Prediction of stand susceptibility and gypsy moth defoliation in Coastal Plain mixed pine–hardwoods

C.B. Davidson, J.E. Johnson, K.W. Gottschalk, and R.L. Amateis

Abstract: The European gypsy moth (*Lymantria dispar* L.) is an introduced defoliator that has become endemic in forests of the northeastern United States. During the last five decades, populations have continued to advance into the southeastern United States. Defoliation outbreaks continue to occur along the leading edge of the infestation, and the potential for extensive defoliation within southern forests remains. A field study was implemented in 1991 to determine the relationship between species composition and gypsy moth defoliation in Coastal Plain mixed pine–hardwood stands and to formulate a defoliation prediction model. Stands in both pine–oak and pine–sweetgum cover types were extensively defoliated during a single defoliation outbreak. Mean stand defoliation in the pine–oak type peaked at 42.6% in 1994, while mean defoliation in the pine–sweetgum type peaked at 32.8% in 1995. Defoliation intensity was significantly related to stand composition, with oaks and sweetgum being defoliated at the greatest intensities. Overall, pines were not heavily defoliated in either cover type. However, moderate to heavy defoliation of a small number of overstory pines was observed in some pine–oak stands and appeared to be due to a threshold level of oak defoliation (>80%). A nonlinear model for the prediction of mean total stand defoliation is also presented. Defoliation is predicted as a function of the number of gypsy moth egg masses, the number of years since the beginning of the outbreak, susceptible species basal area, pine basal area, and total stand basal area.

Résumé : La spongieuse (*Lymantria dispar* L.) est un insecte défoliateur introduit qui est devenu endémique dans les forêts du nord-est des États-Unis. Au cours des cinq dernières décennies, les populations ont continué de progresser vers le sud-est des États-Unis. Des épidémies continuent à survenir le long du front de l’infestation et la possibilité subsiste qu’il y ait des défoliations sévères dans les forêts du sud. Une étude de terrain a été mise en place en 1991 pour déterminer la relation entre la composition en espèces et la défoliation par la spongieuse dans les peuplements mélangés de pins et de feuillus de la plaine côtière et pour élaborer un modèle de prédiction de la défoliation. Les peuplements dont les types de couvert sont dominés par le pin et le chêne ainsi que par le pin et le liquidambar ont été sévèrement défoliés au cours d’une seule épidémie. La défoliation moyenne des peuplements dont le type de couvert est dominé par le pin et le chêne a atteint un maximum de 42,6% en 1994 tandis qu’elle a atteint un maximum de 32,8% en 1995 dans le type de couvert dominé par le pin et le liquidambar. L’intensité de la défoliation était significativement reliée à la composition du peuplement; le chêne et le liquidambar ont été les essences les plus sévèrement défoliées. Le pin n’était généralement pas sévèrement défolié dans l’un ou l’autre des types de couvert. Cependant, une défoliation modérée à sévère d’un petit nombre de pins de l’étage dominant a été observée dans certains peuplements de pin et de chêne. Elle semblait être due au degré de défoliation (>80%) du chêne. Les auteurs présentent un modèle non linéaire pour prédire la défoliation moyenne des peuplements. La défoliation est prédite sur la base du nombre de masses d’œufs de la spongieuse, du nombre d’années depuis le début de l’épidémie, de la surface terrière des espèces sensibles, de la surface terrière du pin et de la surface terrière totale.

[Traduit par la Rédaction]

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. 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 and Michigan (USDA 2000). Although the total area defoliated by the gypsy moth has fallen within the last decade, outbreaks continue to occur along a leading edge. Recent studies indicate there is potential for continued defoliation in southern forests (Barbosa et al. 1983; Cook et al. 1994; USDA 2000; Liebhold et al. 1997).

