

The Great Lakes Entomologist

Volume 33
Numbers 3 & 4 - Fall/Winter 2000 *Numbers 3 &
4 - Fall/Winter 2000*

Article 7

October 2000

Distribution of First Instar Gypsy Moths (Lepidoptera: Lymantriidae) Among Saplings of Four Tree Species Common in the Great Lakes Region

J. L. Stoyenoff
University of Michigan

J. A. Witter
University of Michigan

Follow this and additional works at: <https://scholar.valpo.edu/tgle>



Part of the [Entomology Commons](#)

Recommended Citation

Stoyenoff, J. L. and Witter, J. A. 2000. "Distribution of First Instar Gypsy Moths (Lepidoptera: Lymantriidae) Among Saplings of Four Tree Species Common in the Great Lakes Region," *The Great Lakes Entomologist*, vol 33 (3)

Available at: <https://scholar.valpo.edu/tgle/vol33/iss3/7>

This Peer-Review Article is brought to you for free and open access by the Department of Biology at ValpoScholar. It has been accepted for inclusion in The Great Lakes Entomologist by an authorized administrator of ValpoScholar. For more information, please contact a ValpoScholar staff member at scholar@valpo.edu.

DISTRIBUTION OF FIRST INSTAR GYPSY MOTHS
(LEPIDOPTERA: LYMANTRIIDAE) AMONG SAPLINGS OF
FOUR TREE SPECIES COMMON IN THE GREAT LAKES REGION

J. L. Stoyenoff^{1,2} and J. A. Witter²

ABSTRACT

We examined the inter-tree distribution of first instar gypsy moth larvae under natural dispersal conditions in the field in Michigan in 1991. The study focused on saplings of northern red oak (*Quercus rubra*), white oak (*Q. alba*), red maple (*Acer rubrum*), and witch-hazel (*Hamamelis virginiana*), which are common understory components of forests in the Great Lakes region. Large-volume trees with foliage that is well-developed early in the spring should provide an excellent surface area for catching newly-hatched gypsy moth larvae, which are randomly dispersed by wind in the spring around the time of leaf flush or shortly thereafter. Comparing across tree species in our study, red maples had the largest crown volumes and well-flushed leaf material, but very few larvae were found on these trees at both sampling times in mid-May. Despite the lack of larvae on red maple, these trees were liberally covered with gypsy moth silk, indicating that many larvae landed on these plants but left rapidly when they apparently found the trees to be an unacceptable food source. Among the other three tree species, patterns of larval distribution reflected levels of host phenological development during both sampling periods, with more insects occurring on tree species that had more advanced leaf development. The highest numbers of larvae were found on northern red oak and witch-hazel. Intermediate numbers of insects were present on white oak. Trends in insect distribution also paralleled patterns seen in tree phenology across slope gradients. Defoliation ratings corresponded well to measures of first instar presence for each tree species. Northern red oak and witch-hazel trees experienced more early defoliation on average than did red maple and white oak. For those tree species that are acceptable hosts of the gypsy moth, average level of phenological development for a given tree, species, or forest stand at the time of larval dispersal can be an important predictor of plant or stand susceptibility to gypsy moth establishment and subsequent defoliation.

Gypsy moth (*Lymantria dispar* (L.)) larvae are broadly polyphagous, feeding on 300 different host species (Leonard 1981). In many lepidopterans, choice of the larval food plant is made by the ovipositing adult female. Gypsy moth females, however, are relatively unselective about where they lay their egg masses, readily depositing them even on inedible objects such as rocks,

¹Correspondence address: Dow Gardens, Midland, MI 48640-4292.

