Does Thinning Affect Gypsy Moth Dynamics?

Andrew M. Liebhold, Rose-Marie Muzika, and Kurt W. Gottschalk

ABSTRACT. In northeastern U.S. forests there is considerable variation in susceptibility (defoliation potential) and vulnerability (tree mortality) to gypsy moth (*Lymantria dispar* [L.]). Thinning has been suggested as a way to reduce susceptibility and/or vulnerability. We evaluated how thinning affected the dynamics of gypsy moth populations by experimentally thinning half of each of eight oak-mixed hardwood stands in the Central Appalachians. Population dynamics of gypsy moth were monitored using yearly counts of egg masses, numbers of larvae hatching per mass, estimates of larval density, and weekly collections of larvae and pupae which were reared to quantify mortality due to parasitoids and disease. During the 8 yr study, three stands were heavily defoliated by outbreak populations of gypsy moth, three were sprayed with pesticides accidentally, and two were not disturbed. Egg-mass densities were slightly lower in the thinned portions of the undisturbed stands, but thinning had little or no effect on gypsy moth densities in defoliated and sprayed stands. Variation in mortality of gypsy moth caused by parasitoids and disease was related to variation in egg-mass densities in the current and/or preceding years. After adjusting for the effect of gypsy moth density, thinning had no significant effect on mortality from parasitoids or pathogens. We conclude that any reduction in egg mass densities as a result of thinning is likely related to the reduction in foliar biomass, not increased natural enemy activity. For. Sci. 44(2):239–245.

Additional Key Words: *Lymantria dispar*, silviculture, survivorship, parasitism, disease.

Although gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae) larvae feed on more than 200 species of trees (Montgomery 1991, Liebhold et al. 1995), genera such as *Quercus*, *Larix*, and *Populus* are most preferred. As a result, the susceptibility of stands to defoliation is largely a function of the relative dominance of these preferred species (Bess et al. 1947, Campbell 1974, Houston and Valentine 1977, Herrick and Gansner 1986). Heavy and/or repeated episodes of defoliation by this insect can cause considerable mortality of host trees. The probability of mortality following defoliation is closely related to tree vigor as affected by age, site conditions, drought, and other factors (Campbell and Sloan 1977, Wargo 1981, Herrick et al. 1979).

As gypsy moth expands its range from the northeastern United States to large areas of commercial forests in the Appalachian Mountains, outbreaks are likely to be intense and substantially affect forest resources in those areas. While it is possible to reduce defoliation levels by aerial application of pesticides, other approaches to gypsy moth management are needed because of the expense and ecological impact of pesticides. Silvicultural approaches to managing gypsy moth have been proposed periodically over the last 100 yr (Fiske 1913, Clement and Munro 1917, Behre 1939, Bess et al. 1947, Gottschalk 1993). Most of these studies focused on the use of sanitation thinning to reduce or eliminate host species preferred by gypsy moth, thereby lowering stand susceptibility (defoliation potential). Gottschalk (1993) also proposed the use of presalvage thinning to remove high-risk trees (poor crown conditions) and reduce stand basal area to reduce stand vulnerability (rate of mortality following defoliation).

Although some studies have examined the effectiveness of silvicultural manipulations on reducing stand susceptibility and vulnerability, results have been inconsistent. To develop a better understanding of how these manipulations affect susceptibility, we need to better understand the mecha-

Andrew M. Liebhold, Rose-Marie Muzika, and Kurt W. Gottschalk are with the USDA Forest Service, Northeastern Forest Experiment Station, 180 Canfield St., Morgantown, WV 26505. E-mail: sandy@gypsy.fsl.wvnet.edu; rmm@gypsy.fsl.wvnet.edu; kurt@gypsy.fsl.wvnet.edu.

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nisms by which silvicultural thinnings affect the population dynamics of gypsy moth. In this study we tested how presalvage and sanitation thinning affects various aspects of gypsy moth dynamics, such as changes in egg-mass density, patterns of within-generation survivorship, and the magnitude of mortality caused by various parasitoids and pathogens of gypsy moth. The specific hypotheses tested were: (1) thinning causes a reduction in egg mass densities, and (2) thinning causes an increase in the mortality caused by specific mortality agents. A separate study will report on the effectiveness of these treatments on defoliation and tree mortality.