The preference of gypsy moth larvae for certain tree species has been well documented (Mosher 1915; Bess et al. 1947; Liebhold et al. 1995). As a result, classification systems have been developed that rank forest trees according to

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their susceptibility to defoliation. One of the most recent describes trees as being either “susceptible”, “resistant”, or “immune” based on the likelihood of defoliation (Montgomery 1991; Liebhold et al. 1995). Susceptible trees 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 rarely, if ever, consumed by any larval stage (Montgomery 1991). Field studies in northeastern hardwood forests have confirmed the susceptibility of oaks (*Quercus* spp.) to gypsy moth defoliation (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, sweetgum (*Liquidambar styraciflua* L.), and loblolly pine (*Pinus taeda* L.) are likely to be defoliated (Cook et al. 1994; Gottschalk and Twery 1989). The potential for population expansion prompted renewed interest in host susceptibility studies, and laboratory feeding trials were conducted with southern tree species (Barbosa et al. 1983; Berisford et al. 1993). Results of these studies have identified sweetgum as a highly susceptible host. Loblolly pine is unable to support first instars. However, the development, survival, and fecundity of later instars are excellent (Barbosa et al. 1983; Rossiter 1987; Berisford et al. 1993). These results do not indicate whether mixed stands containing susceptible species are as vulnerable to defoliation outbreaks as pure hardwood stands, however. The dearth of information surrounding the effects of defoliation in mixed pine–hardwood stands led to the design of a field study. Our objectives were to (*i*) determine the relationship between species composition and gypsy moth defoliation in Coastal Plain mixed pine–hardwood stands and (*ii*) formulate a model that would facilitate prediction of defoliation within these stands.

Methods

Study areas

The study was established in the Atlantic Coastal Plain physiographic province, in Dorchester, Somerset, Wicomico, and Worcester Counties, Maryland (38°35′–38°05′N, 75°56′–75°25′W). Research plots were established in 16 mixed pine–hardwood stands in 1991, 1992, and 1993. Stands were selected that contained mixtures of loblolly pine and oak, or loblolly pine and sweetgum. Selection was based on several criteria, the most important being stand composition as a range of species composition from nearly pure hardwood to nearly pure pine was desired. Additionally, stands were required to be fully stocked with 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.

Field measurements

Within each of the 16 stands, three 0.04-ha sample plots were established at random locations, at a minimum separating distance of 50 m from each other and the stand boundary. Tree species, diameter at breast height (DBH, 1.37 m), and percent defoliation were measured for all woody stems ≥5 cm DBH. The 16 stands were classified as either pine–oak or pine–sweetgum based on whether oak or sweetgum was the dominant hardwood, as determined by percent basal area. Individual trees were assigned to one of the three host feeding preference classes, i.e., susceptible, resistant, or immune to defoliation (Montgomery 1991). Percent defoliation was estimated visually for individual trees and trees were placed into one of five defoliation classes: none, 0–10%; light, 11–30%; moderate, 31–60%; heavy, 61–90%; and complete, 91–100%. Defoliation was assessed during the period of time following peak defoliation, i.e., between larval pupation and the start of refoliation. Defoliation measurements were collected each year from 1992 to 1996.

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 within each 0.04-ha plot, and the number of egg masses within each plot were counted; centres of the three 0.01-ha plots were established at predetermined bearings from the center of the 0.04-ha plot. The method proposed by Liebhold et al. (1994) was used to distinguish between egg masses of the current and previous generations to reduce the possibility of overestimating population sizes. This method utilizes the ratio 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. Egg mass surveys were taken in the fall of each year, 1992–1995, following leaf abscission. Finally, increment cores were collected at DBH from overstory loblolly pine trees in mid-June 1997, and approximate stand age was determined.

Data analysis

Annual defoliation estimates obtained 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):

$$[1] \qquad \mathrm{DEF} = \frac{\sum_{i=1}^{n} (D_i^2 \times \mathrm{DEF}_i)}{\sum_{i=1}^{n} D_i^2}$$

where D_i is the individual tree diameter (cm) and DEF_i is the individual tree defoliation estimate (%).

Analysis of variance followed by mean separation using the Ryan–Einot–Gabriel–Welsch multiple *F* test (SAS Institute Inc. 1992) was used to determine differences between defoliation levels for various species groups at the 5% significance level.

Modeling defoliation relationships

An appropriate model expressing the relationship between total stand defoliation and defoliation factors is

$$[2] \qquad \mathrm{DEF_s} = \alpha Y\, \mathrm{e}^{\gamma Y}$$

where $\mathrm{DEF_s}$ is percent stand defoliation at time Y of the outbreak, Y is the number of years since start of the outbreak, and α and γ are parameters to be estimated. In this model, defoliation is constrained to be zero at the start of the outbreak, increase to a maximum, and then diminish asymptotically toward zero. The shape of the defoliation curve is strongly influenced by γ, and the maximum response and time to maximum response depend on the values of α and γ. Sit and Poulin-Costello (1994) discuss the mathematical properties of this function in detail.

