Area-Wide Analysis of Hardwood Defoliator Effects on Tree Conditions in the Allegheny Plateau

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ABSTRACT: *The effects of defoliation caused by three foliage feeding insects, the gypsy moth (*Lymantria dispar*), the cherry scallopshell moth (*Hydria prunivorata*), and the elm spanworm (*Ennomos subsignarius*), on tree mortality and crown conditions were evaluated using data collected from 1984 to 1999 in the Allegheny National Forest located in northwestern Pennsylvania. While previous studies have focused on the effects of defoliation on trees in individual stands, this study differed in that it used exhaustive maps of defoliation and an areawide network of plots to assess these effects. A geographic information system was used to map the coincidence of USDA Forest Service Forest Inventory and Analysis and Forest Health Monitoring plot locations with defoliation polygons derived from aerial surveys to calculate cumulative years of defoliation for each pest. Over 85% of the Allegheny National Forest land area was defoliated at least once during the 16-year period from 1984 to 1999. Frequency of defoliation by specific defoliator species was closely associated with the dominance of their primary hosts in stands. Frequency of defoliation was often associated with crown dieback and mortality, but these relationships were not detectable in all species. These results suggest that when impacts are averaged over large areas (such as in this study) effects of defoliation are likely to be considerably less severe than when measured in selected stands (as is the approach taken in most previous impact studies). North. J. Appl. For. 21(1):31–39.*

Key Words: Defoliation, cherry scallopshell moth, elm spanworm, gypsy moth, tree mortality, crown dieback.

Insects and pathogens play important roles in forest ecosystem dynamics. Most insects and diseases rarely reach epidemic levels, but a few species become problems when their numbers reach outbreak levels and cause significant damage (Mason 1987). Most forest insects have beneficial effects like cycling nutrients from foliage to soils, killing weak or noncompetitive trees, and decomposing dead trees (Mattson and Addy 1975, Haack and Byler 1993).

Outbreaks of insect defoliators can have a significant effect on forest growth and productivity. The most important effects of defoliation are reductions in tree growth, decline in crown vigor, individual tree mortality (Kulman 1971, Davidson et al. 1999), and stand mortality (Osawa 1989). These effects vary considerably, both among tree species and among defoliator species (Alfaro et al. 1982, Fleming and Piene 1992). Foliage age, location of foliage in crowns, time of defoliation, and stage of leaf development all influence defoliation effects on tree growth and mortality. Modeling tree mortality is difficult because it can be caused by many different factors and, in general, is a complex process over time (Herrick and Gansner 1987, Gottschalk et al. 1998). Tree decline and mortality often cannot be attributed to a single cause; Manion and Lachance (1992) describe a decline disease spiral that indicates the interchangeablity of various stressing factors including drought, frost, wind damage, poor sites, old age, etc. Defoliation by insects is considered to be an inciting factor.

The research presented here offers a new approach to evaluating the effects of defoliation on forests. Previous studies have measured defoliation and tree conditions in selected stands by setting up a series of plots in a limited area (e.g., Kegg 1973, Fosbroke and Hicks 1989) rather than estimating over an entire region. In contrast, this study integrated plot level data randomly sampled over a geographical area with aerial survey data to assess effects over a large landscape.

NOTE: Randall Morin can be reached at (304) 285-1522; rsmorin@fs.fed.us; http://www.fs.fed.us/ne/morgantown/4557/randy/. The authors thank the USDA Forest Service Forest Health Monitoring program for funding this project with Evaluation Monitoring moneys. Thanks to Daniel Twardus, Robert White, Stephen Horsley, Robert Acciavatti, and William Smith for their guidance and recommendations during the project.

This study was conducted using data collected from the Allegheny National Forest (ANF) covering 740,500 acres on the Allegheny plateau in northwestern Pennsylvania (Figure 1). The ANF is characterized by an abundance of black cherry (*Prunus serotina*), maple (*Acer* spp.), and other hardwoods. Most of the commercial black cherry timber in the United States originates from the Allegheny Plateau (Marquis 1975) and the Allegheny Mountains. Concerns about forest health on the ANF have been raised recently by the public in part because of an apparent increase in tree mortality in Allegheny hardwood forests between 1985 and 1995 (McWilliams et al. 1996). Some speculation has suggested that this mortality may have been due to extensive forest defoliator outbreaks in the region. Droughts in the late 1980s and early 1990s also coincided with several insect defoliator outbreaks. During the interval 1991–1996, the native insects cherry scallopshell moth (*Hydria prunivorata*), elm spanworm (*Ennomos subsignarius*), forest tent caterpillar (*Malacosoma distria*), and oak leaftier (*Croesia semipurpurana*) defoliated 611,000 acres on the ANF; and from 1985 to 1996 gypsy moth (*Lymantria dispar*) defoliated 317,000 acres on the ANF. In addition, there is some indication that mortality of sugar maple (*Acer saccharum*) in the region is part of a poorly understood general decline in this species occurring throughout the northeast (Horsley et al. 2002).

