Spread of Gypsy Moth (Lepidoptera: Lymantriidae) and Its Relationship to Defoliation

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ABSTRACT Gypsy moth management is divided into three components: eradication, suppression, and transition zone management. All three components require knowledge of the boundaries that delimit these areas. Additional interest is also placed on the relationship between population spread and defoliation to prepare for the gypsy moth advance in new areas and minimize its impact. We developed relationships between advancing population boundaries, which were estimated using an algorithm implemented under the USDA Forest Service Gypsy Moth Slow-the-Spread Project and defoliation records collected by State and Federal agencies. We used current data from Wisconsin, West Virginia, and Virginia and historical data from the lower peninsula of Michigan. We observed that in West Virginia, Virginia, and Michigan, defoliation generally occurred in areas where moth abundance exceeded 300 male moths per pheromone-baited trap (i.e., the 300-moth population boundary), whereas in Wisconsin, it generally occurred between the 100- and 300-moth population boundaries. We also detected temporal changes in Michigan in the relationship between boundaries and defoliation, where the transition time between the 10-moth population boundary and defoliation was 4–5 yr. Recent data from Wisconsin suggest a similar transitional time, whereas recent data from West Virginia and Virginia do not seem to contradict an earlier study suggesting a transition time of roughly 8 yr.

KEY WORDS *Lymantria dispar*, biological invasions, invasive species, forecasting

THE GYPSY MOTH, *Lymantria dispar* L., has been gradually expanding its range in North America since its introduction. It is a highly polyphagous herbivore that can exploit >300 species of deciduous and coniferous hosts (Elkinton and Liebhold 1990). USDA Cooperative Management Programs for gypsy moth fall into one of three categories: (1) eradication in uninfested regions located distant from the expanding population front; (2) suppression of outbreaks in regions that are generally infested; and (3) limitation of range expansion in the transition zone, which is currently realized through the USDA Forest Service Gypsy Moth Slow-the-Spread Project (STS) (Sharov et al. 2002, Tobin et al. 2004). All three programs require an understanding of the boundaries that delimit these areas.

The demarcation of these areas is based on the monitoring of male moths using pheromone-baited traps along the expanding population front (Sharov et al. 1995). Considerable interest is often placed on the timing of the arrival of defoliating populations, particularly those causing economic damage, after initial infestation so that state and federal agencies and landowners can prepare adequately for gypsy moth damage to minimize its inimical effects (McFadden and McManus 1991, Gottschalk 1993). Our primary objective was to analyze the relationship between gypsy moth spread, based on the spatial and temporal properties of population boundaries and recorded defoliation.

In the transition zone, gypsy moth spread is comprehensively measured and estimated through STS (Sharov et al. 2002, Tobin et al. 2004). Gypsy moth populations do not necessarily spread continuously along the population front within this transition zone; instead, individual colonies become established beyond the expanding front, presumably because of inadvertent movement of life stages (Schwalbe 1981, Mason and McManus 1981, Liebhold et al. 1992). Past analyses on gypsy moth spread and the factors that influenced it have occasionally led to conflicting hypotheses. Liebhold et al. (1992) analyzed historical data on the movement of gypsy moth populations from the initial source of infestation near Boston, MA. They observed that for average minimum January temperatures >7°C, spread rates were ≈20.8 km/yr, whereas for the inverse condition, spread rates were ≈7.6 km/yr. In contrast, Sharov et al. (1999) observed that temperatures in Michigan were inversely related to gypsy moth spread and instead associated higher spread rates to increases in forest susceptibility.

A previous study by Sharov et al. (1996) examined the relationship between spread and defoliation records in West Virginia and Virginia from 1988 to

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1994. They observed that the estimated "boundary of defoliation" was ≈80 km from the 10-moth population boundary (i.e., the boundary at which ≈10 male moths are recorded per pheromone-baited trap (cf. Sharov et al. 1995). Sharov et al. (1996) also noted that the 10-moth population boundary was generally lagged by ≈8 yr from the defoliation boundary. Because of the continual importance in understanding the relationship between spread and economically important levels of defoliation, particularly in silvicultural management, our objective was to develop region-specific relationships between spread and defoliation using recent data. We examined these relationships over the expanding front in Wisconsin (2001–2003) and West Virginia and Virginia (2000–2003). We also examined historical data on gypsy moth spread and defoliation in the lower peninsula of Michigan (1985–1995). Here, the range of the data extend from early reports of defoliation to the time at which the entire lower peninsula was considered to be generally infested and under USDA Quarantine (Code of Federal Regulations, Title 7, Chapter III, Section 301.45–3); thus, we were able to use Michigan data to detect temporal relationships between spread and defoliation.