The effects of egg mass numbers and basal area of susceptible species can be incorporated into eq. 2 by making them functions of the parameter α:

Table 1. Total stand basal area, stem density, mean diameter, age, and species basal area of 16 mixed pine–hardwood stands at the time of plot establishment.

Stand type and No.	BA (m^2/ha)	Stem density (stems/ha)	Mean DBH (cm)	Mean age[a] (years)	Species basal area (m^2/ha) Oak	Sweetgum	Pine[b]	Resistant hardwoods	Immune hardwoods
Pine–oak									
1	14.3	683	15.4	40	11.5	0.0	2.1	0.3	0.4
2	30.9	1092	15.8	55	13.5	3.2	11.0	2.5	0.7
3	27.9	992	16.4	68	9.4	0.5	15.8	0.2	2.1
4	34.4	667	20.4	73	10.0	1.5	16.4	5.7	0.9
5	37.1	1483	15.3	88	6.5	4.3	23.4	1.2	1.7
6	40.2	1358	16.6	62	4.6	1.4	30.4	2.6	1.3
7	32.0	1408	13.5	55	1.2	0.1	21.1	4.9	4.9
Mean	31.0	1098	16.2	63	8.1	1.6	17.2	2.5	1.7
Pine–sweetgum									
8	37.8	800	21.4	55	0.0	18.5	10.7	7.2	1.4
9	45.2	1167	18.1	65	0.0	15.0	24.4	3.7	2.0
10	52.8	1283	18.7	59	8.5	16.6	14.7	6.4	6.6
11	51.4	1425	17.9	49	0.0	14.3	27.3	9.3	0.5
12	50.4	1042	21.9	57	0.0	9.3	33.8	6.5	0.8
13	47.9	1142	19.2	54	0.0	7.7	33.0	6.7	0.5
14	40.0	1292	16.7	73	4.6	5.9	22.1	3.8	3.6
15	49.1	1308	18.4	46	0.0	7.2	34.4	7.2	0.3
16	36.8	2029	13.4	30	1.3	2.4	32.3	0.7	0.1
Mean	45.7	1276	18.4	54	1.7	10.8	25.8	5.7	1.8

[a]Stand age is based on the age of dominant or codominant pines.
[b]Pine are classified as resistant species.

$$[3] \qquad \alpha = \left(\frac{BA_S}{BA_T}\right)^{b_1} BA_P^{b_2} [\ln(EM)]^{b_3}$$

where EM is the number of egg masses per hectare at time $Y - 1$ of the outbreak; BA_T is the total stand basal area (m^2/ha) at start of outbreak; BA_S is the basal area of susceptible species (m^2/ha) at start of outbreak; BA_P is the basal area of pines (m^2/ha) at start of outbreak; and b_1, b_2, b_3 are parameters to be estimated. Four years of egg mass data (1992–1995) and defoliation data (1993–1996) were used to estimate the parameters of eq. 2 using nonlinear regression. Defoliation data from each of the three 0.04-ha plots within a stand was used as an observation; egg mass data from the three 0.01-ha plots within each 0.04-ha plot was pooled.

Results

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 (Table 1). Stem density ranged from 667 to 1483 stems/ha in pine–oak stands, and from 800 to 2029 stems/ha in pine–sweetgum stands. In both cover types, sweetgum and various species of southern oaks were the only susceptible tree species encountered (Table 2). Although oaks were the dominant susceptible species in the pine–oak type, sweetgum was also a frequent stand component (Table 1). In the pine–sweetgum type, oaks were less common, occurring in only three of the nine stands. Loblolly pine was the most frequently observed coniferous species. However, pitch pine (*Pinus rigida* Mill.), shortleaf pine (*Pinus echinata* Mill), and Virginia pine (*Pinus virginiana* Mill) were also found within the pine–oak type. Pine–sweetgum stands contained a greater proportion of resistant species, while the mean basal area of immune species was approximately equal in both cover types.