The objective of this study was to determine to what extent forest declines in the Allegheny Plateau can be attributed to the recent series of defoliator outbreaks. This work also explores the potential of using Forest Health Monitoring (FHM) data to identify regional forest declines.

Methods

Tree conditions were assessed using tree measurements taken in 1989 as part of the Forest Inventory and Analysis (FIA) program and in 1998, 1999, 2000, and 2001 as part of the FHM program. FIA plots have been remeasured about every 10 years; in Pennsylvania inventories were conducted in 1968, 1978, and 1989 (Alerich 1993). In most cases, there is approximately one FIA plot for every 6,000 acres (Hansen et al. 1992), but the 1989 sampling intensity was higher in the ANF with about one plot for every 3,000 acres. Plot locations in the ANF, and elsewhere in Pennsylvania, were determined by a two-step stratified random sampling procedure. Aerial photos are used to classify all areas into land-use classes (pasture, urban, forestland, water, etc.). For forested land, a more detailed classification categorized areas based on forest type, volume, stand size, stand density, ownership, and stand age. Estimates of land area in each class were derived from aerial photos and then used to determine the number of plots that were randomly located in each class (Hansen et al. 1992). For the 1989 survey, two different plot designs were used (Alerich 1993). Remeasured plots (from the previous 1978 survey) consisted of 10-point clusters of BAF 37.5 (English) prism plots (Alerich 1993). New plots were five-point mixed clusters of fixed radius and variable radius points. Eighty-nine percent of the 168 plots visited in 1989 were remeasurements from the 1978 inventory. We used the 1989 FIA data to analyze of the effects of gypsy moth defoliation from 1985 to 1987.

The USDA Forest Service FHM program of plot measurements was first implemented in the New England states in 1990 (Brooks et al. 1991) and has gradually been expanded to other states. The objective of FHM is to monitor, assess, and report on the long-term status, changes, and trends in forest ecosystem health at regional and national scales. The FHM plot system was developed in response to increasing concern for the health of the nation's forests and the influence of pollution, insects, diseases, climatic change, and other stressors (Brooks et al. 1991). An intensified network of FHM plots was established in the ANF in 1998. A total of 173 plots (one for every 3,000 acres) were visited, 168 were co-located with the 1989 FIA plots and five were added on the national FHM grid. The cherry scallopshell moth and elm spanworm analyses were performed using the 1998, 1999, 2000, and 2001 FHM data.

The frequency of defoliation at each plot location was calculated using a geographic information system to determine coincidence of plot locations with yearly sets of defoliation polygons. Defoliation layers were compiled by digitizing sketchmaps of canopy defoliation generated during aerial surveys conducted yearly from 1984 to 1999. A sketchmap is created while flying in an aircraft and drawing visible damage on topographic maps (McConnell et al. 2000). The minimum threshold for detectable defoliation is typically ca. 25–30% (Ciesla 2000). The presence and cause of defoliation was confirmed from ground visits at selected locations.

One-way analysis of variance (ANOVA) was used to test the relationship of tree species composition on defoliation. Similarly, one-way ANOVA was used to test the relationship of defoliation on percent standing dead basal area and percent crown dieback. To analyze the effect of mortality, we excluded plots with <10% host species basal area because we expected sampling error of mortality estimates on hosts would be excessively high. In other words, a plot with one tree of a host species that was dead would have 100% mortality; this would inflate the mortality estimates. Crown dieback is defined as recent mortality (3–10 years) of branches with fine twigs and reflects the severity of recent stresses on a tree. Although it serves as one indicator of tree damage, crown dieback may only be measureable for several years. Dead fine twigs or branches usually remain on the tree for a relatively short time. Once they fall, there is no visible indicator of how large the tree crown should have been, though it likely would appear smaller than normal for some time depending on the severity of the dieback. The variable is estimated as a percentage of the live crown area for each tree that is dead (USDA Forest Service 1998).