Materials and Methods

Gypsy moth spread rates were estimated by an algorithm implemented under the STS Project (Sharov et al. 2002, Tobin et al. 2004, Decision-Support System for the Slow-the-Spread Project 2005). Moth abundance was first spatially interpolated using trap catch data from a grid of pheromone-baited traps and median indicator kriging (Isaaks and Srivastava 1989). In Wisconsin, West Virginia, and Virginia, traps were deployed 2, 3, or 8 km apart, depending on the distance from the generally infested area (Tobin et al. 2004): an intertrap distance of 8 km is generally used where gypsy moth densities are ≥10 moths per trap, a 3-km grid is generally used where gypsy moth densities are 2–9 moths per trap, and a 2-km grid is used where gypsy moth densities are ≤1 moth per trap. In the lower peninsula of Michigan, traps were placed ≈6 km apart. Population boundaries of the 1-, 3-, 10-, 30-, 100-, and 300-moth boundaries were estimated from interpolated moth abundance using an optimization technique (Sharov et al. 1995). To iterate, the 10-moth population boundary, for example, is a boundary at which ≈10 male moths are recorded per pheromone-baited trap. The displacement of each population boundary in consecutive years was measured to determine the rate of gypsy moth spread.

Gypsy moth defoliation data from Wisconsin (2001–2003) and West Virginia and Virginia (2000–2003) were obtained from the National Aerial Survey Spatial Database (Forest Health Technology Enterprise Team, USDA Forest Service, Fort Collins, CO). This database is a national GIS database for all aerially detected insect, disease, and abiotic forest damage. For gypsy moth, aerially detected defoliation was collected by state agencies and the USDA Forest Service (on national forest land) and compiled into the National Aerial Survey Spatial Database. More information on survey standards and other documentation related to this program is available online (USDA Forest Service 2005). Defoliation data from the lower peninsula of Michigan (1985–1995) were obtained through Liebhold et al. (1997), in which aerially detected gypsy moth defoliation was collected by the state of Michigan.

To explore the relationship between spread and defoliation, we measured the minimum distance between each recorded area of defoliation and each moth population boundary (1, 3, 10, 30, 100, and 300 moths) in ArcView 3.2 (Jenness 2002, cf. Fig. 1). For consistency across regions, we only used defoliation recorded within 100 km of the 10-moth population boundary. We measured the size of each recorded area of defoliation and converted it first to a proportion based on the total hectares of defoliation recorded in each region and across all years and then to a cumulative proportion over increasing distance from the population boundary. We modeled, by region, the cumulative proportion of defoliation, $\hat{Y}$, over the distance, D, from each population boundary according to an exponential function,

$$\hat{Y} = \frac{1}{(1 + \exp^{(-r \times D + b)})},$$

where r and b are the respective estimated parameters of the rate of increase and lag (Brown and Mayer 1988) in PROC NLIN (SAS Institute 1999).

To detect year-to-year variability in the relationship between the 10-moth population boundary and defoliation, we used data from the lower peninsula of Michigan. In this case, we calculated $\hat{Y}$, the cumulative proportion of defoliation (equation 1), for each year (as opposed to summarizing across all years). Before analysis, $\hat{Y}$ was first subject to a linearizing transformation,

$$Y' = \ln\left(\frac{\hat{Y}}{1.05 - \hat{Y}}\right)$$

(Brown and Mayer 1988), and the effects of year, distance from the 10-moth population boundary, and their interaction were tested in PROC GLM (SAS Institute 1999). The year and interaction effects served as a test for intercept and slope heterogeneity, respectively. We used the 10-moth population boundary because it was previously observed to be the least variable in estimation among all the population boundaries (Sharov et al. 1997b).