During the study period, both cover types were subjected to a single gypsy moth defoliation outbreak. Egg mass density was variable both between stands and among years (Table 3). Most stands experienced an increase in population density to some maximum followed by a decline. Although maximum egg mass density did not occur in the same year in all stands, there was little variability in outbreak chronologies between cover types. Within the pine–oak type, populations peaked in five stands in 1993. One population peaked in 1992 and the other in 1994 in the two remaining stands (Table 3). Among pine–sweetgum stands, the majority experienced population peaks in 1994. Two stands reached maximum density in 1993. The maximum population size achieved by individual gypsy moth populations within both cover types ranged from less than 4000 to over 21 000 egg masses/ha (Table 3). In both cover types, populations had dramatically declined by 1995, and the outbreak appeared to be completely over by 1996.

Stands in both cover types were extensively defoliated during the outbreak period (Table 4). Peak gypsy moth defoliation generally occurred in the year subsequent to the maximum observed gypsy moth egg mass density. Only 3 of 16 stands departed from this trend; two experienced defoliation peaks in the year of peak egg mass density, while in the third, defoliation peaked 2 years after the maximum observed egg mass density. Within these three stands, localized outbreaks of the forest tent caterpillar (*Malacosoma disstria* Hübner) occurred in both 1994 and 1995. Within the pine–oak type, mean egg mass levels were greatest in 1993, resulting in the greatest mean defoliation intensity of 42.6%

Table 2. Listing of all tree species by host feeding preference class in pine–oak and pine–sweetgum stands.

Occurrence	Susceptible species	Resistant species	Immune species
Both stand types	*Liquidambar styraciflua* L., sweetgum; *Quercus alba* L., white oak; *Quercus bicolor* Willd., swamp white oak; *Quercus falcata* Michx., southern red oak; *Quercus michauxii* Nutt. swamp chestnut oak; *Quercus nigra* L., water oak; *Quercus phellos* L., willow oak; *Quercus rubra* L., northern red oak	*Acer rubrum* L., red maple; *Carpinus caroliniana* Walt., hornbeam; *Pinus taeda* L., loblolly pine; *Sassafras albidum* (Nutt.) Nees, sassafras	*Ilex opaca* Ait., American holly; *Magnolia virginiana* L., sweetbay; *Nyssa sylvatica* Marsh., blackgum
Pine–oak stands	*Quercus stellata* Wang., post oak; *Quercus velutina* Lam., black oak*	*Cornus florida* L., flowering dogwood;* *Pinus echinata* Mill., shortleaf pine; *Pinus rigida* Mill., pitch pine; *Pinus virginiana* Mill., Virginia pine*	
Pine–sweetgum stands		*Carya tomentosa* (Poir.) Nutt., mockernut hickory; *Fagus grandifolia* Ehrh., American beech; *Prunus serotina* Ehrh., black cherry*	

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

Table 3. Annual mean gypsy moth egg mass density per hectare at study sites.

Stand type and No.	Egg masses/ha			
	1992	1993	1994	1995
Pine–oak				
1	8463	6 478	7 166	1083
2	851	8 099	5 542	5138
3	2337	7 806	932	1566
4	—	3 291	8 773	1369
5	7653	21 073	1 672	1431
6	2343	14 959	3 300	1221
7	1195	3 742	2 837	920
Mean	3807	9 350	4 317	1818
Pine–sweetgum				
8	—	1 667	18 802	689
9	—	7 333	19 309	3278
10	—	400	9 067	228
11	—	1 300	16 097	1218
12	67	2 400	10 927	1619
13	100	1 713	13 732	1589
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	1141