²University of Michigan, School of Natural Resources and Environment, Ann Arbor, MI 48109-1115.

stumps, and recreational vehicles (Lance 1983). When larvae hatch in spring, they must find their own food. By spinning silk threads, larvae are able to balloon on the wind in an attempt to find an acceptable host plant. Studies of larval behavior have reported that all healthy larvae will undergo at least one such ballooning dispersal, and larvae will generally balloon again if they land on an unsuitable substrate (Lance and Barbosa 1981, Capinera and Barbosa 1976, van der Linde 1971). Typically at the time of gypsy moth first instar larval dispersal in Michigan, tree phenology varies among tree species and individual trees on a given site from tight buds to flattened, expanding leaves (Chilcote 1990, Chilcote et al. 1992).

Several factors affect whether dispersing larvae will encounter a given plant. These include characteristics of the plant community, plant location relative to wind patterns and obstacles, plant size and branchiness, and the level of phenological development of foliage (Stanton 1983, Feeny 1976). Tendency to remain on a particular plant once it is encountered may be affected by factors such as plant species, phenological stage of the foliage, density of larvae on the plant, and the level of food reserves available for re-dispersal attempts remaining in the larva's body.

Some aspects of dispersal by first instar gypsy moth larvae have been more thoroughly investigated, such as the effects of velocity and turbulence of air currents on larval movement, dispersal distances, and settling (Zlotina et al. 1999, Fosberg and Peterson 1986, Taylor and Reling 1986, Mason and McManus 1981, McManus 1973). The effects of differing plant characteristics on dispersal activity and distribution of young larvae within a stand is another important aspect which encompasses many factors (Naidoo and Lechowicz 1998, Weseloh 1998, Ticehurst and Yendol 1989, Lance and Barbosa 1981, Barbosa 1978a, van der Linde 1971). In particular, understanding has been incomplete relative to ways in which the stage of foliar phenological development may affect gypsy moth larval distribution among trees during the ballooning first instar dispersal phase. We undertook this study to examine how first instar gypsy moth larvae are distributed among saplings of various common tree species in the field and how this distribution may be related to patterns of host phenological development.

MATERIALS AND METHODS

Study site and trees. This study was performed in 1991 at a moderately mesic site dominated by 15 to 20 year old trees of northern red oak (*Quercus rubra*), white oak (*Q. alba*), bigtooth aspen (*Populus grandidentata*), trembling aspen (*P. tremuloides*), red maple (*Acer rubrum*), and witch-hazel (*Hamamelis virginiana*) in Kalkaska County, Michigan (T25N, R6W, S26). The vegetation in this area tended to be somewhat open. The site was situated on a slope, so that study trees fell into one of three locations: lower slope (elevation of 353 m), midslope, or hilltop (elevation of 385 m) areas. Natural gypsy moth egg masses were moderately abundant throughout the site. Five minute walks through the site (Eggen and Abrahamson 1983) in each of the three slope locations yielded egg mass counts of 100, 134, and 143 in upper, mid, and lower slope areas, respectively.

The plant material selected for study consisted of 19 saplings of northern red oak and 20 saplings each of white oak, red maple, and witch-hazel. All study species were represented in each of the three slope locations, except in the midslope area where northern red oak trees of the appropriate size and exposure (see below) were not available. Neither aspen species present at the

site was used in this study due to lack of trees of the appropriate size and exposure in the necessary locations.

We chose these particular tree species for study because they are common throughout the Great Lakes region and represent a range of foliage conditions at the time of gypsy moth dispersal from tight buds to flattened, expanding leaves, as well as a range of suitability for gypsy moth larvae from low to high (Chilcote 1990, Chilcote et al. 1992). We used understory-sized trees both to increase ease of sampling and because research by Ticehurst and Yendol (1989) has demonstrated that more than 80% of all early instar gypsy moth larvae may be found in the lower canopy, understory, and forest floor during both day and night.