We also were interesting in estimating the transition time from initial establishment of gypsy moth to economically important defoliating levels. To do this, we examined the relationship between the 10-moth population boundary and cumulative proportion of defoliation when the latter was projected ahead in time, using 0- to 2-yr time lags, in Wisconsin and West Virginia and Virginia and from 0- to 5-yr time lags in Michigan. The cumulative proportion of defoliation (measured by equation 1) was subject to the linearizing transformation (e.g., equation 2) and for each

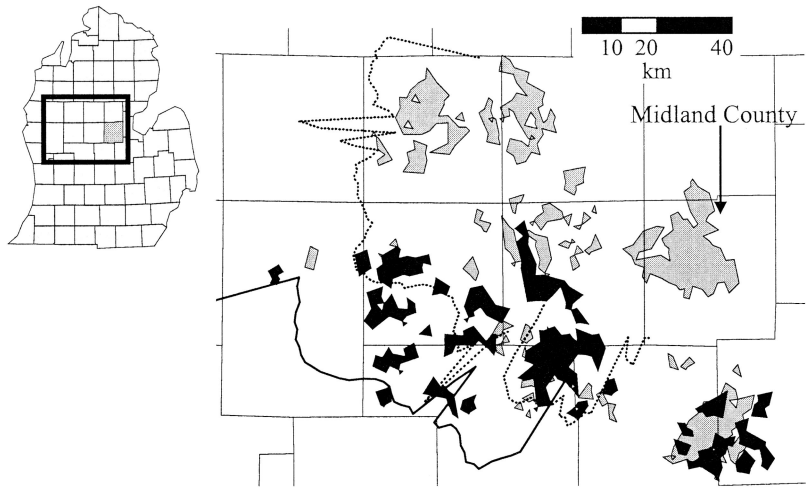

Fig. 1. Example of the displacement in the 300-moth population boundary in 1989 (dotted line) and 1990 (solid line) in the lower peninsula of Michigan. Areas of recorded gypsy moth defoliation are also shown for 1989 (light-colored shapes) and 1990 (dark-colored shapes). The minimum distance between each area of recorded defoliation to the population boundaries was measured, and the cumulative proportion of defoliation, based on the total Ha of defoliation in each region (Michigan, Wisconsin, and West Virginia/Virginia) was related to the distance from the population boundary. Midland County, MI, is indicated as a reference.

region, we tested for slope heterogeneity among the time lags in PROC GLM (SAS Institute 1999) to determine if the rate of this relationship was stable across time. We also used the least regression fit of this relationship to extrapolate the average displacement between the 10-moth population boundary in year t and cumulative proportion of defoliation in year t + time lag.

Results

A summary of the amount of defoliation and rate of gypsy moth spread in Wisconsin, West Virginia and Virginia, and Michigan is presented in Table 1. For each of these areas, the relationship between cumulative proportion of defoliation and gypsy moth population boundaries are shown in Fig. 2. The exponential model for these areas (equation 1 was used to predict the distance at which 10, 25, 50, 75, and 90% of the defoliation occurred with respect to population boundaries). For reporting purposes, these distances are listed for the 10-moth population boundary and the two boundary extremes: 1- and 300-moths (Table 2). The exponential model predicted, for example, that 50% of the defoliation occurred at 60.4, 42.7, and 76.9 km from the 10-moth boundary in Wisconsin, West Virginia and Virginia, and Michigan, respectively.

Table 1. Summary of gypsy moth spread rates (km/yr) and total hectares of defoliation

Year	Michigan		West Virginia/ Virginia		Wisconsin	
	Spread rate	Hectares defoliated	Spread rate	Hectares defoliated	Spread rate	Hectares defoliated
1985	NA	17,218				
1986	21.2	32,046				
1987	15.2	16,935				
1988	21.7	69,936				
1989	24.3	146,470				
1990	11.2	117,030				
1991	12.9	70,631				
1992	−0.9	17,760				
1993	31.5	10,072				
1994	−1.9	7,837				
1995	11.2	44,596				
2000			16.6 (3.1)	27,192	6.7 (1.8)	12
2001			15.9 (11.8)	75,374	15.4 (4.1)	1,545
2002			−14.2 (7.0)	26,654	33.5 (3.2)	15,051
2003			6.8 (16.2)	33,647	35.6 (12.0)	44,453

Data shown are those used in the analyses of this paper.
NA, not available.

