Q. velutina***
	%								
1	0 (16)	---	0 (29)	---	0 (2)	---	50 (2)	63 (8)	---
2	34 (29)	0 (1)	---	---	0 (1)	50 (2)	40 (5)	---	---
3	100 (1)	---	98 (40)	---	76 (17)	---	---	---	---
4	50 (10)	---	---	0 (1)	---	20 (5)	---	100 (3)	---
5	---	---	64 (25)	---	31(26)	33 (3)	---	---	---
6	---	---	64 (12)	---	64 (25)	---	100 (1)	---	100 (1)
7	100 (1)	---	0 (1)	---	40 (5)	---	---	---	---

distributed. In some stands the number of oaks sampled was low (in some cases a single tree), however, the overall trend indicates that oak mortality in Coastal Plain sites can approach the levels observed in defoliated stands of the northeast. For example, if stands with less than five sample trees are eliminated from consideration, oak mortality still ranged from a low of 31% to a high of 98%.

In the pine-sweetgum cover type, resistant species contributed more to the total observed mortality than susceptible species (Figure 5.3b). Of the total number of trees that died, 58.1% were resistant species, 40.3% were susceptible species, and 1.6% were immune species. However, these results were more a reflection of the preponderance of small, resistant trees in the original stands than anything else; on an individual stand basis susceptible species were still the hardest hit. They lost an average of 7.2% of the original basal area and 12.6% of the original number of stems; while resistant species basal area mortality was 4.8% and stem mortality was 8.9%. (Table 5.4). The majority of the resistant species affected were loblolly pines and red maple (*Acer rubrum* L.). Prior to defoliation, red maple was widely distributed in the understory of many pine-sweetgum stands and during times of exceptionally heavy defoliation this species was also defoliated. Previous studies have identified red maple as a species that is highly vulnerable to mortality following defoliation (Campbell and Sloan, 1977; Campbell, 1979), and this may explain the mortality observed here.

Foresters working in the southeastern United States are keenly interested in the effects of gypsy moth defoliation on overstory pines. Table 5.6 shows basal area and stem mortality of understory and overstory pines in pine-oak and pine-sweetgum stands. In both cover types, the

Table 5.6: Initial number of stems, initial basal area, stem mortality, and basal area mortality of overstory and understory pines in six pine-oak and four pine-sweetgum stands in which pine mortality was observed; overstory consists of dominant and codominant trees, understory consists of intermediate and suppressed trees.

Stand No.	**Initial Stem Density**		**Stem Mortality**		**Stem Mortality**		**Initial BA**		**BA Mortality**		**BA Mortality**	
	Under.	**Over.**	**Under.**	**Over.**	**Under.**	**Over.**	**Under.**	**Over.**	**Under.**	**Over.**	**Under.**	**Over.**
	------------------------ stems/ha	----------------------			------------ %	------------	------------------------------- m^2/ha			-----------------------------	--------------- %	--------------
Pine/oak												
2	17	117	8	0	47.0	0.0	0.6	10.4	0.4	0.0	63.9	0.0
3	67	133	33	17	49.2	12.8	3.1	12.6	0.5	1.1	14.9	8.4
4	0	125	0	17	0.0	11.2	0.0	16.4	0.0	2.6	0.0	15.6
5	67	250	8	25	12.5	10	2.6	20.8	0.1	1.7	3.5	8.0
6	58	333	8	25	13.8	7.5	1.7	28.6	0.2	2.5	10.6	8.6
7	58	200	8	0	13.8	0.0	1.8	19.2	0.2	0.0	9.6	0.0
mean	44.5	193	11	14	22.7	6.9	1.6	18.0	0.2	1.3	17.1	6.8
std. dev.	28.7	85.9	11.3	11.4	20.3	5.6	1.2	6.5	0.2	1.2	23.5	6.0
Pine-sweetgum												
13	0	225	0	58	0.0	25.8	0.0	33.0	0.0	7.6	0.0	23.0
14	33	192	8	8	24.2	4.2	1.2	20.8	0.2	1.0	17.9	4.6
15	42	275	17	0	33.3	0.0	2.1	32.2	0.7	0.0	34.6	0.0
16	225	859	125	50	55.5	5.8	4.1	28.2	2.4	1.1	57.0	3.9
mean	75	388	38	29	28.2	9.0	1.8	28.6	0.8	2.4	27.4	7.9
std. dev.	88	274	51	25	19.9	10.0	1.5	4.8	0.9	3.0	21.0	8.9

greatest pine mortality was observed among suppressed and intermediate trees. Mean basal area and stem mortality of understory pines was greater in pine-sweetgum stands than in pine-oak stands. However, mortality rates among individual stands was quite variable. Some stands lost a large percentage of the understory, while in others understory pine mortality was relatively low (Table 5.6). In general, overstory pine mortality was quite low; in both cover types, mean basal area and stem mortality was less than 10% (Table 5.6). However, in some stands, mortality was greater than 10%, and one stand (Stand 16) lost 23.0% of the original basal area and 25.8% of the original number of stems (see section on other factors influencing tree mortality).

Figure 5.4 highlights the importance of initial stand conditions on subsequent tree mortality. In both cover types, as the proportion of susceptible basal area increased, there was a visible shift in mortality between host preference classes. Stands with a large proportion of susceptible species basal area before the outbreak tended to have a greater proportion of these species contributing to total mortality. Because oaks and sweetgum were the only susceptible species observed within this study, these results reflect the importance of these species in determining the effect of gypsy moth defoliation within these cover types. Linear regression analysis confirmed this relationship within both the pine-oak cover type ($r^2 = 0.73$, $p = 0.0139$) and the pine-sweetgum type ($r^2 = 0.79$, $p = 0.0014$).

Influence of canopy position and tree vigor

Canopy position, whether an individual is in the understory or overstory, often has considerable influence on tree response subsequent to defoliation (Campbell and Sloan, 1977; Gansner et al.,