Materials and Methods

Study Sites

The study area was located at the West Virginia University (WVU) Forest, Monongalia and Preston counties, West Virginia (Appalachian Plateau province). In 1989, eight stands were established that reflect a range in oak overstory (Table 1). Some stands were mixed hardwoods with as little as 15% oak basal area in the overstory; others were nearly pure oak. In the winter of 1989–1990, half of each stand was thinned. In stands 1–4, where oaks made up a low proportion of stand basal area (mostly <50%), a sanitation thinning was applied. The guidelines followed when marking trees were to reduce total stand basal area and preferentially remove host species favored by gypsy moth (Gottschalk 1993). In stands 5–8, oaks made up a higher proportion of stand basal area (mostly >50%), and presalvage thinning was applied. The primary objective was to remove trees in poor condition irrespective of tree species or suitability to gypsy moth (Gottschalk 1993).

Gypsy Moth Sampling

Gypsy moth populations were sampled in 1989 before thinning (1990) and each year until 1996. Egg-mass populations were sampled each year by counting all egg masses in 0.01 ha (1/40 ac) plots in each stand (Liebhold et al. 1994). Within each stand, plots were located in a grid with 100 m between sampling points. Depending on the size of the stand, 11–19 permanent plots (0.1 ha) were used in each of the thinned and unthinned halves of each stand. At each sampling point, the two egg masses nearest the plot center were selected to estimate larval hatch. Each egg mass was collected just prior to hatch in the spring and placed in a 30 ml cup. The samples were returned to the laboratory, and the number of first instars was counted. First-instar density was estimated as the product of egg-mass density and larvae/egg mass. Confidence intervals for these estimates were obtained using methods in Buonaccorsi and Liebhold (1988).

Densities of late-instar larvae were sampled using frass traps to coincide with the predominance of fifth instars. At each egg mass sampling point, a 0.25 m^2 plastic cone was used to measure frass drop (Liebhold and Elkinton 1988a, b); 30 ml cups were attached to each frass trap in late afternoon and recovered the next morning. These samples were returned to the laboratory, and the number of pellets collected overnight was counted. Simultaneously, frass yield (number of pellets per insect) was estimated by individually caging 40 field-sampled larvae on foliage in a cup placed in the forest. The number of pellets per larva was counted. Larval density was measured as the ratio of frass drop to frass yield (Liebhold and Elkinton 1988b). Confidence intervals for larval densities were estimated using Fieller's inequality (Buonaccorsi and Liebhold 1988). Because reliable estimates of gypsy moth larval densities can be obtained only in moderate to high populations (Liebhold and Elkinton 1988b), sampling for late-instar density was restricted to stands with egg-mass densities greater than 100/ac.

In stands where larval densities were sufficiently high, larvae were collected weekly to quantify mortality caused by parasitism and disease. The first larval sample coincided with egg hatch; the last sample was taken when adult eclosion began. One hundred larvae were collected in each stand per week; twenty larvae were collected at each of five sampling locations distributed uniformly throughout the stand. Early instars were collected by sampling foliage of saplings and seedlings. Late instars and pupae were collected under burlap bands placed around trees at each sampling location. These sampling procedures presupposed that larvae collected from

Table 1. Stand characteristics in paired stands before and after thinning in 1990.