The above models represent summarized estimates over the entire periods reported in Table 1. In the lower peninsula of Michigan, the relationship between defoliation and the 10-moth population boundary through time is presented in Fig. 3. An analysis of this relationship revealed significantly different intercepts ($F = 67.1$; df = 1,342; $P \leq 0.01$) and slopes ($F = 26.1$; df = 1,342; $P \leq 0.01$) among some of the years. Post hoc analyses revealed that this relationship was unique for 1985, 1986, and 1987, although 1985 and 1986 had a common slope ($F = 0.01$; df = 1,32; $P = 0.93$). There was an also unique relationship for 1992 and for 1995. The relationship did not differ significantly in either intercept ($F = 0.92$; df = 1,254; $P = 0.34$) or slope ($F = 0.02$; df = 1,254; $P = 0.90$) for the years 1988–1991 and 1993–1994 (Fig. 3); moreover, during these years, one-half of the defoliation occurred at ≈78 km from the 10-moth boundary. In contrast, one-half of the defoliation occurred at roughly 34, 48, and 57 km from the 10-moth line in

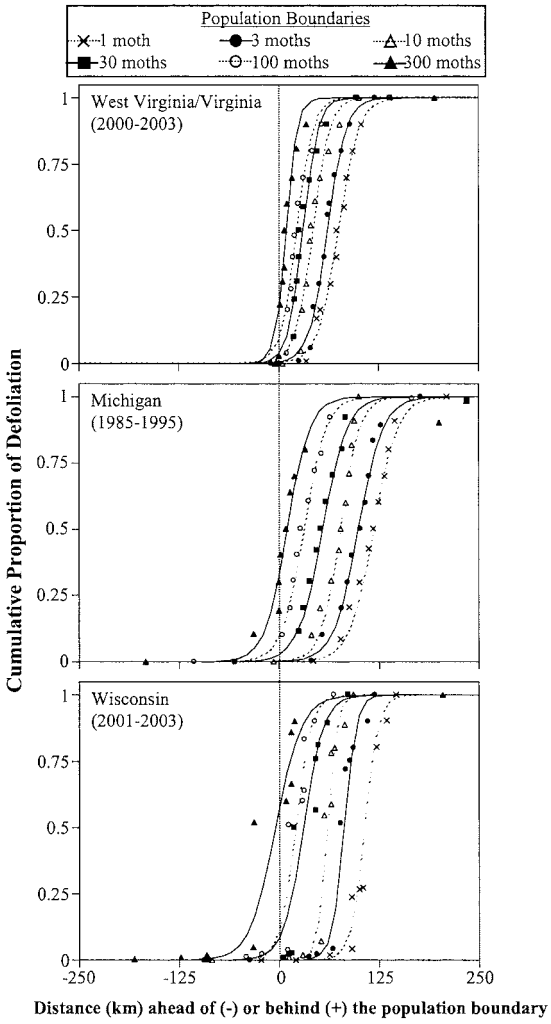

Fig. 2. Relationship between cumulative proportion of gypsy moth defoliation and the distance to gypsy moth population boundaries. Although model predictions (lines) were estimated using all data points, only the approximate deciles are shown (as symbols) for each predicted line for graphical purposes.

1985, 1986, and 1987, respectively. The years 1992 and 1995 represent interesting anomalies during which defoliation was either unexpectedly closer to (1992) or farther from (1995) from the 10-moth boundary.

The relationship between the 10-moth population boundary and defoliation when the latter is projected ahead in time is presented in Fig. 4. In West Virginia and Virginia, there was no significant difference between the 1- and 2-yr lags ($F = 2.2$; df = 1,889; $P = 0.14$); moreover, defoliation was slightly farther from the 10-moth boundary when projected ahead in time. The average displacement between defoliation and the 10-moth population boundary, when the former was projected ahead in time by 1 or 2 yr, was –9.9 km (Fig. 4).

Table 2. Predicted distances (km) from the 1-, 10-, or 300-mothline to 10, 25, 50, 75, and 90% of reported defoliation in West Virginia and Virginia, Michigan, and Wisconsin

Quantile (%)	1-mothline			10-mothline			300-mothline		
	WV/VA	MI	WI	WV/VA	MI	WI	WV/VA	MI	WI
10	46.6	85.8	87.9	19.4	50.6	47.0	−6.0	−20.2	−40.5
25	60.7	102.3	97.7	31.2	64.0	53.8	1.9	−5.0	−22.3
50	74.9	118.6	107.2	42.7	76.9	60.4	9.4	10.8	−4.5
75	88.9	135.2	116.7	54.4	90.4	67.1	17.0	25.7	13.2
90	103.2	152.8	125.8	66.0	102.8	73.6	24.5	41.4	30.5

Negative distances indicate that the defoliation occurred ahead of the population boundary.