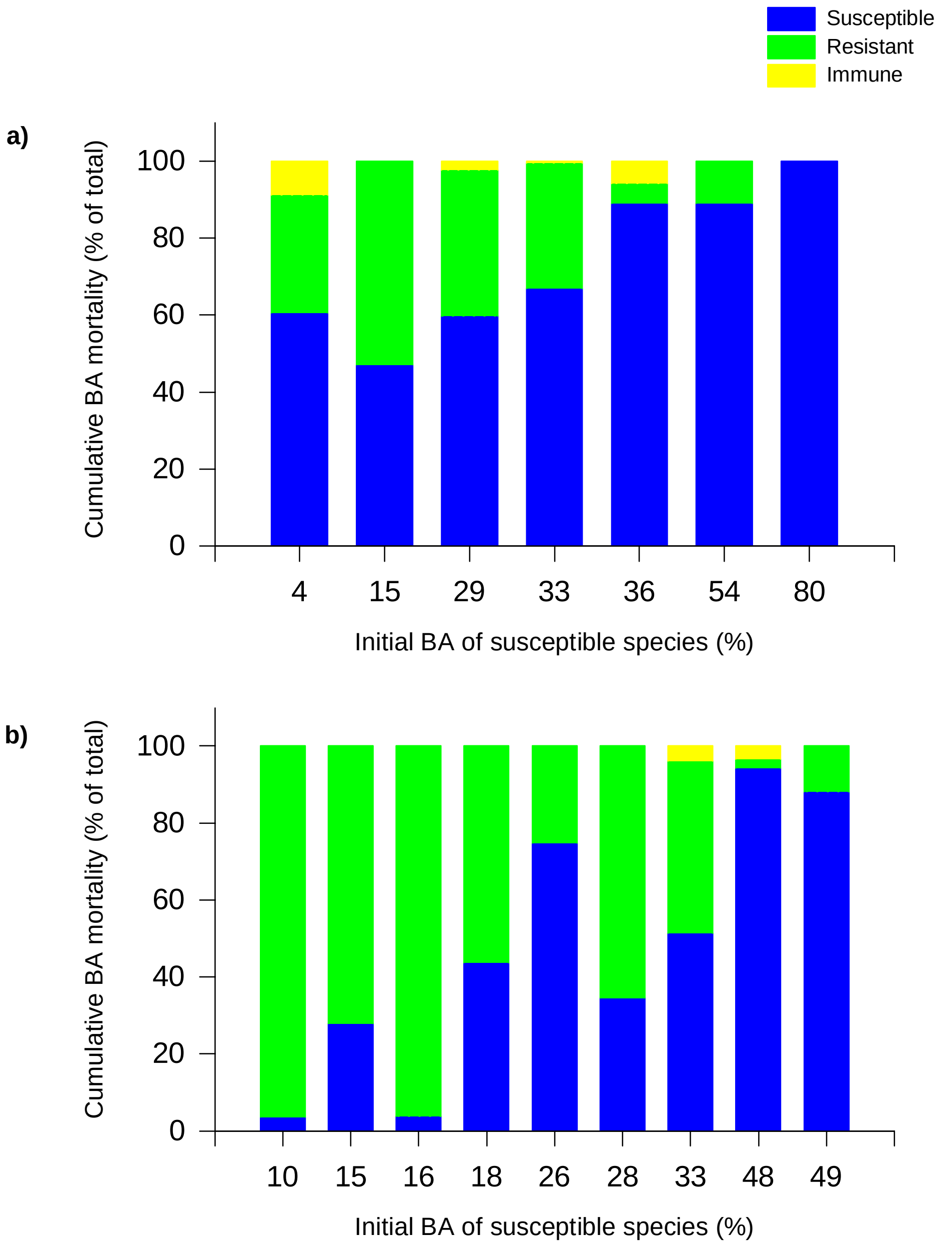

Figure 5.4 Distribution of basal area mortality among host preference classes in a) seven pine-oak stands and b) nine pine-sweetgum stands

1993). In the majority of cases, trees in the suppressed and intermediate crown classes succumb to defoliation-induced mortality at higher rates than those in the codominant and dominant crown classes (Campbell and Sloan, 1977; Brown et al., 1979; Gansner et al., 1993). However, some studies have shown that both large, old trees and small, suppressed trees may be killed (Kegg, 1971; Stalter and Serrao, 1983). In this study, trees were assigned to one of the four recognized crown classes, suppressed, intermediate, codominant, or dominant. For ease of interpretation, suppressed and intermediate trees were combined into a single category and classified as understory; codominants and dominants were combined to form a single category, the overstory. Table 5.7 provides understory and overstory cumulative basal area and stem mortality losses within the two cover types. Within the pine-oak cover type, mean basal area mortality rates of understory (15.3%) and overstory (15.4%) trees were not significantly different (t = 0.9805). Stem mortality rates of overstory trees were slightly greater than those in the understory; mean overstory stem mortality was 23.8% compared to a loss of 19.7% of the understory stems. However, this difference was not significant (t = 0.6964).In the pine sweetgum cover type, there was a significant difference between understory and overstory basal area mortality (t = 0.0585). Approximately 11.1% of the understory basal area was lost while only 4.5% of the overstory was killed. Interestingly, though understory stem mortality (11.2%) was nearly twice that of the overstory (6.4%), the difference was not statistically significant (t = 0.1474).

Another important factor in mortality subsequent to defoliation, and one that is often correlated with crown class, is crown condition prior to defoliation. Trees that are in poor or fair condition are more likely to succumb to mortality following a defoliation episode than those in

Table 5.7: Cumulative basal area and stem mortality of understory and overstory trees in pine-oak and pine-sweetgum stands defoliated by the European gypsy moth.

Cover Type	**Basal Area Mortality**				**Stem Mortality**			
and Stand #	**Understory**	**Overstory**	**Understory**	**Overstory**	**Understory**	**Overstory**	**Understory**	**Overstory**
	--------------- m^2/ha --------------		---------------- % ---------------		-------------- stems/ha -----------		----------------- % ----------------	
Pine-oak								
1	0.2	0.3	4.1	3.2	33	17	8.2	6.0
2	1.4	3.2	13.0	15.9	100	50	11.9	20.0
3	4.8	6.3	39.8	39.7	467	108	56.6	64.7
4	0.5	7.6	14.3	24.6	58	58	14.5	21.7
5	1.8	3.0	11.3	14.1	233	92	19.0	35.7
6	2.1	2.9	21.0	9.6	241	42	24.1	11.7
7	0.4	0.2	3.4	1.0	42	8	3.5	6.8
mean	1.6	3.4	15.3	15.4	168	54	19.7	23.8
std. dev.	1.6	2.8	12.4	13.3	158	37	17.6	20.8
Pine-sweetgum								
8	0.4	0.5	8.5	1.5	42	8	10.5	2.0
9	0.7	0.2	8.2	0.6	67	8	8.5	2.1
10	0.7	0.5	4.1	1.4	42	8	4.2	2.7
11	1.0	0.2	12.4	0.5	108	8	13.6	1.3
12	0.7	0.0	6.4	0.0	67	0	10.6	0
13	0.8	7.5	7.4	20.2	117	58	13.5	21.1
14	2.1	2.8	13.1	11.7	108	50	10.2	21.5
15	1.6	0.0	12.2	0	150	0	15.4	0
16	2.3	1.3	27.3	4.2	175	58	14.3	6.7
mean	1.1	1.4	11.1	4.5	97	22	11.2	6.4
std. dev.	0.7	2.4	6.8	7.0	47	25	3.5	8.7

good condition (Campbell and Sloan, 1977). In both cover types, the greatest concentration of tree mortality was among individuals that were in poor or fair condition in the year prior to their death (Table 5.8, Figure 5.5). In the pine-oak cover type, 45% of all the trees that died had crowns that were in poor condition, 38% were in fair condition and 17% were in good condition.In the pine-sweetgum type, 60% of all dead trees had crowns in poor condition, 31% were in fair condition, and only 9% were in good condition. Though in current usage it is one of the more subjective measures of physiological condition, crown condition is still an effective tool when attempting to gauge vulnerability. Figure 5.5 also indicates that there may be a possible relationship between stem mortality, crown condition and the proportion of susceptible species prior to defoliation. In pine-oak stands, a greater proportion of trees in good condition were killed in stands with a low initial basal area of susceptible species. This trend was less obvious in pine sweetgum stands. These results are understandable if the dynamics of defoliation in mixed stands is examined. Mixed stands with a high percentage of susceptible species experience greater defoliation intensities than stands with a low percentage of susceptible species. This has been shown to be true in this study and by previous researchers (Campbell and Sloan, 1977; Brown et al., 1979, Brown et al., 1988.). However, as the proportion of susceptible species decreases within a stand, there is an increasing likelihood that during a defoliation outbreak resistant species may be defoliated. These resistant species are often more vulnerable to defoliation than their susceptible neighbors. As a result, in a mixed stand with a low proportion of susceptible species, resistant trees that are in good condition prior to the outbreak may be defoliated and these defoliated trees have a greater probability of dying. In stands where the proportion of susceptible species is greater, a larger food base is available for larvae and resistant species are less likely to experience heavy defoliation and resultant mortality.