	Before thinning			After thinning	
Stand	Area (ha)	Basal area (m^2/ha)	Preferred species (%)	Basal area (m^2/ha)	Preferred species (%)
1 (thinned)	12.2	33.8	42	23.8	35
1 (unthinned)	11.2	31.1	32	—	—
2 (thinned)	12.6	34.6	39	24.4	33.6
2 (unthinned)	11.6	31.2	40	—	—
3 (thinned)	10.8	33.4	11	22.7	12
3 (unthinned)	11.7	31.7	34	—	—
4 (thinned)	9.0	30.6	41	24.6	35
4 (unthinned)	7.9	25.6	52	—	—
5 (thinned)	9.2	31.2	60	20.0	65
5 (unthinned)	9.8	31.1	48	—	—
6 (thinned)	9.7	29.2	55	18.2	53
6 (unthinned)	9.9	28.7	51	—	—
7 (thinned)	7.8	30.0	81	20.3	85
7 (unthinned)	8.0	28.2	79	—	—
8 (thinned)	12.4	28.5	67	19.2	68
8 (unthinned)	11.7	28.2	79	—	—

small trees and under burlap bands were representative of the entire population. We are unaware of any studies that negate this assumption. Larvae were placed in individual 1 oz cups containing artificial diet. The cups were placed in an outdoor insectary located on the WVU Forest so that temperature and phenological development were approximately the same as for field populations. Each cup was checked twice weekly until an adult emerged. If the specimen died before adult emergence, the presence of parasitoids in the cup was recorded and cadavers were inspected by microscopy for viral polyinclusion bodies or fungal spores.

For each mortality agent, we computed peak sample percentage mortality as the maximum percent mortality over all weekly samples taken at each stand in each year. Peak percentage mortality is the best measure of parasitoid and disease impact under the sampling plan used here (Gould et al. 1989). A paired t-test was used to compare peak percentage mortality between thinned and unthinned portions of stands. However, mortality due to parasitoids and diseases of gypsy moth is sometimes density dependent (Elkinton and Liebhold 1990, Williams et al. 1992, 1993). If there are systematic differences in gypsy moth densities as a result of thinning, there may be spurious differences in parasitism and disease levels. Instead, we wished to test for the effect of thinning on mortality using an analysis that adjusted for variation in host density. We first used stepwise regression (Draper and Smith 1981) to model peak mortality (transformed using an arcsine-square root transformation) as a linear function of: (1) N_t, gypsy moth density [$\log(x + 1)$] at the beginning of the current generation, and (2) N_{t-1}, gypsy moth density [$\log(x + 1)$] at the beginning of the prior generation. Both independent variables were added successively to the model; the probability associated with the F statistic ($P < 0.05$) for each independent variable was the criterion for entering and retaining each term in the model. These selected variables were then included as covariates in an analysis of covariance where we assumed a randomized complete-block design (Steel and Torrie 1980). Peak percent mortality was the response, N_t and N_{t-1} were included as covariates (only if they were significant in the stepwise regression); treatment (thinning) and block were the effects. Block was defined as a particular stand in a given year. Thus, the 24 collections listed in Table 2 represent 2 collections (thinned and unthinned) from 12 blocks.

Results and Discussion

Thinning resulted in a decline in the total basal area of all species, including preferred species, by about 26% (Table 1). Presalvage thinning (stands 5–8) did not substantially change the proportion of basal area of preferred species. However, in stands where sanitation thinning was applied (1–4), the proportion of preferred species in the overstory declined except in stand 3 where the proportion of preferred species already was low.

Over the period 1989–1996, the expanding front of the gypsy moth was moving through the study area. Thus from 1989–1990, population densities were rapidly increasing (Figure 1). In stands 4, 7, and 8, populations continued to increase in 1991. Substantial defoliation occurred in these stands in 1990 and 1991. However, populations collapsed in 1991, apparently as a result of a virus epizootic. By contrast, populations collapsed in 1990 in stands 2, 5, and 6 due to an accidental application of pesticides in these stands that year by the West Virginia Department of Agriculture. Populations in these sprayed stands rebounded to moderate densities (ca. 100 egg masses/ha) by 1994, but then declined through 1996. In stands 1 and 3, populations remained at moderate densities

Table 2. Peak percent mortality from weekly collections of larvae. Data were only collected at sites where densities were adequate for sampling.