In contrast, in Wisconsin and Michigan, there was a consistent, and more expected, pattern through time. In Michigan, one-half of the defoliation occurred at the 10-moth population boundary from 4 to 5 yr ago (Fig. 4), suggesting that once populations obtained the 10-moth threshold, these populations can reach economically important defoliating levels within 4–5 yr. We were not able to predict a corresponding lag between the 10-moth boundary and defoliating populations in Wisconsin because of the range of the existing data, but we did observe that 50 and 90% of the defoliation occurred at ≈22 and 35 km, respectively, from the 10-moth boundary from 2 yr ago. For comparison, in Michigan, 50 and 90% of the defoliation occurred at ≈38 and 63 km, respectively, from the 10-moth boundary from 2 yr ago. In Michigan and for the 0-, 1-, and 2-yr lags, the mean displacement between the 10-moth population boundary and defoliation was 17.5 km/yr, whereas at the 3-, 4-, and 5-yr lags, it was 13.5 km/yr. Moreover, the overall rate of gypsy moth spread in Michigan during this time was 14.6 km/yr (Table 1), which is not too dissimilar to the rate at which the 10-moth population boundary transitioned to defoliating population levels. In Wisconsin, the mean displacement at the 1- and 2-yr lags was 20.3 and 19.6 km, respectively (Fig. 4), whereas the average spread rate was 22.8 km/yr (Table 1).

Discussion

We elucidated the relationship between gypsy moth spread and defoliation, which has important management ramifications. Although under the STS program the management philosophy of gypsy moth is uniform across states, specific management tactics of gypsy moth is generally addressed at local levels so that local conditions can be considered. An ongoing concern in local gypsy moth management is the timing of economically important defoliating levels of gypsy moth populations subsequent to its first arrival.

This study and a previous one (Sharov et al. 1996) of the relationship between population boundaries and defoliation yielded similar results. Defoliation was generally behind the estimate of the 300-moth population boundary in the Central Appalachians (1988–1994; Sharov et al. 1996), and we measured a similar relationship in the lower peninsula of Michigan (1985–

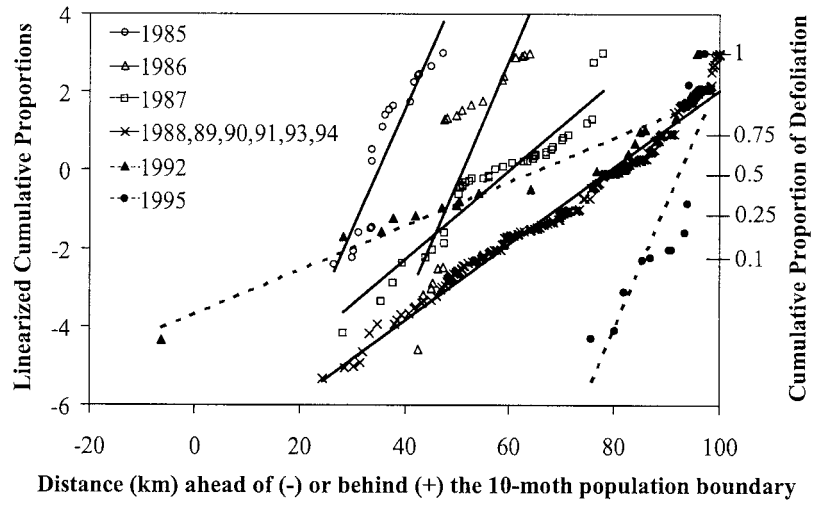

Fig. 3. Yearly relationship between cumulative proportion of gypsy moth defoliation and the distance to the 10-moth population boundary in the lower peninsula of Michigan, 1985–1995.