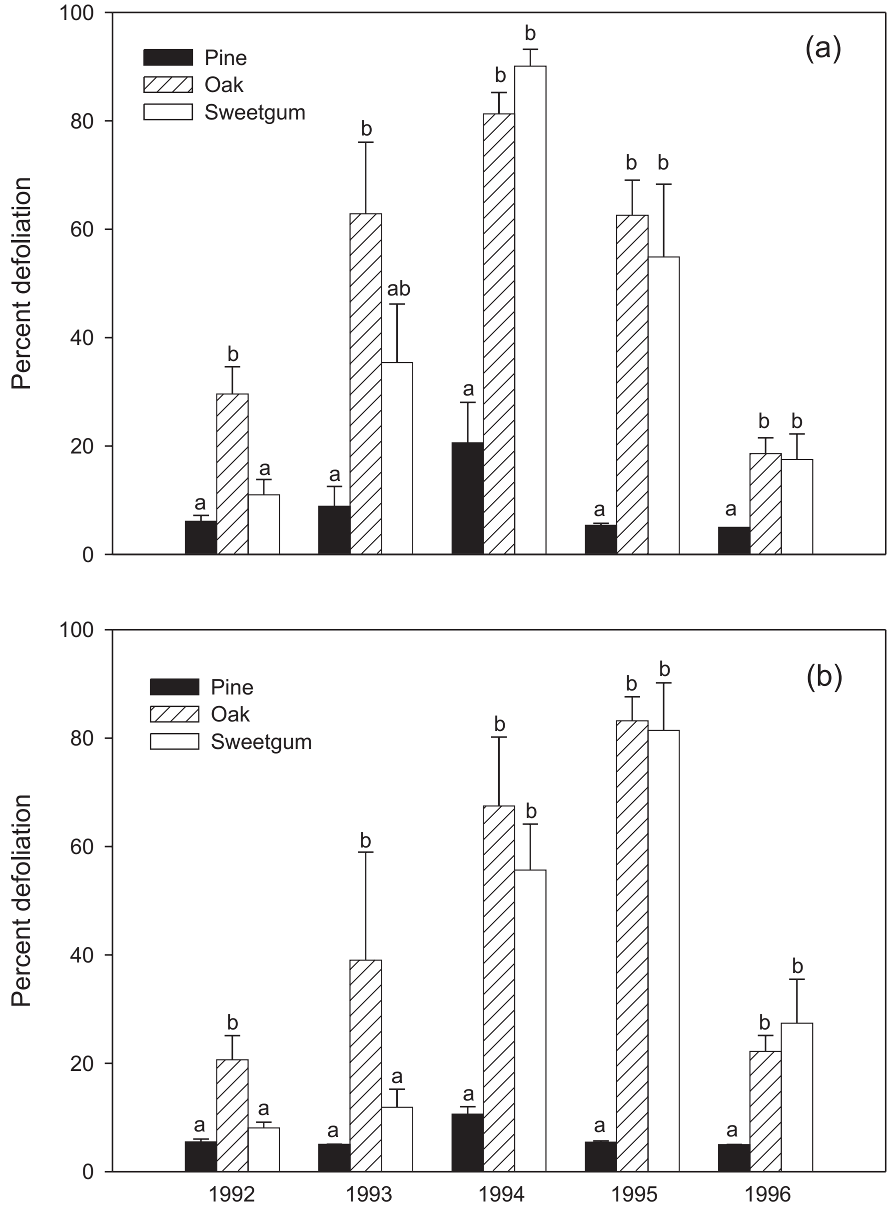
Table 4. Mean percent gypsy moth defoliation within individual pine–oak and pine–sweetgum stands during a single defoliation outbreak from 1992 to 1996.

Stand type and No.	Mean stand defoliation (%)				
	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	8.5
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	32.7	12.5

occurring in 1994 (Table 4). In the pine–sweetgum type, mean egg mass levels were greatest in 1994, and defoliation intensities did not peak within the majority of these stands until 1995, when mean total stand defoliation reached 32.7% (Table 4). Mean defoliation was positively related to the preceding fall's egg mass density in both pine–oak (p = 0.0471) and pine–sweetgum (p = 0.0001) stands.

In pine–oak stands the susceptible oaks and sweetgum were defoliated at the greatest intensities during each of the outbreak years from 1992 to 1996 (Fig. 1*a*). Pines were not defoliated at any appreciable level until 1994. An analysis of variance using the Ryan–Einot–Gabriel–Welsch multiple F test (SAS Institute Inc. 1992) revealed significant differences in mean defoliation levels between these species groups 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. As defolia-

Fig. 1. Mean annual defoliation of all pines, oaks, and sweetgum between 1992 and 1996 in (*a*) pine–oak and (*b*) pine–sweetgum stands. Error bars are SE. For each year, means with the same letter are not significantly different at the 0.05 alpha level using the Ryan–Einot–Gabriel–Welsch multiple *F* test.



tion levels decreased in 1995 and 1996, defoliation of the susceptible oaks and sweetgum remained significantly greater than pine defoliation.

Susceptible species also experienced the greatest defoliation intensities in pine–sweetgum stands (Fig. 1*b*). Although sweetgum was the dominant susceptible species in these stands, defoliation trends observed in pine–oak stands were also observed here. During the early years of the outbreak (1992–1993), oak defoliation was significantly greater than both pine and sweetgum defoliation, and sweetgum defoliation did not differ significantly from pine defoliation (Fig. 1*b*). In 1994, mean defoliation of sweetgum increased and significant differences between sweetgum and pine defoliation were observed throughout the remainder of the outbreak.