Year	Stand	*Blepharipa pratensis*	*Brachymeria intermedia*	*Compsilura concinnata*	*Cotesia melanoscela*	*Phobocampe unicincta*	*Parasetigena silvestris*	*Entomophaga maimaiga*	Nucleo-polyhedrosis virus (NPV)	Unidentified
1989	8 (thinned)	0	0	1.7	0	[a]	2.9	0	47.5	33.9
1989	8 (unthinned)	0	0	5.5	0	[a]	2.9	0	44.2	42.3
1990	4 (thinned)	19.6	0	0	0	0	1.1	0	34.7	67.0
1990	4 (unthinned)	21.0	0	1.0	0	0	1.0	0	34.4	71.0
1990	8 (thinned)	19.8	3.4	0	0	0	1.1	0	31.2	57.0
1990	8 (unthinned)	22.7	0	0	0	0	0	0	22.9	70.7
1991	4 (thinned)	6.4	18.3	14.3	1.7	0	0.9	0	76.0	46.7
1991	4 (unthinned)	7.0	12.8	16.2	1.2	0	2.3	0	78.6	39.2
1991	8 (thinned)	13.4	13.4	6.0	1.0	0	19.8	0	86.3	47.5
1991	8 (unthinned)	6.6	19.8	6.1	0	0	8.1	0	76.5	41.9
1992	1 (thinned)	20.3	2.9	6.9	11.4	1	12.0	0	25.7	81.0
1992	1 (unthinned)	11.2	0	6.0	11.6	1.9	11.2	0	51.4	79.5
1992	3 (thinned)	2.8	0	0.9	5.0	6.8	23.0	5.7	10.1	83.6
1992	3 (unthinned)	5.2	0	6.3	11.5	1.0	25.2	2.0	14.0	86.8
1993	1 (thinned)	5.1	3.0	3.9	20.3	0	26.9	4.9	30.3	77.2
1993	1 (unthinned)	8.4	0	4.1	16.1	1.0	7.5	1.9	41.5	70.1
1993	3 (thinned)	5.8	0	3.9	18.0	3.0	30.3	12.7	12.1	76.7
1993	3 (unthinned)	6.1	0	5.9	28.7	1.0	25.4	11.1	16.6	91.1
1993	5 (thinned)	1.0	0	6	16.2	0	14.2	36.7	11.7	86.4
1993	5 (unthinned)	0	0	5.6	13.1	0	21.2	28.2	8.9	86.1
1994	1 (thinned)	[a]	[a]	14.1	19.8	1.0	35.5	0	12.8	76.2
1994	1 (unthinned)	[a]	[a]	16.8	19.6	1.0	36.2	0	17.6	74.0
1994	3 (thinned)	[a]	[a]	5.2	6.4	9.2	22.3	0	10.2	90.1
1994	5 (thinned)	[a]	[a]	8.9	16.1	2.7	12.0	2.0	8.0	82.7

[a] Inadequate data.

from 1990 through 1994 and then declined from 1994–1996.

There was little or no evidence that the 1990 thinnings affected egg-mass densities in paired stands that were defoliated (4, 7, and 8) or sprayed (2, 5, and 6) (Figure 1). However, in stands that remained at moderate densities (1 and 3), densities tended to be lower in the thinned stands. The effect of thinning on egg-mass densities in all stands from 1990–1996 was tested using analysis of variance based on a repeated measures experiment (Snedecor and Cochran 1980). Results indicated that over all stands there was no significant effect of thinning on egg-mass density ($P = 0.128$, df = 7).

Survivorship patterns were variable among stands and years, though they generally were similar to those from previous studies (Figure 2). Mortality seemed greatest between the late-instar/pupal periods. It was not possible to estimate very low larval densities, and therefore survivorship curves are only provided for populations at stands and years when populations were at moderate or high levels. Survivorship patterns did not differ substantially between thinned and unthinned stands.