Table 5.8: Cumulative basal area and stem mortality of trees in good, fair, and poor condition, as a percentage of the initial basal area and number of stems, in pine-oak and pine-sweetgum stands defoliated by the European gypsy moth.

Cover Type and Stand #	**Basal Area Mortality**			**Stem Mortality**		
	Good	**Fair**	**Poor**	**Good**	**Fair**	**Poor**
	-- % --					
Pine-oak						
1	3.2	10.8	0.0	6.6	25.0	0.0
2	13.6	88.6	0.0	12.6	50.0	0.0
3	34.1	100.0	100.0	53.7	100.0	100.0
4	20.6	33.8	25.7	9.6	26.1	60.0
5	11.9	14.3	86.4	21.2	50.0	50.0
6	11.6	60.8	87.5	16.7	70.0	66.7
7	0.8	20.4	15.8	1.8	50.0	50.0
mean	13.7	47.0	45.1	17.5	53.0	46.7
std.dev.	11.2	36.5	44.4	17.2	25.9	36.1
Pine-sweetgum						
8	2.0	6.7	100.0	2.8	13.0	100.0
9	0.9	7.4	52.4	2.8	10.0	60.0
10	2.3	0.0	0.0	3.9	0.0	0.0
11	0.3	7.1	100.0	0.8	15.6	100.0
12	0.7	18.4	100.0	2.6	36.4	100.0
13	17.2	16.0	97.6	11.7	57.1	100.0
14	10.3	96.9	98.2	7.5	83.3	100.0
15	1.2	11.8	98.1	6.2	42.9	100.0
16	4.5	86.5	100.0	5.9	83.3	100.0
mean	4.4	27.9	82.9	4.9	38.0	84.4
std. Dev.	5.7	36.7	34.7	3.3	31.3	34.3

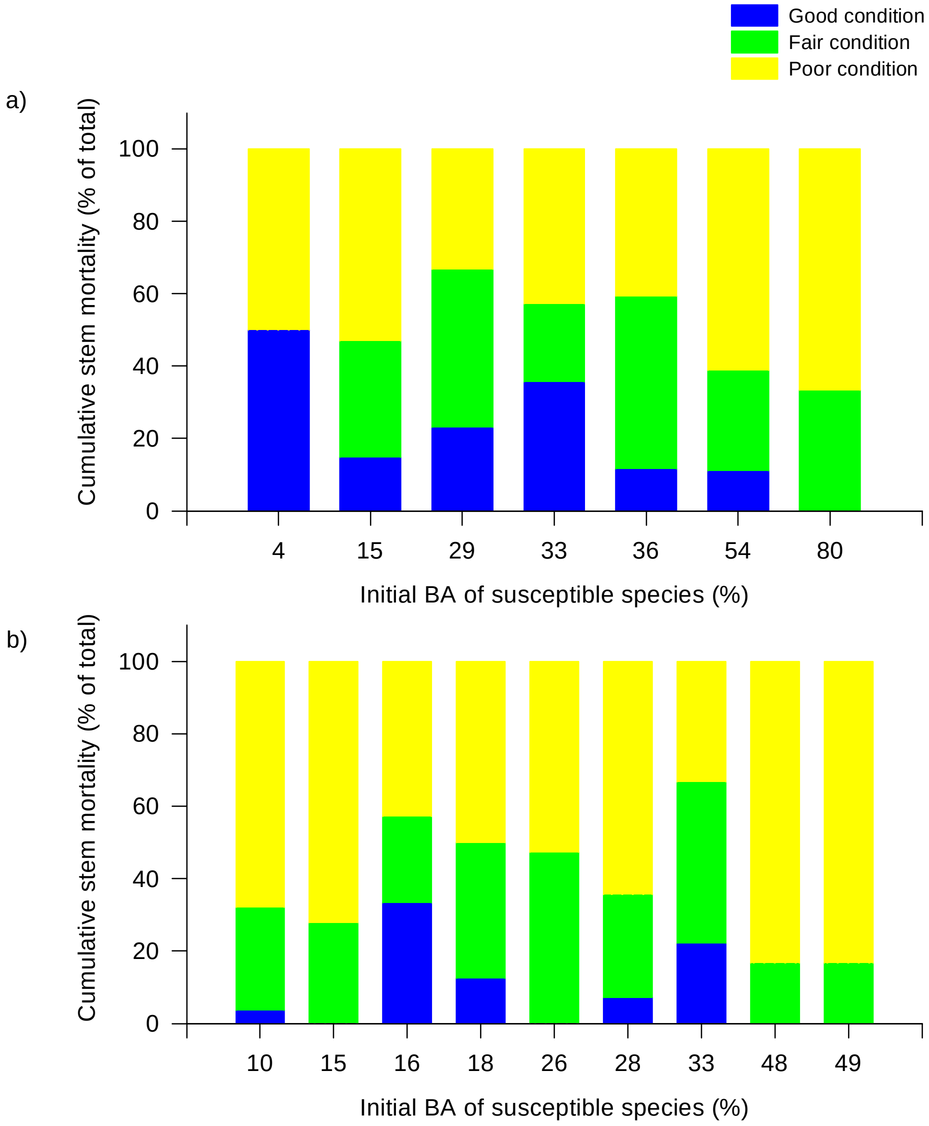

Figure 5.5: Proportion of dead trees (stems/ha) in which crown condition was rated as good, fair, and poor, in a) seven pine-oak stands and b) nine pine-sweetgum stands.

Influence of factors other than defoliation

Subsequent to defoliation, tree mortality occurred in both cover types, and in some stands mortality rates were very high. However, whether these results could be attributed solely to gypsy moth defoliation is in doubt. In the pine-oak type, Stand 3 lost 39.6% of the original basal area and 58% of the original number of stems. While Stand 3 was heavily defoliated during the outbreak, it was also subjected to an additional stress factor. In 1993, during one of the periods of extremely heavy defoliation, this stand was also burned by a wildfire. Consequently, a large number of understory trees were killed as a direct result of fire injury. These included both susceptible oaks and American holly, a species which is immune to gypsy moth defoliation, but which lost 28% of the original basal area (Table 5.4). For many of the remaining trees, the combination of these two stress factors, defoliation and a wildfire, probably combined to cause their death.

Within the pine-sweetgum cover type a large percentage (66%) of the total loblolly pine mortality occurred within a single stand (Stand 16). However, the stand characteristics and defoliation history indicate that gypsy moth defoliation was not the primary causal factor in the observed mortality. Prior to the outbreak, loblolly pine comprised 88% of the initial stand basal area (Table 5.2). The majority of the pine mortality subsequent to defoliation consisted of suppressed and intermediate trees in the understory. Fifty-seven percent of the original understory basal area and 55.5% of the understory pine stems were killed (Table 5.6). However, only 3.9% of the original overstory basal area (codominants and dominants) and 5.8% of the stems died. Among the suppressed and intermediate classes, 78% of the trees never experienced more than a light defoliation (11-30%), while the maximum defoliation for the remaining trees was only moderate (31-60%). Defoliation levels prior to mortality of the codominant pines were more variable. Twenty-eight percent were not defoliated, 43% received light defoliation, 14% percent received moderate defoliation, and another 14% sustained heavy defoliation. Results similar to those described above have been reported in the northeastern U.S. In describing the effects of gypsy moth defoliation on pine-hardwood stands in western Connecticut where eastern white pine (*Pinus strobus* L.) was the dominant species, Stephens (1988) suggested that the effect of defoliation was simply to accelerate tree mortality that was inevitable. In Stand 16 this also appears to be true. Rather than defoliation being the primary cause of death, for the majority of loblolly pines, the data implicates an interaction between defoliation and competition-induced mortality. However, individual trees that experienced moderate or heavy defoliation may have been rendered more vulnerable through the act of defoliation.