1995; Fig. 2; Table 2). In contrast, slightly more than one-half of defoliation occurred between the 100- and 300-moth population boundaries in Wisconsin (Fig. 2; Table 2). Moreover the rate of gypsy moth spread has been higher in Wisconsin than in the Appalachian states (Decision-Support System for the Slow-the-Spread Project 2005). Sharov et al. (1999) previously measured a positive correlation between gypsy moth spread and forest susceptibility. Spatially interpolated models of the basal area density of gypsy moth preferred hosts (Morin et al. 2005) indicate that the Great Lakes region has a fairly high composition of preferred hosts. However, Appalachian states, such as West Virginia and Virginia, are likewise rich, and in fact richer, in the density of preferred hosts (Morin et al. 2005). Instead, topography may likely play an important role in explaining differences in gypsy moth spread. Sharov et al. (1997a) reported that, outside the generally infested area, higher colony abundance was associated with lower elevations, where colonization rates were possibly higher because of increased human movement. Gypsy moth dispersal, whether active or passive, may be more limited in the Appalachian terrain than in Wisconsin, but this question has not yet been sufficiently explored.

Previous work by Sharov et al. (1996) on gypsy moth spread in the Central Appalachians, and specifically, areas of West Virginia and Virginia, showed that the 1-moth and 10-moth population boundaries were ≈110 and 81 km from the "defoliation boundary," respectively. Although their methods differ slightly from ours, an appropriate analogy in our approach is to examine the distance at which 50% of the defoliation occurs. Using historical data from Michigan, our results (Table 2) are similar to what Sharov et al. (1996) reported from the Central Appalachians. Also, we provide an update to Sharov et al. (1996) by using current data from West Virginia and Virginia. From 2000 to 2003, 1-moth and 10-moth population boundaries of West Virginia and Virginia were ≈75 and 43 km, respectively, from 50% of the defoliation (Table 2). Although these distances have declined from earlier work (Sharov et al. 1996), this is consistent with the concept of "boundary compression," which relates the distance between population boundaries with rates of spread. Sharov et al. (1996) described a model of gypsy moth spread that suggests that, when spread is reduced, the distance between population boundaries should likewise be reduced and thus "compressed." This phenomenon is supported by the data in Fig. 2, where in West Virginia and Virginia the observed population boundaries are more compressed than those in Michigan or Wisconsin, whereas spread rates in West Virginia and Virginia have also been slower (Table 1).

Data from the lower peninsula of Michigan provides the most complete picture of the relationship between gypsy moth spread and defoliation, although we do recognize that past management of gypsy moth in Michigan from 1985 to 1995 does differ from the current philosophy implemented under STS. The 10-moth population boundary and defoliation were closer to each other when the latter was first reported and increased through time and became relatively stable (Fig. 3). Some degree of stability among moth population and defoliation boundaries was also observed in West Virginia and Virginia (Sharov et al. 1996). Although Michigan has a long history of gypsy moth, and first applied DDT against an infestation in 1954, the Michigan Department of Agriculture adopted a position of containment, in lieu of eradication, of an established population in Midland county in 1981 (Dreistadt 1983). After 1981, gypsy moth spread radially from Midland, and all but one county in the lower peninsula was under USDA quarantine by 1989. Thus, the smaller distances between the 10-moth