Ordinary kriged surfaces of mortality and species abundance were created and visually compared to defoliation maps. Kriging is a geostatistical method that provides unbiased estimates at unsampled locations as weighted averages of values from nearby locations (Issaks and Srivistava 1989, Liebhold et al. 1993). In this analysis, we generated maps from the plot data by calculating kriged estimates on

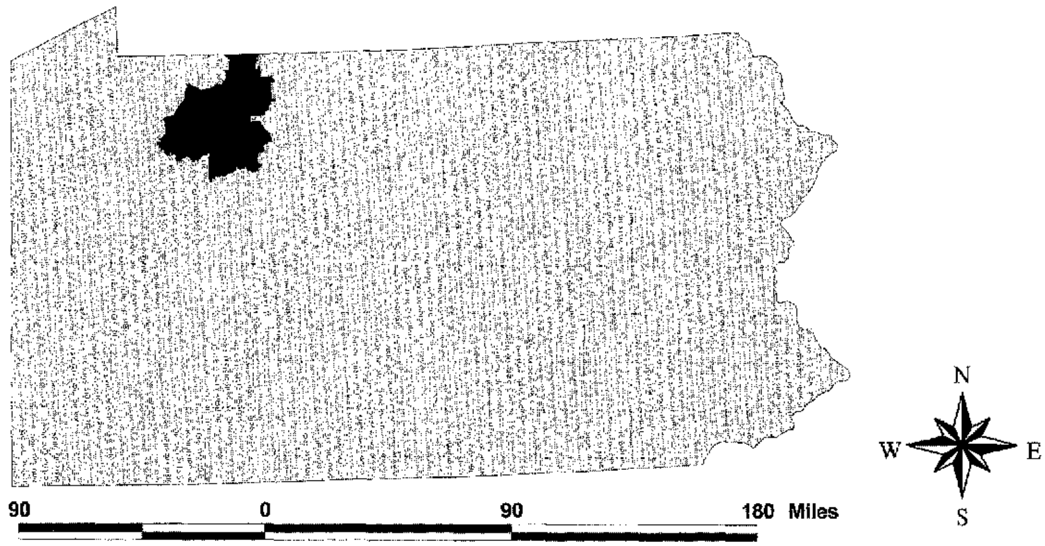

Figure 1. Location of the Allegheny National Forest in northwestern Pennsylvania.

a grid of 1 × 1-km cells. Variograms used in the kriging procedure were generated using the VARIOWIN software (Pannatier 1996), and the GSLIB software (Deutsch and Journel 1998) was used for the kriging.

Results

The cumulative frequency of defoliation (1984–1998) for the ANF is shown in Figure 2. Approximately 85% of all land area was defoliated at least once. Land area values in this report include the entire area within the proclamation boundary of the ANF (not just federal land). The land area defoliated by each of the three pests is displayed in Figure 3.

An outbreak of the cherry scallopshell moth occurred from 1993 to 1996, defoliating a cumulative total of 360,643 acres (Figure 3a). Historically, cherry scallopshell moth outbreaks occur approximately every 10 years in the region and generally last 2–3 years; previous outbreaks occurred in 1972–1974 and 1982–1984 (Bonstedt 1985). An outbreak of the elm spanworm occurred from 1991 to 1993, defoliating a cumulative total of 434,998 acres (Figure 3b). An outbreak of the gypsy moth occurred from 1985 to 1987, defoliating a cumulative total of 245,852 acres (Figure 3c). This was the first gypsy moth outbreak on the ANF and occurred when the invading population initially moved through the region (Liebhold et al. 1992). A second smaller

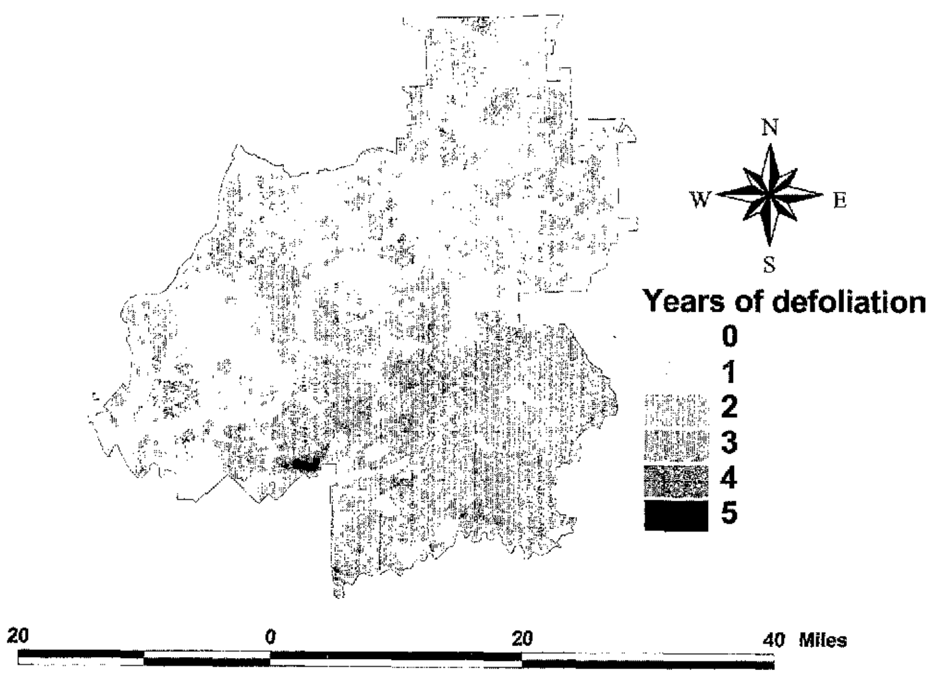

Figure 2. Frequency (years) of defoliation by all insect species (1984–1998).