Within the pine-sweetgum type, Stand 13 had the largest basal area mortality. Most of this mortality consisted of resistant loblolly pines (Tables 5.4, 5.6). These trees were all large diameter, dominants, that were killed as a direct result of an outbreak of the southern pine beetle (*Dendroctonus frontalis* Zimmerman). In many instances, mortality subsequent to defoliation is not a direct result of the defoliation per se, but is due to secondary action organisms that opportunistically attack the weakened tree. These interactions are common in northeastern forests among oaks, *Armillaria* spp. and *Agrilus bilineatus* (Weber) (Dunbar and Stephens, 1975; Wargo, 1977; Dunn et al., 1986). Some researchers have hypothesized that as gypsy moth populations move further into the southeastern United States interactions with the southern pine beetle may occur, thereby increasing the overall number of outbreaks (Gottschalk and Twery, 1989). Within this stand none of the loblolly pines had experienced more than 30 percent defoliation prior to their death. Previous research in mixed pine-hardwood stands has shown that greater defoliation intensities are required before there is a noticeable impact upon the pine component (Turner, 1963; Stephens, 1988). There is a possibility that defoliation contributed to loblolly pine vulnerability, however, without further study this relationship will remain unclear.

Prediction of the Probability of Tree Mortality

Logistic regression was used to estimate the probability of tree mortality within both pine-oak and pine-sweetgum types. Prior to the regression analysis, a correlation analysis was conducted. This indicated that two of the ten independent variables, (MAXDEF and SUSCBA) were highly correlated ($r = 0.85$, $p = 0.0001$). Thus, to avoid problems with multicollinearity in further analyses, these variables were not included in the same equation. Though mortality rates in Stands 3 and 13 were quite high, both were excluded from the model development process for the following reasons. During the outbreak, Stand 3 experienced a wildfire and Stand 13 suffered a southern pine beetle outbreak.. While secondary factors are often implicated in the death of trees following gypsy moth defoliation, these two events were believed to be primarily responsible for the mortality observed, rather than mortality resulting from the interaction of defoliation with the wildfire or the SPB outbreak.

Model development

In both cover types stepwise logistic regression identified several possible candidates. Of these only three equations were selected for further consideration, two within the pine-oak data (Model 1 and 2) and a single equation from the pine-sweetgum data set (Model 3). The significance of the overall logistic model can be determined with the –2 Log Likelihood statistic (SAS, 1995). This has a chi-square distribution under the null hypothesis that all of the coefficients within the model are zero. Using the –2 Log Likelihood, Models 1, 2, and 3 were all found to be significant at the 0.0001 level (Table 5.8). Though significance of the overall model is important, researchers agree that the adequacy of a logistic model is best determined by how well the parameters explain variation in the dependent variable, i.e. their significance; and by the fit of the predictions to data (Trexler and Travis, 1993). Of the three models selected by stepwise regression, all parameter estimates were significant at the 0.05 level (Table 5.9).

One of the most common measures of the predictive accuracy of logistic regression is the Hosmer and Lemeshow (1989) goodness-of-fit test. The null hypothesis for the test is that the model under investigation fits the data well, thus significance indicates a lack of fit. Based on the Hosmer and Lemeshow goodness-of-fit test models 1 and 3 were found to provide good fit to the data; p = 0.7924 for Model 3, and p = 0.0942 for Model 1. However, Model 2 did not provide a good fit according to this test, p = 0.0270.

Another measure of the predictive accuracy of a logistic regression model is the receiver operating characteristic (ROC) curve (SAS, 1995). This is a graphical display and is related to the ***c*** statistic, which measures the area under the ROC curve. In addition to indicating predictive ability, these two measures can be used to compare competing models to determine which is a better predictor. The ROC curve is computed using two values, sensitivity and specificity (SAS, 1995). Sensitivity refers to the proportion of dead trees that the model correctly predicts to be dead at a specified probability cutpoint. The specificity is the proportion of living trees that the model correctly predicts to be alive at a specified cutpoint. The cutpoint is the assigned probability level at which a tree is determined to be dead. With a cutpoint of 0.50, trees with a calculated probability of mortality less than 0.50 are alive, while those with a probability of 0.50 and greater are classified as dead. To avoid bias in interpretation the validation data set for each cover type was used to compute the sensitivity and specificity values used in computing the ROC curve. Interpretation of the ROC curve and the ***c*** statistic is relatively simple. Ideally, the ROC curve should rise rapidly and then slowly approach an asymptote. A curve that rises slowly is indicative of a model with low predictive accuracy. The ***c*** statistic can vary between 0 and 1.

Table 5.9: Results of stepwise logistic regression using the development data sets for the pine-oak and pine-sweetgum cover types; variable abbreviations are those used in Table 5.1 and the text.

Model #	**-2 Log Likelihood *p* value**	**Variables**	**Parameter Estimate**	**Prob > Chi Square**
Model 1	0.0001	INTERCEPT	2.5314	0.0224
		YRSOFDEF	-0.6028	0.0049
		HOST	-0.0634	0.0001
		CRCOND	0.9038	0.0029
		MAXDEF	-0.0156	0.0227
Model 2	0.0001	INTERCEPT	-1.1489	0.0180
		HOST	-1.1407	0.0001
		CRCOND	0.8558	0.0016
Model 3	0.0001	INTERCEPT	-1.8935	0.0080
		CANOPY	-1.4707	0.0004
		HOST	-0.6349	0.0028
		CRCOND	1.9054	0.0001

Values of ***c*** close to 1 indicate a model with high predictive accuracy. ROC curves for the three models and their associated ***c*** statistics are shown in Figure 5.6. All three models appear to have good predictive value based on the appearance of the ROC curve and the value of the ***c*** statistic. Based on the ***c*** statistic, of the two pine-oak models, the predictive accuracy of Model 1 is slightly greater than Model 2.

Model validation

Using the validation data sets, each of the three models was used to predict tree mortality based on stand and tree characteristics within the respective cover types. The results of these classification tests utilizing three probability cutpoints are shown in Table 5.9. The correct dead tree classification rate (CDR) and the correct live tree classification rate (CLR) are the number of dead and live trees to which the model correctly assigns dead or alive status. The overall correct classification rate (CCR) is the total number of trees that the equation correctly assigns to either living or dead status. As seen in Table 5.10, CDR, CLR and CCR can be manipulated through the selection of different cutpoints. At a cutpoint of 0.25, all three models achieve their greatest CDR. With a cutpoint of 0.50, the CDR's of all three models are reduced, CLR's of Models 2 and 3 increase while Model 1 decreases, and CCR's of all three models increase. At the 0.75 cutpoint, the CDR, CLR, and CCR of Model 3 is unchanged, while for Models 1 and 2, CLR's increase and CDR's and CCR's decrease. Hassler et al. (1986) noted that the choice of cutpoint often varies depending on the use of the equation and the potential costs of misclassification. In this study, the objective was to achieve the greatest possible CDR without significantly compromising the CLR and CCR and this was achieved at a cutpoint of 0.25.