The two major causes of mortality observed in most collections were nucleopolyhedrosis virus and "unidentified" (Table 2). Virus mortality was highest in stands 4 and 8 in 1991. This mortality represented an epizootic that caused populations to drop from high densities in 1991 to low densities in 1992 (Figure 1). Overall, virus mortality was positively related to both density in the current (N_t) and the previous generation (N_{t-1}) (Table 3). This result is in general agreement with the existing knowledge of NPV epizootiology (Doane 1970, Woods et al. 1991)

That unidentifiable causes account for much of the mortality (Table 2) is problematic in a study such as this, though this phenomenon is common in life-table studies of the gypsy moth and other forest defoliators (Morris and Miller 1954, Royama 1992). Godwin and ODell (1984) reported that *Blepharipa pratensis* and *Parasetigina silvestris* often parasitize gypsy moths without producing puparia or adults. However, it is unlikely that this was the major cause of the unidentified mortality observed here, because the amount of unknown mortality did not seem correlated with that caused by these or other known agents (Table 2). Thus, we cannot draw conclusions about the cause of this mortality nor state with certainty whether it was an artifact of rearing on artificial diet.

In weekly samples of larvae and pupae, mortality also was caused by the parasitoids, *Parasetigina silvestris, Blepharipa pratensis, Phobocampe unicincta, Compsilura concinnata,* and *Cotesia melanoscela* (Table 2). Parasitism levels of *P. sylvestris* and *C. melanoscela* generally increased from 1989 through 1994. One explanation for this phenomenon is that population densities generally were increasing over this period. Another reason for the increase in parasitism levels is that they tend to be low in newly founded populations along the leading edge of the expanding population; range expan-