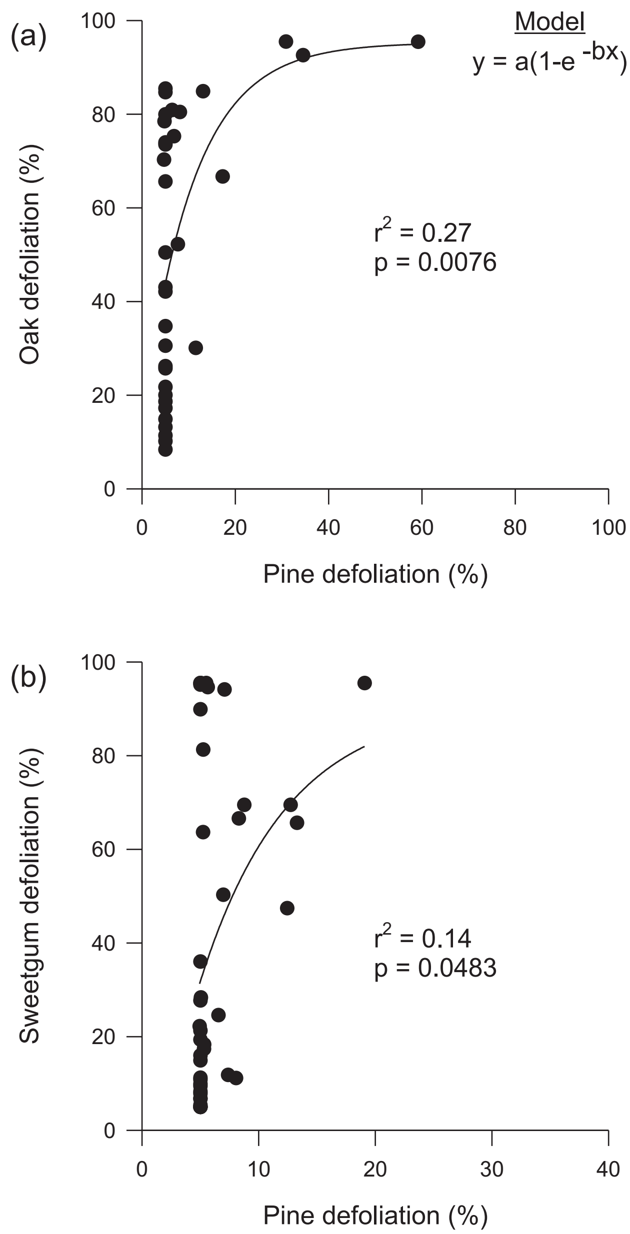
Mean pine defoliation exhibited a marked increase in pine–oak stands in 1994 (Fig. 1*a*). This increase was due primarily to intensive defoliation within three of the seven stands where moderate to heavy defoliation of a small number of overstory pines caused mean pine defoliation levels to increase to 17, 34, and 59%. In each case, the susceptible species within the stand were completely defoliated. This increase in pine defoliation appears to be related to a threshold level of oak defoliation (Fig. 2*a*). When oak defoliation exceeded 80% in pine–oak stands the intensity of pine defoliation increased dramatically. This relationship was not as well defined within pine–sweetgum stands (Fig. 2*b*). Although defoliation intensities and the basal area of susceptible species were similar to those of pine–oak stands, pine defoliation never exceeded 20%.

Pine basal area displayed a negative relationship with mean stand defoliation in both pine–oak (p = 0.0094) and pine–sweetgum (p = 0.0452) stands. Within individual stands, mean defoliation over the course of the outbreak increased significantly as the proportion of either oak (p = 0.0021) or sweetgum (p = 0.0107) increased (Fig. 3). The relationship between defoliation and susceptible species basal area (combined oak and sweetgum) was also positive in pine–oak (p = 0.0083) and pine–sweetgum (p = 0.0278) stands.

Within both cover types, a second susceptible hardwood species frequently occurred as a minor stand component. In pine–oak stands, sweetgum was often present, while in pine–sweetgum stands, different species of southern oak could be found. However, the species that accounted for the minor portion of the susceptible hardwood component did not have a significant influence on defoliation intensity in either pine–oak (p = 0.2197) or pine–sweetgum (p = 0.6675) stands.