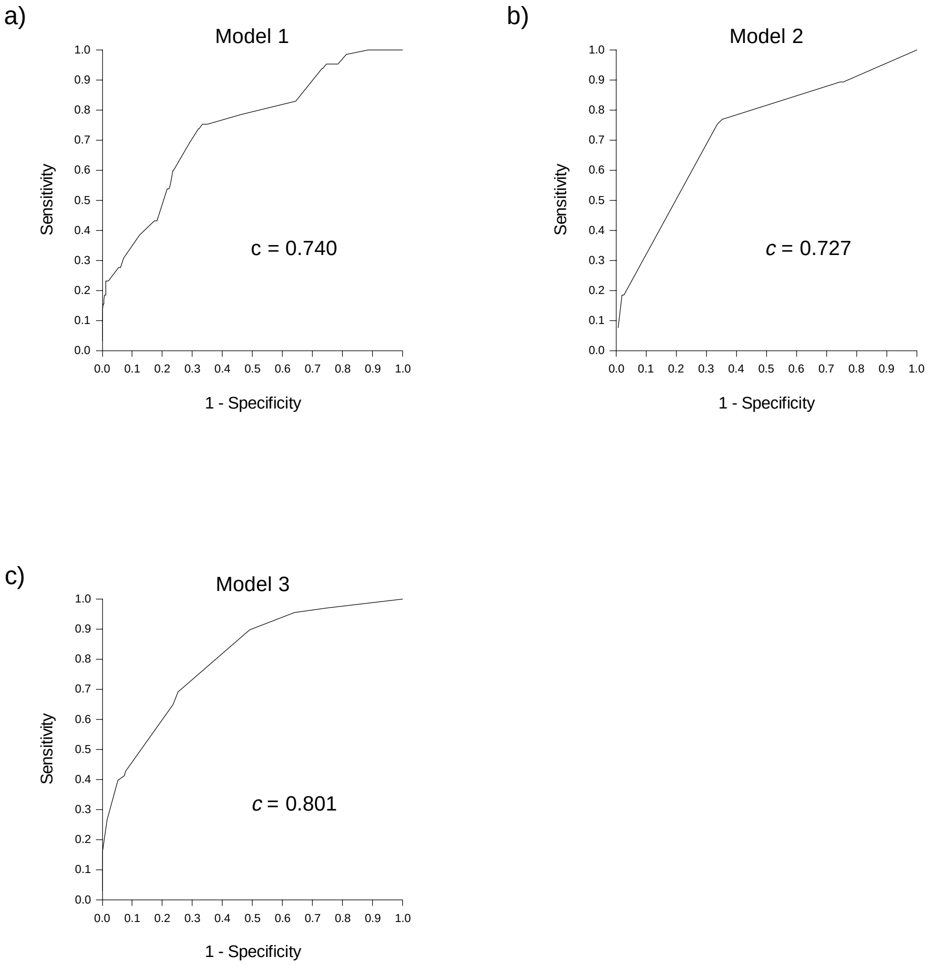

Figure 5.6: Receiver operating characteristic curves for three logistic regression equations, a) Model 1, b) Model 2, c) Model 3.

Table 5.10: Classification results for Models 1, 2, and 3, using the pine-oak and pine-sweetgum validation data sets.

Model #	Probability Cutpoint	Correctly Classified		Incorrectly Classified Trees		Correct Dead Tree Classification	Correct Live Tree Classification	Overall Correct Classification
		Dead	Live	Dead	Live	%	%	%
1	0.25	28	177	24	27	54	87	80
	0.50	13	203	39	1	25	79	84
	0.75	3	204	49	0	6	100	81
2	0.25	44	142	8	62	85	70	73
	0.50	9	203	43	1	17	99	83
	0.75	1	204	51	0	2	100	80
3	0.25	25	388	15	23	62	94	92
	0.50	11	411	29	0	28	100	94
	0.75	11	411	29	0	28	100	94

Stepwise logistic regression identified Model 3 as the best predictor of tree mortality subsequent to gypsy moth defoliation in pine-sweetgum stands. Validation with an independent data set confirmed this selection, as the equation proved itself quite robust. At the 0.25 cutpoint,accuracy of the prediction of tree mortality was 63%, CLR was 95% and the overall CCR of 92% was excellent. CCR's in the 70's and 80's are frequently reported in the literature, and the recommendation of previous researchers has been to choose cutpoints that maximize the CCR (Hassler et al., 1986). Stepwise logistic regression identified two possible candidates among models for the pine-oak type. Model 2 had the greatest CDR at the 0.25 cutpoint, however, the CLR & CCR of Model 1 were superior. Based on the ROC curve and the ***c*** statistic, predictive ability of both models were approximately equal; however, the results of the Hosmer and Lemeshow (1989) goodness-of-fit test demonstrated that Model 1 had the best fit. Based on the results of the classification tests, both models tended to fluctuate over the range of probability cutpoints; however, this trait was more noticeable with Model 2.

Partial regression curves were produced for all three models using a range of values for the individual parameter estimates. It was at this point that the inherent instability of Model 1 was revealed. The predicted probabilities of tree mortality did not follow expected trends, resulting in reductions in predicted tree mortality as the intensity and duration of defoliation increased. These results could not be justified based on the results of this study or previous studies. Conversely, the probabilities predicted by Model 2 followed expected trends and gave reasonable predictions of tree mortality for susceptible and resistant species based on the initial crown condition (Figure 5.7). Therefore Model 1 was rejected and Model 2 as shown below was selected for the prediction of individual tree mortality in the pine-oak cover type.

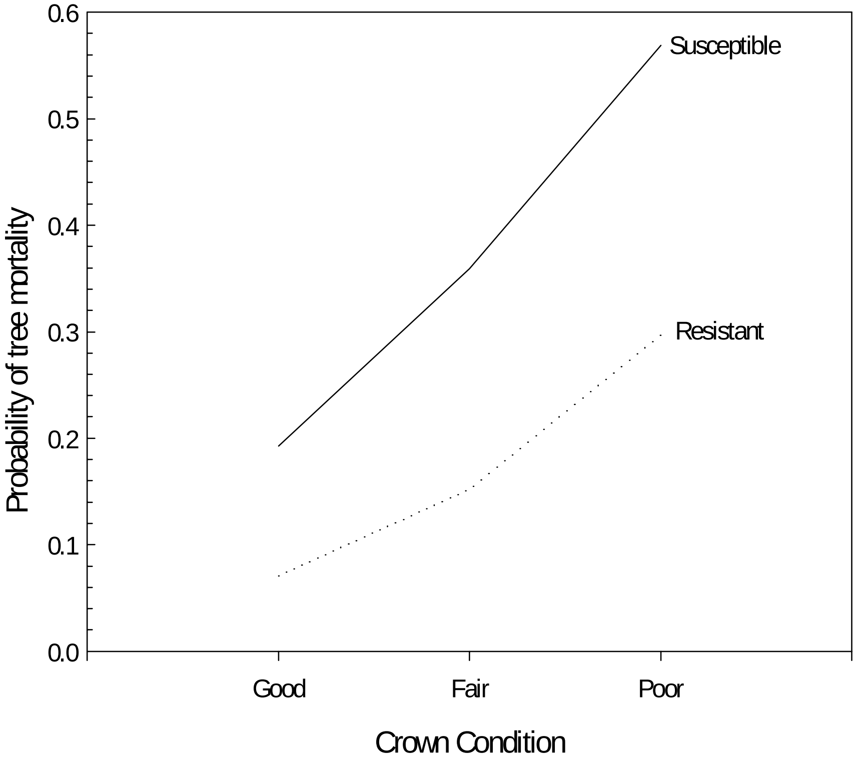

Figure 5.7: Partial regression curves for the prediction of the probability of tree mortality based on host preference class and crown condition in Coastal Plain mixed pine-oak stands.