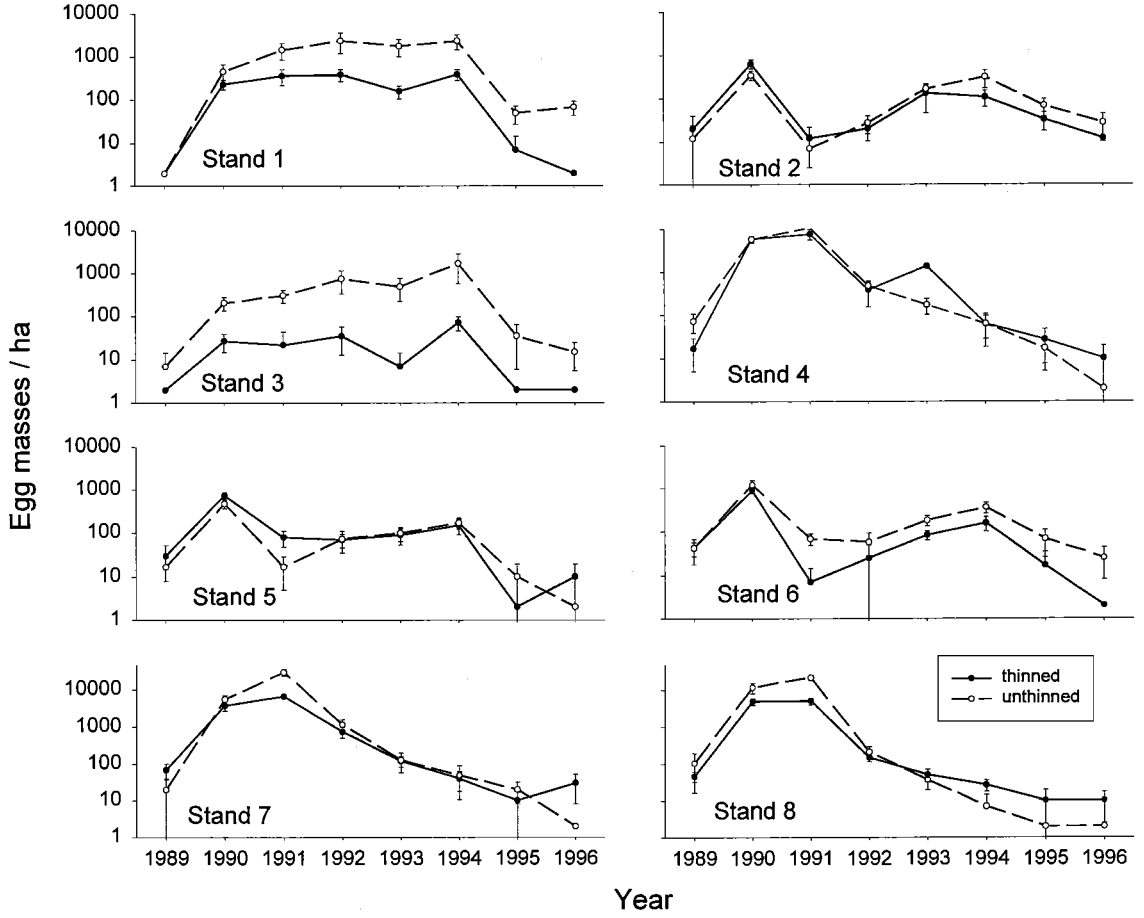

Figure 1. Gypsy moth egg-mass densities in paired thinned and unthinned stands, 1989–1996. Bars depict 95% confidence intervals.