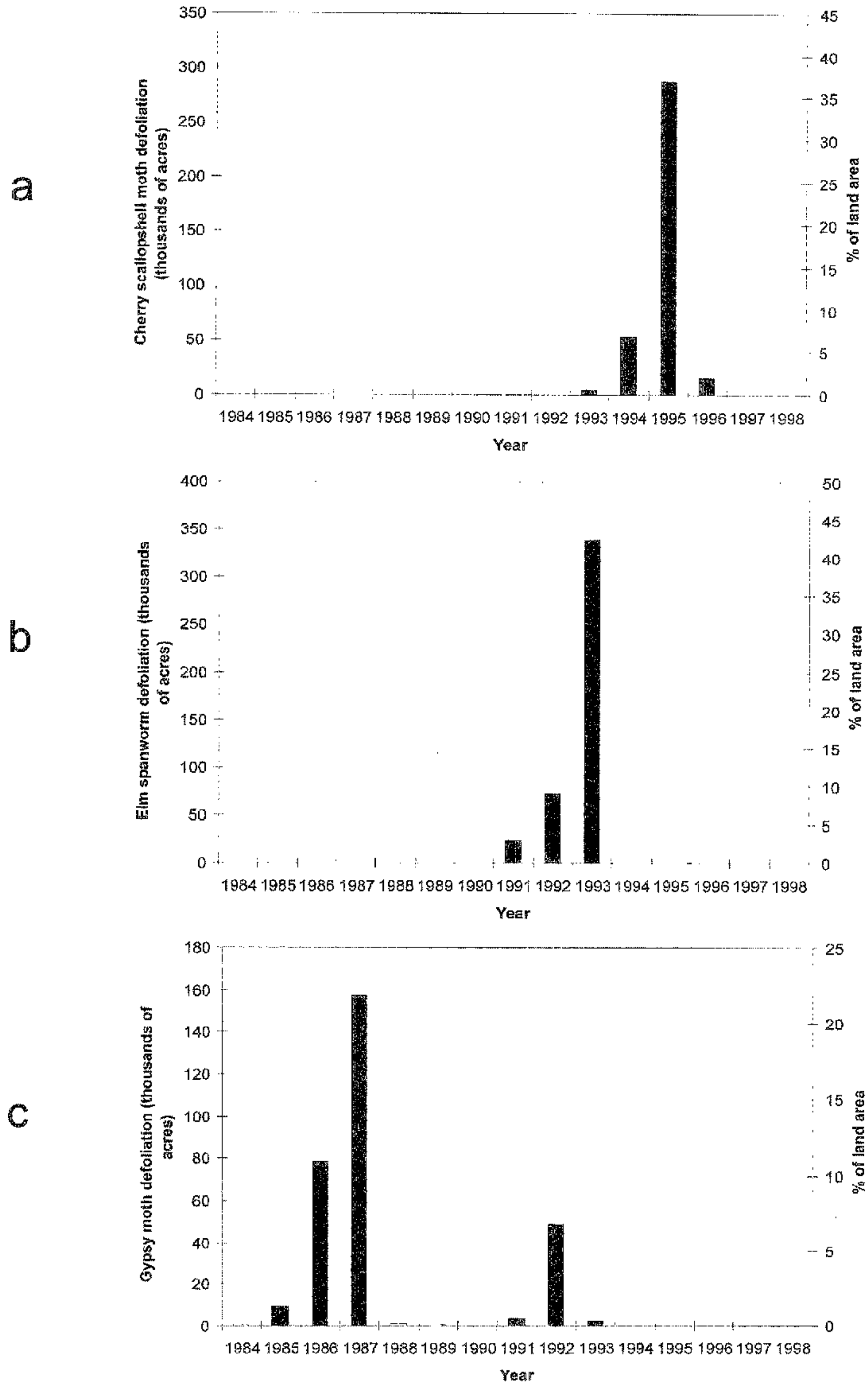

Figure 3. Land area defoliated by major insect species, between 1984 and 1998. (a) Cherry scallopshell moth, (b) elm spanworm, (c) gypsy moth. Total area inventoried was 740,500 acres.

TABLE 1. Mean stand characteristics averaged over FIA/FHM plots grouped by total number of years of defoliation by insects. Mean dieback was estimated as the average dieback among all trees at all plots, and numbers in parentheses are the number of trees. For all other means, estimates were calculated as averages of plot values, and numbers in parentheses are the number of plots. Plots with less than 10% host basal area were excluded from mortality analyses. *P* values are given for one-way analyses of variance.