Model 2:

$$\pi(x) = [\ 1 + e\ (-\ (-1.1489 - 1.1407\ X1 + 0.8558\ X2\ )\ )\ ]^{-1}$$

where,

$\pi(x)$ = probability of tree mortality (0 to 1)

e = the base of natural logarithms

X1 = HOST (1 =susceptible 2 = resistant)

X2 = CRCOND (1 = good, 2 = fair, 3 = poor)

When the above techniques were applied to Model 3 the resulting probability predictions were as expected. Trees in good condition were predicted to have a smaller probability of dying than those in fair or poor condition; and the predicted mortality of understory trees was greater than that of overstory trees (Figure 5.8). Based on these results Model 3 as shown below was selected for the prediction of individual tree mortality in pine-sweetgum stands.

Model 3:

$$\pi(x) = [\ 1 + e\ (-\ (-\ 1.8935 - 1.4707\ X1 - 0.6349\ X2 + 1.9054\ X3\ )\ )\ ]^{-1}$$

where,

$\pi(x)$ = probability of tree mortality (0 to 1)

e = the base of natural logarithms

X1 = CANOPY (1 = suppr./interm., 2 = codom./domin.)

X2 = HOST (1= susceptible, 2 = resistant)

X3 = CRCOND (1 = good, 2 = fair, 3 = poor)

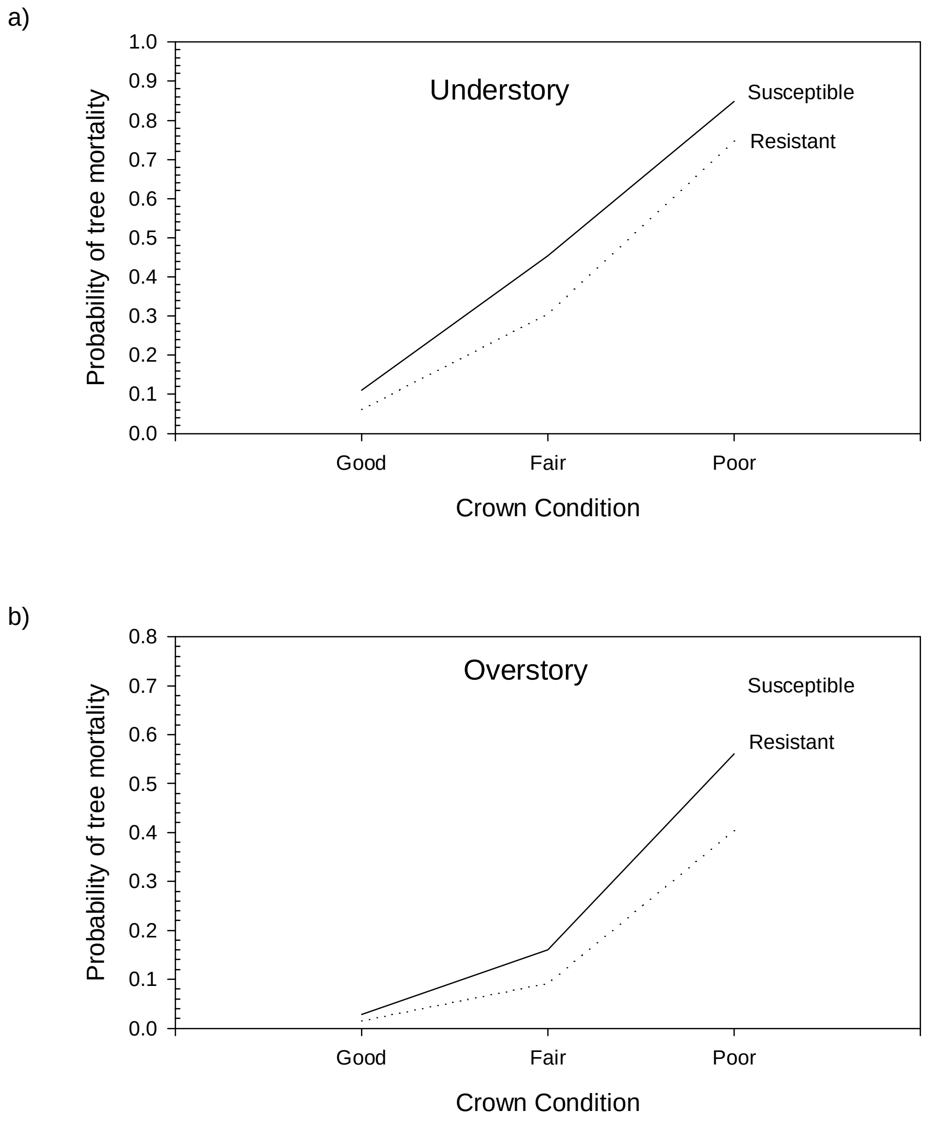

Figure 5.8: Partial regression curves for the prediction of the probability of tree mortality based on host preference class and crown condition in a) understory trees (suppressed and intermediate), and b) overstory trees (codominant and dominant), in Coastal Plain mixed pine-sweetgum stands.

CONCLUSIONS

Trends in mortality that have been described in mixed hardwood stands in the northeastern United States and Pennsylvania, were also observed in mixed pine-hardwood stands of the Atlantic Coastal Plain. There was considerable interspecific variation in tree response subsequent to the outbreak. Susceptible species were heavily impacted and oaks displayed greater vulnerability than sweetgum. Loblolly pine mortality was observed, but it was difficult to isolate the source, and thereby determine whether gypsy moth defoliation was a primary causal factor. In general, the potential for extensive overstory pine mortality in mixed pine-hardwood stands defoliated by the gypsy moth does not appear to exist.

In addition to interspecific variation, variation was observed between cover types in the response to defoliation. The pine-oak type exhibited greater mortality among individual stands, indicating that this type is more vulnerable to gypsy moth defoliation. Crown class and crown condition prior to the outbreak have been shown to be important determinants of tree response to defoliation. In this study, significant differences in basal area mortality rates were only observed between understory and overstory trees in the pine-sweetgum cover type. Under- and overstory basal area mortality rates were not significantly different in the pine-oak type, and stem mortality rates were not significantly different in either type. Suppressed and intermediate trees in the understory, and trees that were in poor or fair condition, had a much higher probability of dying subsequent to defoliation. The role of additional stress factors was also revealed. Fire appeared to increase tree mortality in defoliated stands; and the possibility of interactions between the gypsy moth and the southern pine beetle is a consideration.

Logistic regression was found to be a useful tool in the prediction of tree mortality subsequent to defoliation in Coastal Plain pine-hardwood stands. Two logistic regression equations were derived and validated for use in pine-oak and pine-sweetgum cover types. Model 2 predicts the probability of tree mortality in stands where the hardwood component is dominated by oaks. Model 3 predicts mortality in stands where sweetgum is the dominant hardwood.

The above equations when used with cutpoints of 0.25 to determine assignment of tree status (live or dead) provide good predictive ability within both cover types. For consideration in future studies, it is suggested that a more precise estimate of the equation parameters would be obtained if the original data set had been retained for model development and a completely independent set of data had been used for model validation.