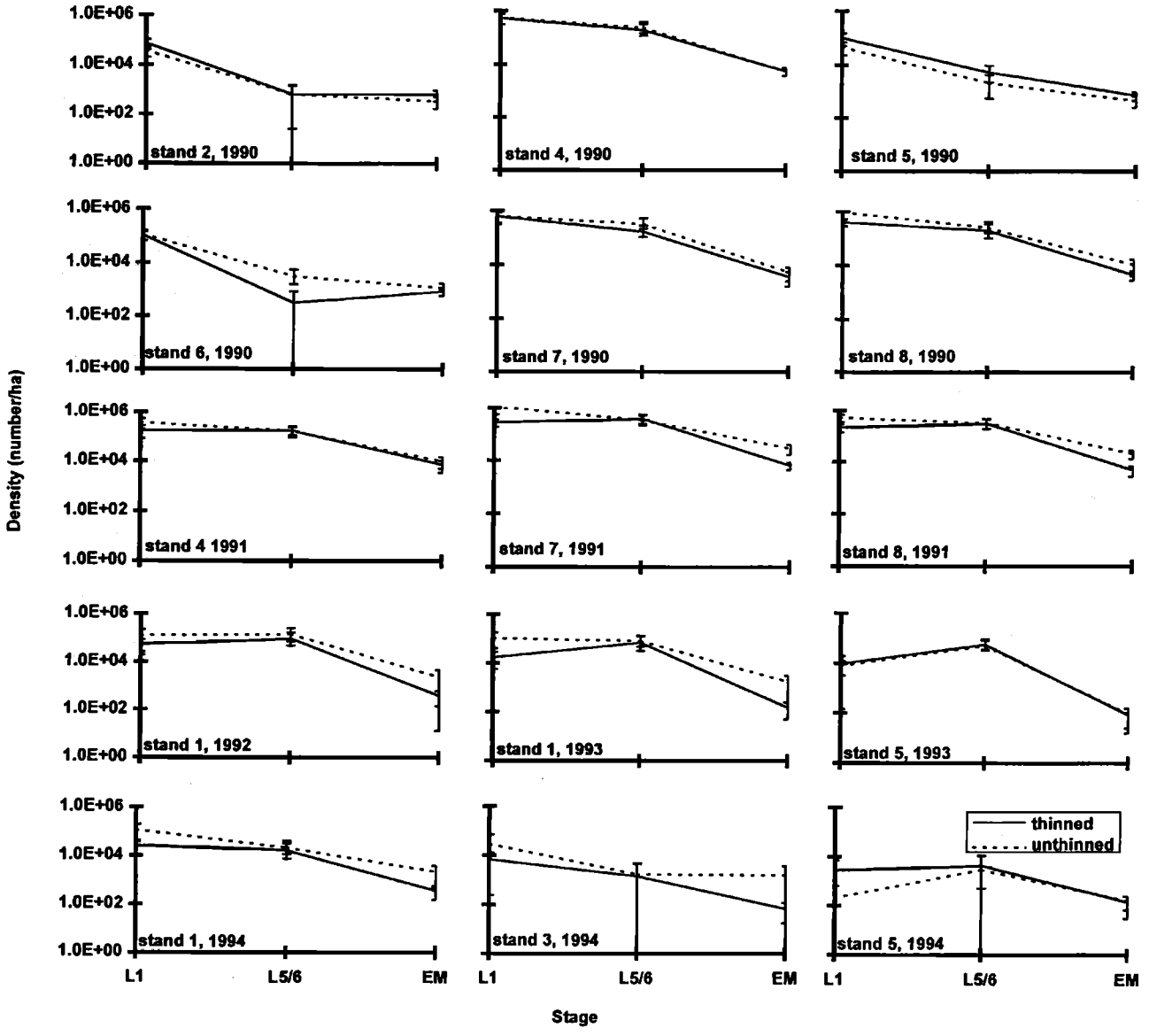

Figure 2. Generation survivorship curves in paired thinned and unthinned stands. Bars depict 95% confidence intervals.

Table 3. Results of stepwise regression of peak mortality on egg mass density (N_t) and log egg mass density (N_{t-1}). Independent variables that were not significant are not listed. When neither independent variable was significant, no results are shown.

Dependent variable	Independent variable[a]	Estimate	Probability of a > F
Blepharipa pratensis	N_t	−0.070	0.047
	N_{t-1}	0.12	0.002
Brachymeria intermedia	N_t	0.14	0.0006
Compsilura concinnata	N_t	0.12	0.0001
	N_{t-1}	−0.077	0.006
Cotesia melanoscela	N_t	0.12	0.003
	N_{t-1}	−0.20	0.0001
Phobocampe unicincta	N_{t-1}	−0.061	0.002
Parasetigena silvestris	N_t	0.10	0.012
	N_{t-1}	−0.20	0.0001
Nucleopolyhedrosis virus (NPV)	N_t	0.16	0.003
	N_{t-1}	0.13	0.009
Unknown	N_{t-1}	−0.14	0.0001

[a] N_t = egg mass density at the beginning of the same generation [log(1 + egg mass/ha)], N_{t-1} = egg mass density at the beginning of the previous generation [log(1 + egg mass/ha)].

sion by parasitoids tends to lag that of host gypsy moth populations (Ticehurst et al. 1978). The relationship between parasitism and host density varied considerably among parasitoid species (Table 3). Parasitism *by B. intermedia, C. concinnata, C. melanoscela* and *P. silvestris* were positively related to density in the current generation, N_t, and parasitism by *B. pratensis* was inversely related to N_t. Parasitism by *C. concinnata, C. melanoscela, and P. silvestris* was inversely related to host density in the previous generation, N_{t-1}, but parasitism by *B. pratensis* was positively related to N_{t-1}. For most species, these patterns are mostly in agreement with those of previous studies (Elkinton and Liebhold 1990, Williams et al. 1992, 1993).

One aspect of this study that differentiates it from previous studies was that only populations of moderate and high density were sampled. This may explain some of the differences in these relationships. It also is important to point out that the replicates listed in Table 2 are stratified in both space and time. Thus, any density dependence detected in these data may be the combination of spatial and temporal density dependence. Data in this study were insufficient to differentiate between these two types of density dependence. It also is worth pointing out that the observations listed in Table 2 may not be completely independent of each other because of autocorrelation in space or time. If present, such autocorrelation would violate the assumptions of independence among samples implicit in the simple linear regression used here. Pollard et al. (1987) and Dennis and Taper (1994) proposed methods for testing for density dependence in the presence of temporal autocorrelation, but we are unaware of similar methods for testing density dependence of specific mortality sources.

Entomophaga maimaiga caused considerable mortality in 1993, but much less in 1992 and 1994, and no mortality from 1989–1991 (Table 2). Mortality caused by *E. maimaiga* was first noticed in North America in New England in 1989; by about 1992, this pathogen seemed to have expanded its range to encompass nearly the entire range of the gypsy moth (Hajek et al. 1995). Thus, its absence in our samples from 1989–1991 can be explained by its general absence from the region during that period.