	Years of cherry scallopshell moth defoliation			
Stand characteristic (%)	0	1	2 or 3	*P* value
Black cherry basal area	16.33 (81)	30.62 (80)	38.87 (12)	0.0002
Black cherry mortality	5.45 (30)	5.65 (58)	17.38 (8)	0.0209
Black cherry dieback	6.02 (288)	6.59 (392)	10.5 (86)	0.01

	Years of elm spanworm defoliation			
	0	1	2 or 3	*P* value
Black cherry basal area	15.35 (75)	31.46 (86)	31.85 (12)	0.0003
Black cherry mortality	8.94 (31)	7.54 (59)	15.36 (10)	0.3782
Black cherry dieback	5.14 (270)	7.55 (442)	9.26 (54)	0.0118
Red maple basal area	22.93 (75)	23.79 (86)	3.57 (12)	0.02
Red maple mortality	4.71 (58)	4.95 (56)	9.93 (8)	0.2891
Red maple dieback	4.1 (464)	4.2 (528)	5.58 (60)	0.499
Sugar maple basal area	6.39 (75)	10.29 (86)	7.12 (12)	0.3444
Sugar maple mortality	8.22 (15)	15.84 (31)	31.05 (4)	0.1119
Sugar maple dieback	3.04 (125)	7.15 (243)	1.85 (27)	0.0031
American beech basal area	9.65 (75)	10.4 (86)	7.83 (12)	0.9382
American beech mortality	3.6 (28)	11.5 (27)	9.56 (5)	0.237
American beech dieback	5.18 (234)	6.6 (199)	5.11 (38)	0.4889

	Combined years of cherry scallopshell moth and elm spanworm defoliation				
	0	1	2	3 or 4	*P* value
Black cherry basal area	12.02 (52)	21.38 (48)	36.35 (53)	33.06 (20)	0.0001
Black cherry mortality	13.13 (17)	6.71 (27)	6.78 (40)	13.34 (15)	0.3398
Black cherry dieback	3.84 (166)	7.79 (185)	6.98 (302)	9.14 (113)	0.0016

	Years of gypsy moth defoliation		
	0	1 or 2	*P* value
Basal area of all oaks	2.18 (129)	32.83 (35)	0.0001
Mortality of all oaks	2.85 (6)	9.39 (22)	0.1164

gypsy moth outbreak occurred from 1991 to 1992, causing 52,156 acres of cumulative defoliation.

Cherry Scallopshell Moth

The preferred host for cherry scallopshell moth larvae is black cherry (USDA Forest Service 1979), and black cherry-dominated stands were most frequently defoliated during outbreaks (Table 1); there was a significant relationship between percent black cherry basal area and years of cherry scallopshell moth defoliation (Table 1). The number of years of cherry scallopshell defoliation was significantly associated with percent standing dead black cherry and percent crown dieback on black cherry trees (Table 1).

Figure 4a shows a kriged surface of percent black cherry basal area on the ANF (1998–2001 FHM data). The central and southeastern parts of the forest had the largest black cherry components. Not surprisingly this area generally coincided with the area defoliated by the cherry scallopshell moth shown in Figure 4b. In the kriged map of percent standing dead basal area from the 1998–2001 FHM data, the greatest proportion of standing dead basal area on the ANF also appeared to generally correspond to area defoliated by cherry scallopshell moth (Figure 4c).

Elm Spanworm

The most highly preferred hosts for elm spanworm on the ANF are black cherry, red maple (*Acer rubrum*), sugar maple, and American beech (*Fagus grandifolia*). However, our analysis indicated that frequency of defoliation was only significantly associated with the proportion of black cherry and red maple in stands; proportion of other hosts did not vary significantly among defoliated and undefoliated stands (Table 1).

As with the cherry scallopshell moth, there was a tendency for greater levels of host crown dieback and tree mortality in stands defoliated by elm spanworm (Table 1). However, the only statistically significant associations observed were between years of defoliation and percent crown dieback of black cherry and sugar maple trees (Table 1). The relationship between sugar maple mortality and years of elm spanworm defoliation was marginally significant.