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CHAPTER 6

SUMMARY

The objective of the research contained in this dissertation was to examine both the potential for, and the effects of, European gypsy moth defoliation in mixed pine-hardwood stands in the Atlantic Coastal Plain of Virginia and Maryland. The rationale for the study was the continued advance of gypsy moth populations into the southeastern United States and the perceived potential for defoliation of both mixed stands and pine plantations based upon laboratory studies of southern tree species (Barbosa et al. 1983). In addition to the southern oaks (*Quercus* spp.), these studies identified loblolly pine (*Pinus taeda* L.) and sweetgum (*Liquidambar styraciflua* L.) as species that would be affected by advancing populations. Sweetgum was found to be susceptible to defoliation by all larval instars. Loblolly pine was classified as resistant to defoliation, however, it was observed that once larvae had reached the second instar they could complete their life-cycle on a diet of pine foliage.

Many pine plantations within the southeastern United States contain a hardwood component of either oaks or sweetgum within the understory. Thus, in theory the possibility existed for first instar larvae to become established on the understory hardwoods and then to move onto the pines and defoliate them. In order to elucidate these relationships, research plots were established in forty-one Coastal Plain stands in between 1991 and 1993 and measurements of stand characteristics, defoliation, and tree mortality were conducted through the summer of 1996. Sixteen stands were defoliated and detailed results are presented in Chapters 4 and 5.

The results of this study have shown that as gypsy moth populations move south into pine, mixed pine-hardwood and hardwood stands, defoliation outbreaks will occur. The climate and species mix in these stands is favorable for the insect and southern oaks and sweetgum have been found to be susceptible to defoliation. The intensity of the outbreak and its duration will depend upon a number of factors, but the most important appears to be species composition. Stands with a moderate (40-50% of the BA) to high (>80%) basal area component of susceptible species will experience the most defoliation, and complete defoliation of individual trees of susceptible species can be expected.

Southern pines, specifically loblolly and pitch pine (P. *rigida* Mill.) have been found to sustain gypsy moth larvae within the laboratory. Larval consumption of pines in the field was also observed within this study. However, measurable defoliation was confined to a small number of isolated individuals. What this means for the timber manager is that currently there are no indications that widespread pine defoliation will follow the movement of gypsy moth populations into the Southeast. This does not mean that individual trees or even isolated groups within a stand may not be affected; however, the majority of the stand can be expected to withstand even heavy gypsy moth infestations. This is contrary to earlier reports of heavy white pine (*P.strobus* L.) defoliation in the northeast, but is similar to early observations of pitch pine defoliation (Hall, 1935; Turner, 1963).

Another possibility is that the pines within these stands may derive some benefit from a gypsy moth outbreak. For instance, suppose an outbreak were to occur within a 15 year old loblolly pine stand with an understory hardwood component of oaks and sweetgum comprising 20% of the total basal area. During the outbreak these hardwoods would be defoliated; if the oaks and sweetgum were killed, the reduction in competition for resources (light, water, and nutrients) may provide the same effect as the mid-rotation woody release that would normally be prescribed for a stand in this condition. Campbell and Garlo (1982) found this type of relationship within pine-oak stands in New Jersey. Results from this study indicate that sweetgum is not as vulnerable following defoliation as the southern oaks. However, even if the trees were not to die the simple reduction in hardwood growth caused by defoliation, and the temporary increase in water and nutrients during the growing season may still provide the pines with an advantage and thereby increase their growth.

Tree mortality following defoliation within these stand types will also favor the growth of pines. Southern oaks were found to be as vulnerable to mortality as their counterparts in the northeast, but sweetgum appeared to be less vulnerable following defoliation. However, where these susceptible species comprised a significant percentage of the total initial basal area, they also tended to comprise a greater proportion of the total mortality. Results from this study did not clearly implicate gypsy moth defoliation in pine mortality. Pine mortality was observed, however, the majority occurred among suppressed and intermediate trees. A significant amount of overstory pine mortality was observed within a single stand, but none of the dead trees had experienced more than 30% defoliation prior to their death. Previous research in mixed pine-hardwood stands in the Northeast has shown that defoliation intensities greater than 80% were required before significant tree mortality was observed (Turner, 1963; Stephens, 1988).

USING THE MODELS TO PREDICT DEFOLIATION AND TREE MORTALITY

The results of this study have demonstrated that both susceptibility and vulnerability of individual trees and stands are dependent upon numerous interrelated factors. Thus, the accurate prediction of either is very difficult. Nevertheless, as gypsy moth populations move into the southeastern United States, forest managers need to be able to determine the potential for stand damage. The models presented in chapters 4 and 5 were formulated to assist forest managers in the determination of the susceptibility and/or vulnerability of Coastal Plain mixed pine-hardwood stands, both prior to and following the arrival of gypsy moth populations. They are based upon observations in mixed pine-oak and pine-sweetgum stands that were subjected to a single defoliation outbreak. Therefore, extrapolation to other stand types or to areas experiencing multiple outbreaks is not advisable.

The susceptibility of individual stands can be estimated using the graph in Figure 4.13. The basal area of susceptible species is calculated as the proportion of the total stand basal area that consists of those susceptible tree species listed in Table 3.1. A more complete listing of susceptible species may be found in Liebhold et al. (1995). Estimation of gypsy moth egg mass density may be accomplished using fixed-area plots and the method outlined by Liebhold et al. (1994). In areas where information on gypsy moth egg mass density is unavailable, forest managers may choose to use the heaviest egg mass densities in their estimation and thereby create the “worst case” defoliation scenario for a stand of interest. As the predicted average stand defoliation increases, defoliation of both susceptible and resistant species within a stand will also increase.

If a particular stand is determined to be susceptible to defoliation the flowcharts in Figures 6.1 and 6.2 can be used to determine the probability of individual tree mortality within a particular cover type. Figure 6.1 is designed to be used to estimate mortality in pine-oak stands and uses host preference class and crown condition (Table 6.1) to determine vulnerability. For example, following a gypsy moth outbreak in a pine-oak stand, a southern red oak (*Q.falcata* Michx.) in fair condition would have a 36 percent probability of dying, while a loblolly pine in good condition would have a 7 percent probability of dying. These charts were designed to be used with a 0.25 probability cutpoint, (i.e. if the assigned probability is ≥ 0.25 then the tree is