When mortality levels were compared between thinned and unthinned stands using a paired *t*-test (Sokal and Rohlf 1981), parasitism by *B. intermedia* and *C. melanoscela* was significantly higher in thinned stands, and mortality caused by NPV was significantly lower in thinned stands (Table 4). However, we knew from the results given in Table 3 that mortality often is closely associated with gypsy moth densities, so any difference in densities between thinned and unthinned stands might explain the differences in mortality levels. Therefore, we reassessed the significance of thinning on mortality levels using analysis of covariance where gypsy moth density and/or lagged density were used as covariates. The least-squares means given in Table 4 adjust mortality levels based on the known relationship(s) with gypsy moth density. None of the least-squares means indicated a significant effect of thinning. Thus, the adjusted analysis indicated that thinning had no effect on mortality levels.

Weekly collections of larvae provided adequate estimates of mortality caused by parasitism and disease, but did not provide information on predation. Results from a concurrent study of predation (Grushecky 1995) indicated that small mammals were significantly more abundant in thinned than in unthinned stands. However, exclosure studies indicated that levels of predation on tethered larvae and pupae by small mammals and invertebrates did not differ significantly between thinned and unthinned stands.

Neither we nor Grushecky were able to determine that thinning significantly altered levels of mortality caused by specific parasitoids, predators, or pathogens. Thus, it seems unlikely that these silvicultural operations can reduce the frequency or intensity of gypsy moth outbreaks by enhancing the activity of the natural enemies of the insect.

Results from stands that were not defoliated or sprayed (1 and 3) suggest that gypsy moth densities declined as a result of thinning (Figure 1). It is possible that these differences were not observed in the defoliated stands (4, 7, and 8) because densities already were at outbreak levels. Following 2 yr of defoliation in these stands, populations collapsed to low densities such that it probably would be difficult to detect differences in densities caused by thinning (Figure 1). Similarly, the accidental application of pesticide in stands 2, 5, and 6 may have obscured any effect of thinning on gypsy moth populations.

Because a significant decrease in gypsy moth densities following thinning was detected in only 2 of the 8 stands (Figure 1), we cannot conclusively state that densities were reduced by thinning. However, numerous researchers have reported that outbreak frequency is closely related to the proportion of stand basal area represented by preferred gypsy moth host-tree species (Bess et al. 1947, Houston and Valentine 1977, Herrick and Gansner 1986). Perhaps one reason

Table 4. Unadjusted means and least squares means (adjusted for covariates listed in Table 3) for transformed peak percentage mortality.

	Unadjusted mean		Least-squares mean	
Dependent variable	Unthinned	Thinned	Unthinned	Thinned
Blepharipa pratensis	0.291	0.306	0.270	0.327
Brachymeria intermedia	0.0919	0.150*	0.0872	0.154
Compsilura concinnata	0.238	0.213	0.232	0.236
Cotesia melanoscela	0.261	0.271*	0.243	0.309
Phobocampe unicincta	0.0539	0.0926	0.0984	0.0751
Parasetigena silvestris	0.334	0.385	0.357	0.370
Nucleopolyhedrosis virus (NPV)	0.631	0.549*	0.555	0.583
Unknown	0.973	1.00	0.994	1.01

* Significant difference between means for thinned and unthinned ($\alpha = 0.05$).

why we did not see a more dramatic decrease in gypsy moth densities in thinned stands is that the proportion of preferred species basal area did not decline substantially in any stand following thinning (Table 1). Nevertheless, our results suggest that any reduction in gypsy moth density caused by thinning most likely is not a result of differential effects by natural enemies but of another factor, for example, mortality during dispersal and/or effects on fecundity.

The lack of a detectable effect of thinning on the action of the natural enemies of gypsy moth does not preclude the viability of silvicultural approaches to managing this insect pest. Rather, these results indicate that thinnings are more likely to affect stand susceptibility simply by reducing the total or relative amount of host foliage (Gottschalk 1993). Further, silvicultural manipulations can be useful tools in gypsy moth management because they remove trees that are likely to die following defoliation (e.g., those with poor crowns).

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