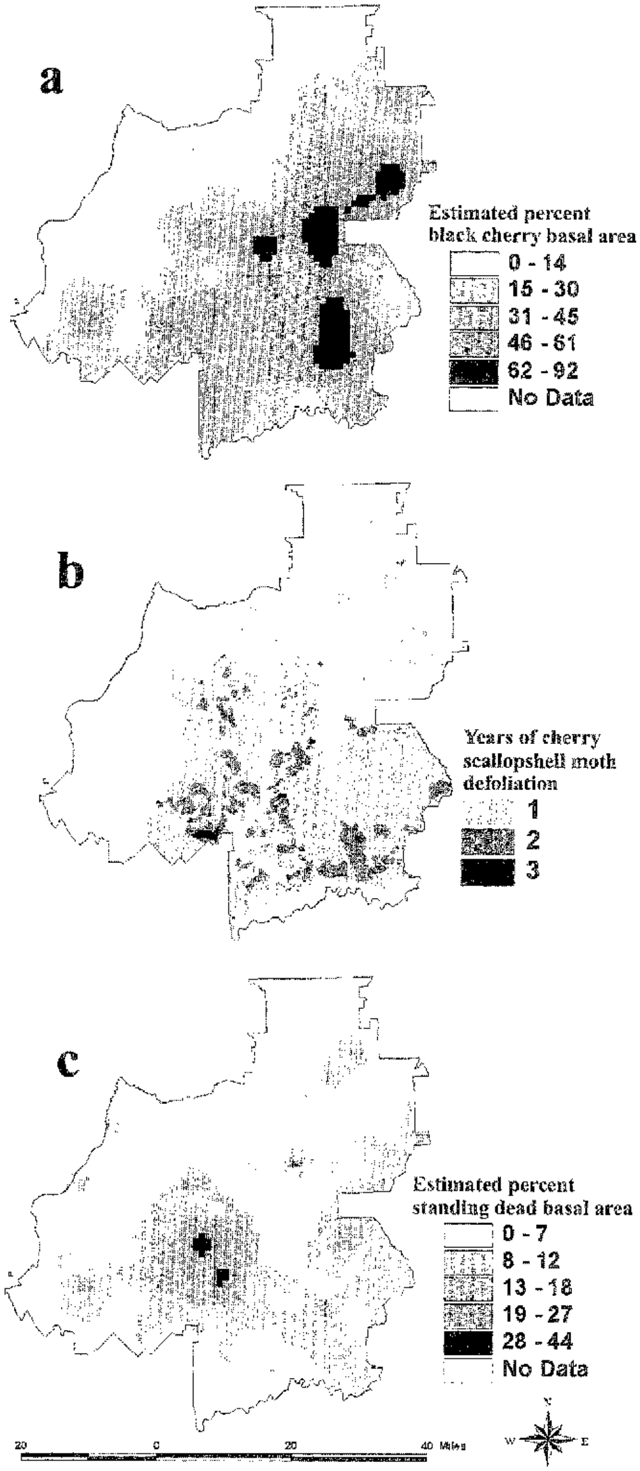

Figure 4. Maps of cherry scallopshell moth host abundance, defoliation, and damage (host and damage were mapped using 1 × 1-km cells). (a) Kriged surface of percent black cherry basal area from 1998 to 2001 FHM data (exponential model, nugget = 300, sill = 350, range = 45 km), (b) map of frequency of cherry scallopshell moth defoliation (total number of years defoliated) from 1993 to 1996 on the ANF, and (c) kriged surface of percent standing dead basal area, all species from 1998 to 2001 FHM data (exponential model, nugget = 0, sill = 110, range = 15 km).