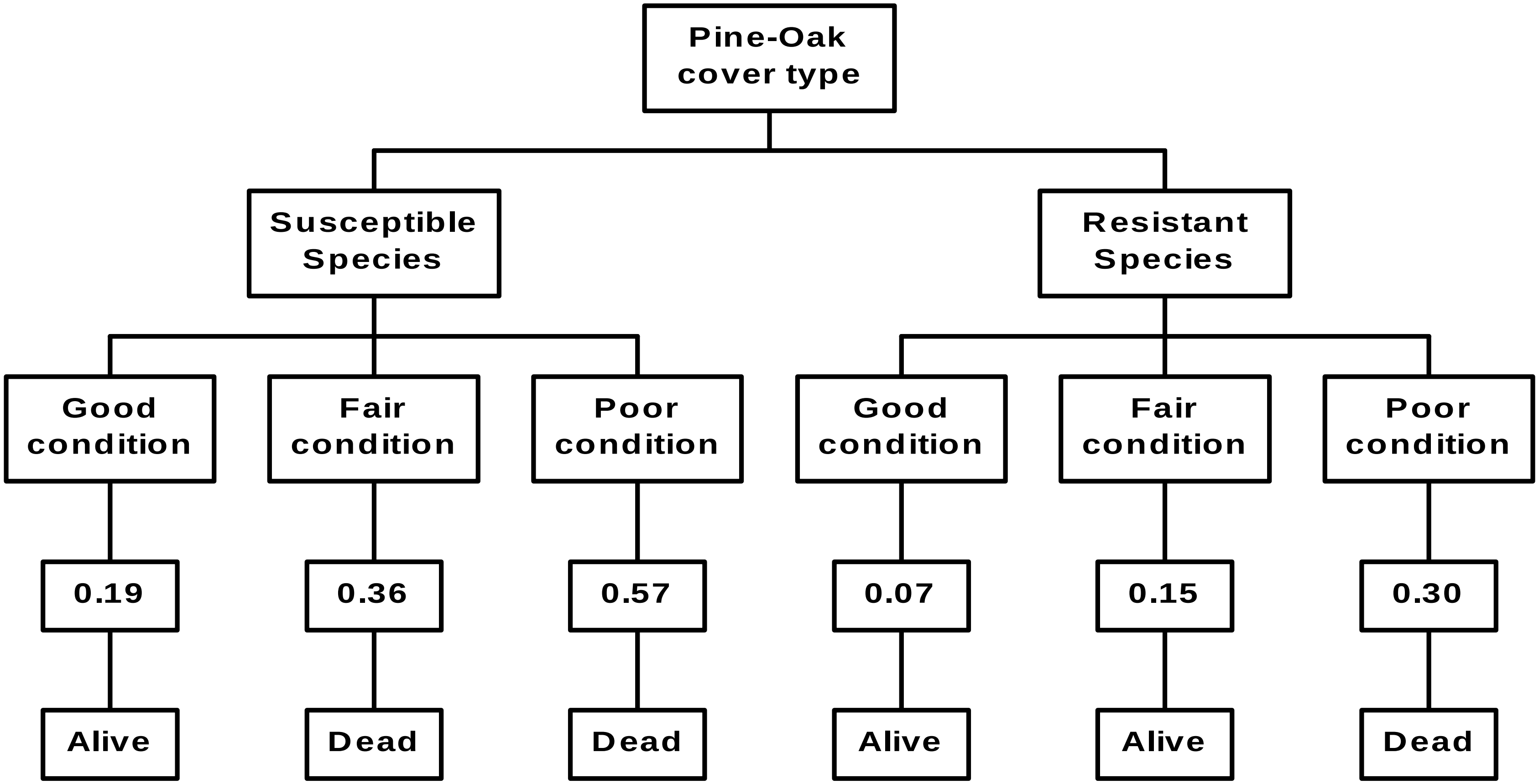

Figure 6.1: Flowchart for use in estimating the probability of individual tree mortality in mixed pine-oak stands following a single gypsy moth outbreak; probability of mortality is dependent upon host preference class (susceptible or resistant), and crown condition (good, fair, or poor), the final boxes show tree classification status based upon a cutpoint of 0.25.

Table 6.1: Characteristics used in assigning individual trees to a crown condition class for the determination of vulnerability to gypsy moth defoliation (Gottschalk and McFarlane, 1992).

Condition Class	**Tree Characteristics**
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

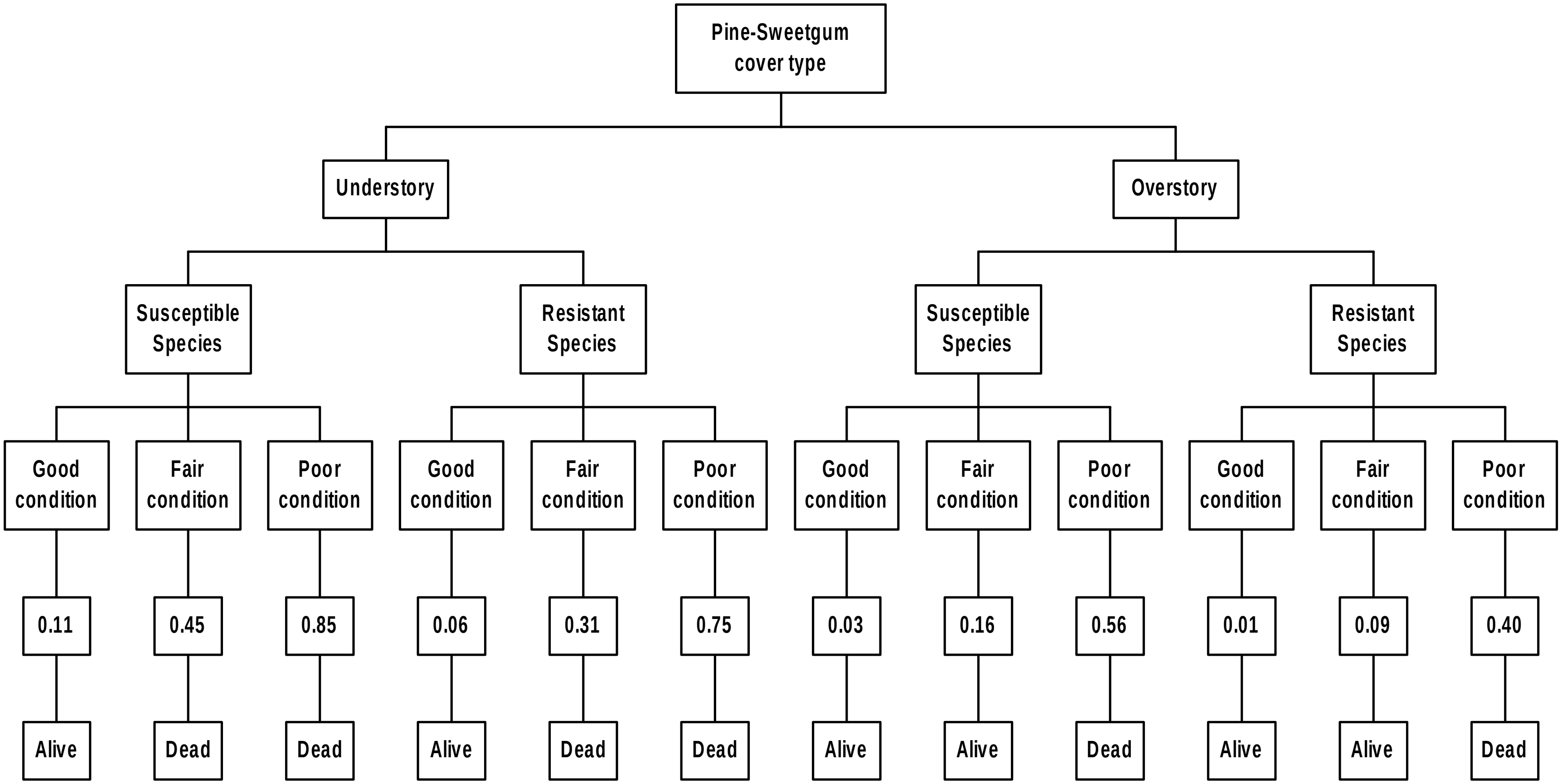

Figure 6.2: Flowchart for use in estimating the probability of individual tree mortality in mixed pine-sweetgum stands following a single gypsy moth outbreak; probability of mortality is dependent upon crown class (understory or overstory), host preference class (susceptible or resistant), and crown condition (good, fair, or poor), the final boxes show tree classification status based upon a cutpoint of 0.25.

considered dead), therefore the southern red oak would be classified as dead while the pine would be alive. Figure 6.2 is designed for use in pine-sweetgum stands and uses canopy position, host preference class, and crown condition to assign a probability of mortality. The method is the same as that for Figure 6.1 except that trees must be classified as either understory (suppressed or intermediate) or overstory (codominant or dominant) first. Once individual tree probabilities have been assigned, stand tables may be utilized to produce stand-level mortality estimates.

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