The parameters of eq. 3 were estimated (Table 5) and predicted versus observed percent defoliation was compared for four randomly selected study plots (Fig. 4). The deviation between observed and predicted values ranged from 2 to 10%. The index of fit (one-residual sum of squares/corrected total sum of squares) for the regression was 0.39, and the mean squared error was 180.2.

Fig. 2. 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.



Discussion

Numerous studies have confirmed the importance of species composition in determining stand susceptibility and subsequent defoliation intensity, with defoliation increasing as the proportion of susceptible species increases (Campbell and Sloan 1977; Brown et al. 1979; Herrick and Gansner 1986; Houston and Valentine 1985). The stands within this study exhibited similar patterns. Defoliation intensity was significantly related to stand composition. This is consistent with 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). Gypsy moth larvae seek out suitable foliage when feeding, and laboratory studies have classified both oaks and sweetgum as suitable hosts. Therefore, stand susceptibility is dependent upon whether oaks, sweetgum, or other susceptible species are present and in what proportion. Pine basal area was shown to have a negative effect on mean stand defoliation in both cover types, while the relationship between defoliation and oak, sweetgum, and susceptible species basal area was positive. In eq. 3, the influence of tree species on defoliation is accounted for through basal area. A higher ratio of susceptible species basal area to total basal area results in more stand defoliation; conversely, increased pine basal area reduces defoliation.

Among individual species, the susceptible oaks and sweetgum were defoliated at the greatest intensities. Pines were not heavily defoliated in either cover type, regardless of total pine basal area. The uncharacteristically heavy defoliation of pines observed in three stands occurred in conjunction with the complete defoliation of all susceptible species. This probably resulted in gypsy moth larvae switching to the more resistant pines when the supply of susceptible host foliage was depleted (Gottschalk and Twery 1989). 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 identified throughout the years and because they are frequently correlated. Climate, site factors, inter- and intra-specific susceptibility to defoliation, and the dynamics of predator–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 our 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 is a distinct possibility.

The selected model appears to adequately simulate defoliation over a range of susceptible species and pine basal ar-

Fig. 3. Relationship between cumulative mean defoliation and susceptible species basal area in (*a*) pine–oak stands and (*b*) pine–sweetgum stands.

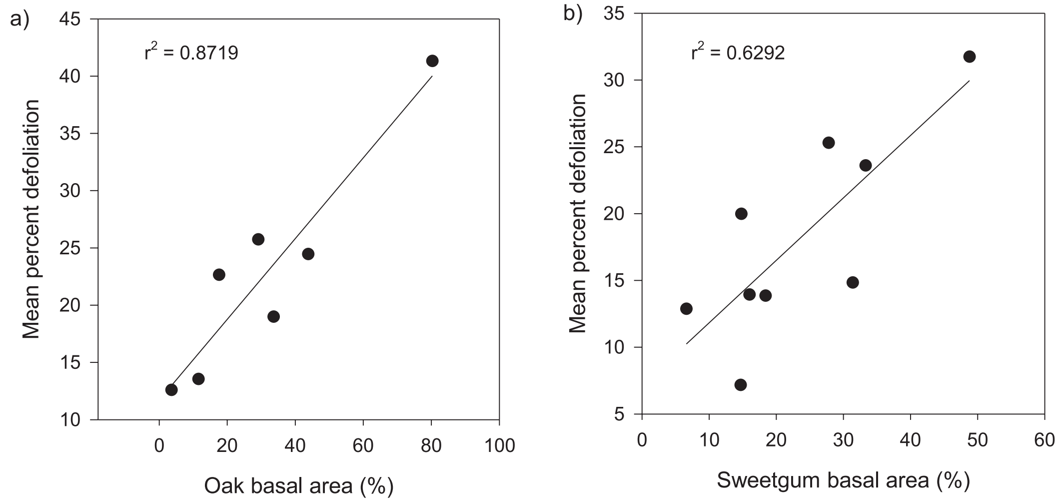


Fig. 4. Observed and predicted stand defoliation values of four randomly selected study plots using a nonlinear model.