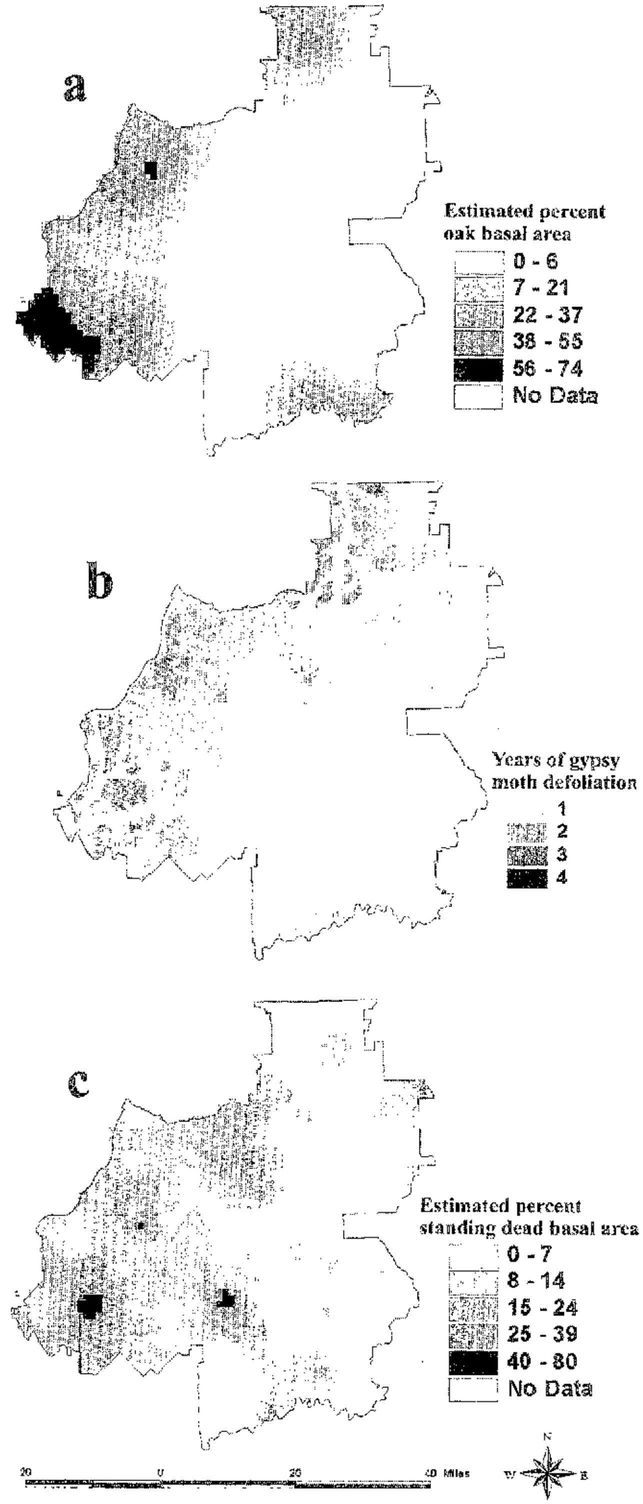

Figure 5. Maps of gypsy moth host abundance, defoliation, and damage (host and damage were mapped using 1 × 1-km cells). (a) Kriged surface of percent oak basal area from 1989 FIA data (exponential model, nugget = 0.108, sill = 0.4, range = 50 km), (b) map of frequency of gypsy moth defoliation (no. years), and (c) kriged surface of percent standing dead basal area, all species from 1989 FIA data (spherical model, nugget = 0.328, sill = 0.655, range = 8 km).

Combined Effects of Cherry Scallopshell Moth and Elm Spanworm

Between 1991 and 1996, black cherry on the ANF was affected by outbreaks of both elm spanworm and cherry scallopshell moth. Black cherry was the primary host of the cherry scallopshell moth and one of several elm spanworm hosts. Because outbreaks of cherry scallopshell moth and elm spanworm occurred consecutively, the black cherry condition in the 1998–2001 FHM surveys might be most clearly understood by considering the combined effects of both species.

There were statistically significant associations between total number of years of cherry scallopshell moth and elm spanworm defoliation with percent black cherry basal area (Table 1). There was a significant trend between black cherry crown dieback and years of defoliation (Table 1).

Gypsy Moth

The gypsy moth primarily defoliates hardwood trees, especially oak (*Quercus* spp.) and aspen (*Populus* spp.) and sometimes beech, although large larvae will feed on other species, especially during outbreaks (Liebhold et al. 1995). Small larvae will feed readily on beech, although large larvae avoid beech due to the toughness of leaf foliage. On the ANF, plots with a higher percentage of oak were defoliated more often by gypsy moth (Table 1). The average amount of crown dieback and standing dead oak basal area appeared to increase with frequency of defoliation, but these effects were not statistically significant (Table 1).

A kriged surface of oak basal area is shown in Figure 5a. The majority of the oak basal area was located on the western third and along the southern and northern boundaries of the ANF. This area, with the largest oak component, coincided with the area defoliated by gypsy moth (Figure 5b). As shown by the kriged map of percent standing dead basal area from the 1989 FIA survey, the area with the greatest relative amount of standing dead basal area also appeared to generally coincide with defoliation by gypsy moth (Figure 5c).

Discussion

There are approximately 85 species of insects in the orders Lepidoptera and Hymenoptera that periodically cause widespread defoliation of forest trees in North America (Mattson et al. 1991). There are probably few areas of comparable size and diverse forest composition that have been defoliated as frequently as the ANF (85% of the land area defoliated at least once over a 12-year period).

Cherry scallopshell moth is a native and widely distributed species in the eastern United States and Canada. Given the preference of this species for black cherry (USDA Forest Service 1979) and the abundance of black cherry on the ANF, it is not unexpected that outbreaks occur. In this study, we found a significant association between cherry scallopshell moth defoliation and black cherry composition, black cherry mortality, and black cherry crown dieback.