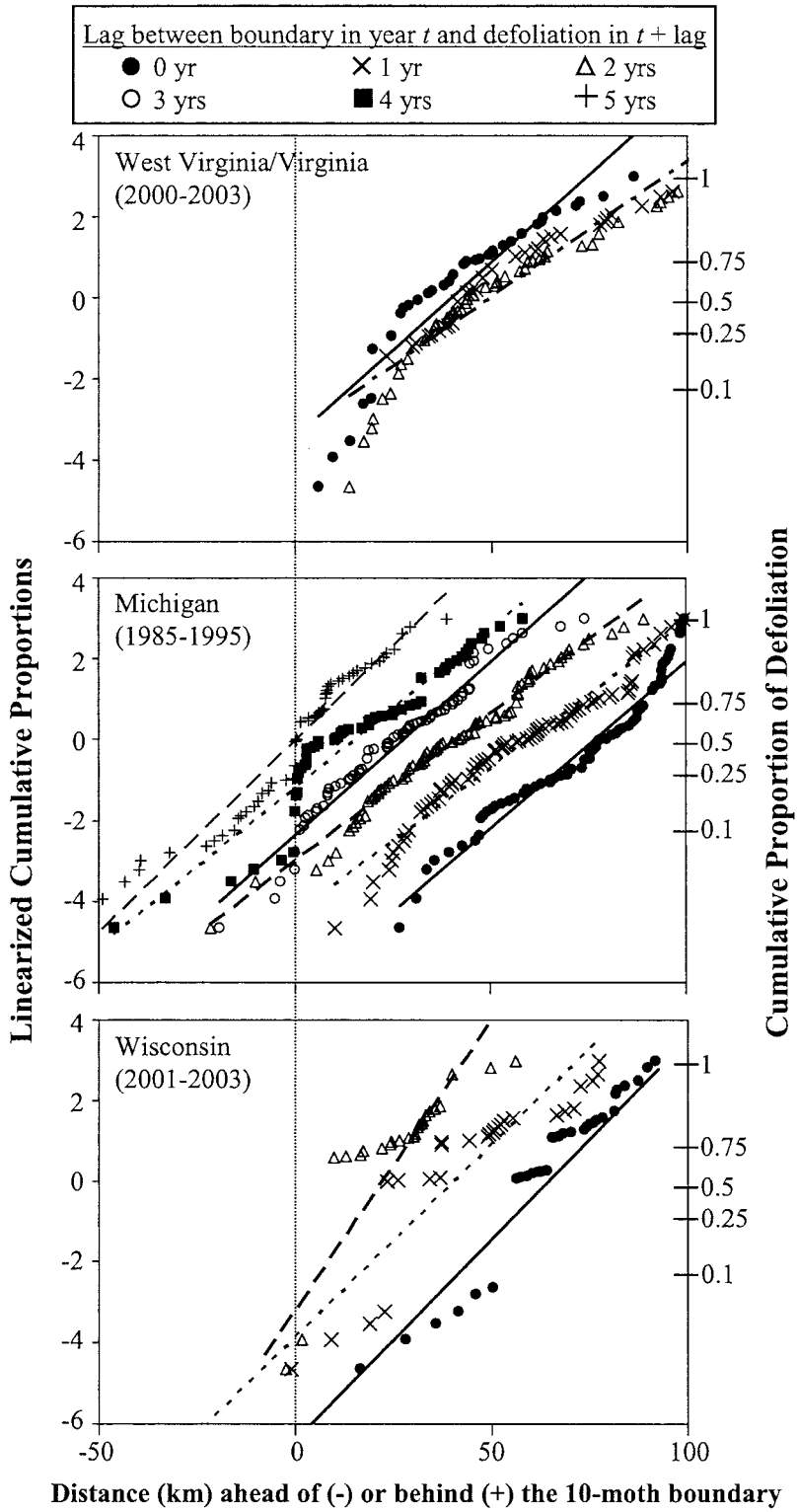

Fig. 4. Relationship between cumulative proportion of gypsy moth defoliation and the distance to the 10-moth population boundary when defoliation is lagged ahead in time.

population boundary and defoliation during the mid-1980s (Fig. 3) may be explained by the smaller extent of the generally infested area during this time.

Nevertheless, an analysis of the historical Michigan data may provide some insight to the current situation in Wisconsin, in which defoliation is fairly new. Moreover, 33 of Wisconsin's 72 counties are not yet under USDA quarantine as of January 2005 (Code of Federal Regulations, Title 7, Chapter III, Section 301.45–3). As spread continues through Wisconsin, we may be able to detect temporal patterns in the relationship between spread and defoliation in future studies and perhaps even detect the influence of the STS program compared with Michigan.

The transition of population boundaries to defoliation is useful in the timing of gypsy moth management strategies (McFadden and McManus 1991, Gottschalk 1993). Sharov et al. (1996) previously observed an ~8-yr lag between the transition from the 10-moth population boundary and the defoliation boundary in West Virginia and Virginia. Recent data (2000–2003) from this area do not contradict this estimation, and both spread and defoliation boundaries have been fairly spatially stagnant. Recent data from Wisconsin (2001–2003) suggest that it would have a transitional lag similar to the ~4- to 5-yr lag observed in Michigan (1985–1995). Thus, given the data currently available, it would seem that the window of opportunity for implementing silvicultural practices in advance of gypsy moth is considerably narrower in Wisconsin and was narrower in the lower peninsula of Michigan than what was previously (Sharov et al. 1996) and currently observed from the Appalachian states of West Virginia and Virginia. However, in this paper, we focused on the general relationship between spread and defoliation and observed some year-to-year variability in this relationship in the lower peninsula of Michigan. Future studies that incorporate local measures of population dynamics, such as growth rate, in conjunction with locally based spread models may improve our understanding of the relationship between gypsy moth spread and defoliation.

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