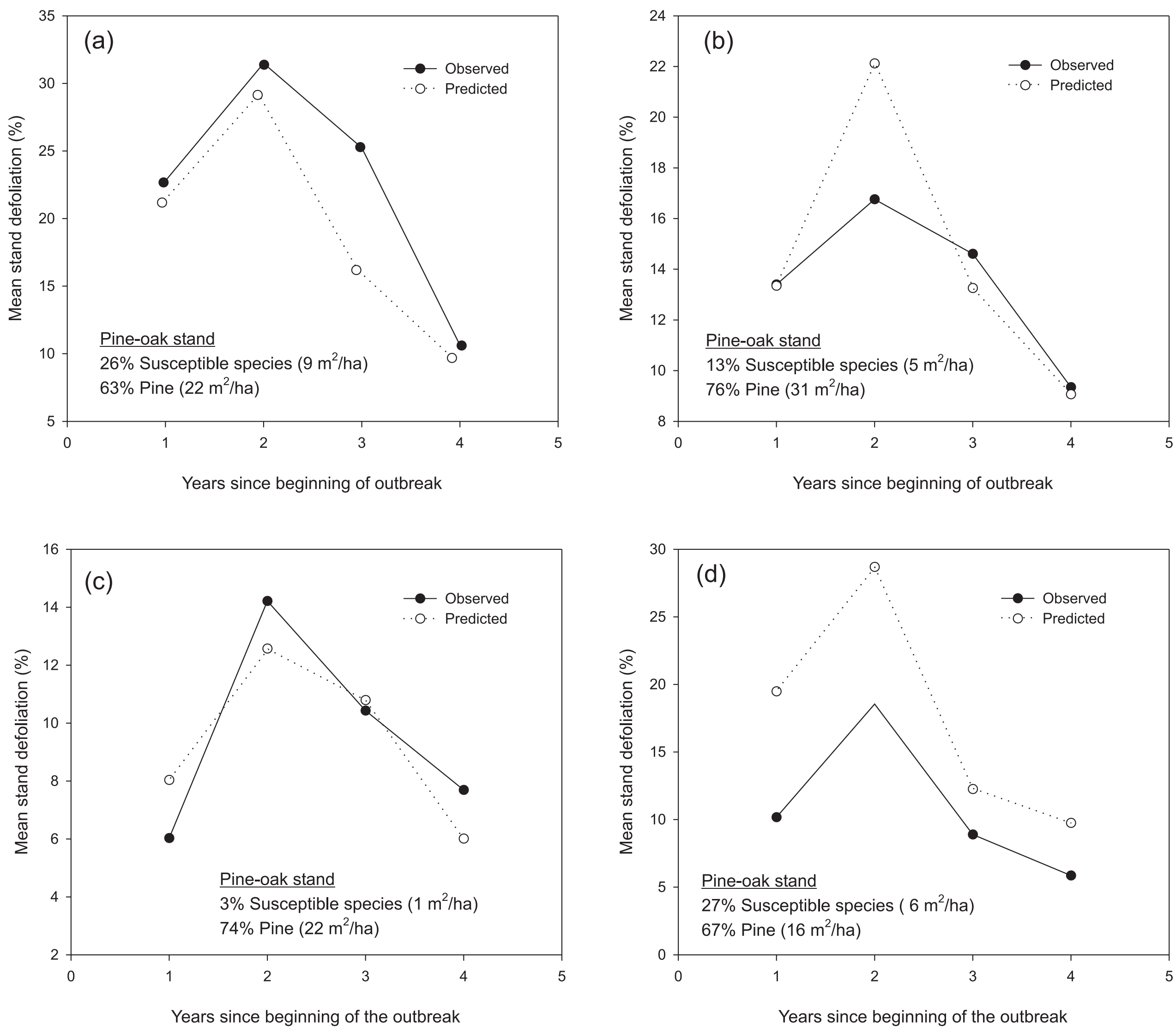


Table 5. Parameter estimates and asymptotic standard errors for the estimates of eq. 4 fitted to the defoliation data set.

Parameter	Estimate	Asymptotic SE
b_1	0.2226	0.1036
b_2	–0.2684	0.0579
b_3	2.0792	0.0647
γ	–0.5781	0.0530

eas. The range in deviations between predicted and observed values in the four randomly selected plots is relatively small. Although the model explains only 39% of the variation in total stand defoliation, no extreme deviations in prediction were observed and residual plots did not indicate any deviations from the regression assumptions. The model's limitations are due both to the variation in species basal area in the development data set and its relatively small size. Gypsy moth defoliation is dependent upon a complex of interacting and often interrelated factors making accurate prediction difficult.

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