Elm spanworm is also a native species that is common throughout the eastern United States and into Canada. Sporadic outbreaks of the elm spanworm have been recorded in the eastern United States since the 1800s; at least 18 major elm spanworm infestations took place between 1900 and 1961 (Fedde 1964, Ciesla 1964). This species is highly polyphagous, and nearly all major tree species on the ANF except yellow-poplar (*Liriodendron tulipifera*) (Drooz 1980) and cucumbertree (*Magnolia acuminata*) are hosts. The most highly preferred hosts for elm spanworm on the ANF during this outbreak were black cherry, red maple, sugar maple, and American beech. The only significant associations between forest composition and elm spanworm defoliation were for black cherry and red maple. However, the only significant association of the defoliation with mortality or crown dieback were the relationships between elm spanworm defoliation and black cherry and sugar maple crown dieback.

Since the time of its accidental introduction near Boston, Massachusetts in 1868 or 1869, the gypsy moth has been slowly expanding its range. The current rate of spread is estimated to be about 13 miles per year, and the gypsy moth first became established on the Allegheny Plateau in the early 1980s (Liebhold et al. 1992). Gypsy moth is an outbreak pest species that has been recognized as the most destructive forest defoliating insect in the United States (Davidson et al. 1999, Liebhold and McManus 1999). Though the gypsy moth is polyphagous, it primarily defoliates hardwood trees, especially oak, aspen (*Populus* spp.), American basswood (*Tilia americana*), paper birch (*Betula papyrifera*), and sometimes beech (Montgomery 1990). In this study, we found a significant association of gypsy moth defoliation with percent oak composition.

Impacts of insects on forests can be positive or negative depending on their feeding strategies and population levels, but defoliation by outbreak levels of leaf-feeding insects generally has a detrimental effect on tree conditions (Haack and Byler 1993). Defoliation affects trees both via reduction of photosynthesis and increased evapotranspiration (Kulman 1971). The magnitude of this effect varies considerably among tree and defoliator species, depending on various aspects of tree physiology and the seasonal timing of defoliation. The ultimate effect of defoliation episodes is a reduction in growth and vigor that may lead to crown dieback and in some cases tree mortality. Secondary agents (e.g., pathogenic fungi or woodboring insects) are typically associated with defoliation-induced dieback and mortality (Dunbar and Stevens 1975, Davidson et al. 1996).

A stand's risk associated with a particular defoliator species is represented both by stand susceptibility and vulnerability (Hicks et al. 1987). Susceptibility represents the probability of defoliation and is usually closely related with stand species composition as illustrated by the three insect species described above. The likelihood of tree mortality after a defoliation episode is termed vulnerability (Crow and Hicks 1990).

According to a study by Schultz and Allen (1977), mortality of black cherry following defoliation by cherry scallopshell moth varied from 4.3 to 83.3%. Likewise, Fedde (1964) reported that repeated elm spanworm defoliation results in weakened trees and slower growth rates. Losses of 50% in radial growth increment have been observed after two seasons of severe defoliation, while two or more consecutive summers of complete defoliation often result in tree mortality (Fedde 1964). Significant mortality has been reported due to gypsy moth defoliation as well (Baker 1941, Kegg 1973, Brown et al. 1979). Thirty percent of the favored host trees died during a 10-year period due to gypsy moth defoliation (Baker 1941). During a gypsy moth outbreak in New Jersey, oak mortality increased with each successive defoliation, from 6% to 69%, over a 4-year period (Kegg 1973). Brown et al. (1979) found that 17% of the basal area in a mixed-oak stand was dead after 4 years of gypsy moth defoliation. The research presented here indicated a relationship between years of elm spanworm defoliation and percent standing dead red maple, as well as a relationship between combined years of cherry scallop-shell moth and elm spanworm defoliation and percent standing dead black cherry (Table 1).

The results reported here are largely consistent with previous studies; areas that were defoliated by all three species were generally associated with higher levels of crown dieback and tree mortality when compared to areas that were not defoliated. However, using estimates of dieback and mortality averaged over the entire land area, these effects were often not large. While many studies of defoliator impacts have documented instances of mortality (e.g., Baker 1941, Schultz and Allen 1977, Brown et al. 1979, Gansner et al. 1983, Gansner and Herrick 1984, Gansner et al. 1987), these impacts may not necessarily extend over large areas. Our plot data included some stands where crown dieback and tree mortality were heavy and others where it was negligible; when averaged over the entire land area, most results indicated at least some effects on dieback and mortality.

The analyses reported here represent a slightly different approach to measuring defoliation impacts. The bulk of previous studies are based on analysis of forest conditions following defoliation in a few selected forest stands. The approach reported here is different because both the defoliation data (aerial sketch maps) and forest condition data (FIA and FHM plot data) were collected on an areawide basis and, as such, they can be used to generalize impacts over specific large land areas. While the intensity of FHM sampling in the ANF has been much greater than most regions, this type of analysis could be applied to assess forest changes and defoliation impacts across larger geographical regions as well. This study thus illustrates the use of plot and survey data to make meaningful measures of defoliation impacts over large geographical areas.

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