Because tree volume is an important component of how apparent any given plant is to food-seeking herbivores, we attempted to choose experimental trees that were naturally of similar sizes (Lance 1983). Some pruning was done during April 1991 on almost all study trees from the ground or from ladders to remove portions of branches that extended beyond the height that could easily be viewed from a 2.5 m ladder (average total tree height after pruning: 2.35 ± 0.26 m for witch-hazel, 2.82 ± 0.29 m for northern red oak, 2.88 ± 0.30 m for white oak, and 3.19 ± 0.34 m for red maple). No sample trees were pruned heavily, however. After all pruning was completed, the diameter of each tree crown was measured in two directions and averaged, and the crown height and total tree height were each estimated to the nearest 0.3 m. The crown height and average crown diameter were used in the equation of volume for a cone to estimate the volume for each tree crown.

Trees selected for use in the study were in relatively exposed locations so that larvae could readily blow onto them but could not crawl or drop onto the experimental trees from other overhanging trees. In a few cases, portions of nearby large trees were pruned away to avoid blockage of study trees and to help equalize amounts of exposure. Before eggs began hatching in May in the area of the study site, the study trees were inspected for gypsy moth egg masses, which were scraped off when encountered. Also, circles of forest floor at least 2 m in diameter around each sample tree were cleared of all woody debris and leaf litter prior to egg hatch. This helped isolate study trees from sources of potential colonizers in the forest floor litter, since egg masses may be found there as well. These measures were taken so that caterpillars encountered on the trees during the course of the experiment could reasonably be expected to have reached the trees through aerial dispersal activity, rather than being present simply because a given tree was in direct contact with or in close proximity to a large number of egg masses.

Sampling procedures. Daily monitoring revealed that peak egg hatch occurred at the study site on 12 May 1991. The weather was very warm and dry (12 May maximum: 27°C, minimum: 16°C), and larvae began to disperse soon after hatch. By the following day, a large portion of the larvae were moving about among potential host plants at all levels of the slope.

We began the first sample of the study trees during mid-morning of 13 May. Each tree was given an overall rating of leaf development according to the phenological scoring system employed by Chilcote (1990) (Table 1), and a complete count was made of all larvae located anywhere on the tree from the groundline to the tips of the branches. To be counted, larvae had to be in direct contact with the bark or leaves of the tree; larvae suspended from branches by silk strands were not included in the counts. Upper portions of the trees were inspected with the help of 2.5 m ladders, which allowed us to easily view all branches. As larvae were counted, they were removed from the tree and killed. The first sample of all 79 trees was completed on 14 May.

A second sample was planned to take place near the end of major gypsy

Table 1. Phenological scoring system for budbreak and leaf expansion of hardwood trees based on Chilcote (1990).

Score	Foliar Conditions
1	Winter condition; buds tight.
2	Buds swelled but no expansion of scales.
3	Buds and scales expanding.
4	Scale expansion greater than 2 mm.
5	Leaf material showing at tip of bud.
6	Leaves exposed beyond scales but blades not flat.
7	Leaves exposed and blades flattened.
8	Leaves expanding and soft.
9	Leaves expanding and tough.
10	Leaves fully expanded and tough; dark and leathery.

moth egg hatch and dispersal at the field site in order to confirm patterns seen at the first sample. Warm temperatures and steadily increasing degree day accumulations during mid-May (Fig. 1) facilitated a rapid hatch. Observations of egg masses in the area indicated that most eggs were hatched by 16 May. Therefore, trees were sampled a second time on 16–17 May, using the same procedures and following the same pattern through the site. On 18 May, percent defoliation of each study tree was scored as one of five classes based on visual estimation of all foliage on each tree (1 = defoliation < 10%, 2 = 11–25% defoliation, 3 = 26–50% defoliation, 4 = 51–75% defoliation, and 5 = 76–100% defoliation).

Statistical procedures. Statistical analyses were performed with the General Linear Models procedure in SAS (SAS 1996). A two-factor analysis of variance (ANOVA) design was used, which included factors of tree species, slope location, and the interaction of these factors. The sampling unit was individual trees (20 for each species, except 19 for northern red oak).

Assumptions were tested using plots of residuals versus predicted values, normal probability plots, stem-and-leaf plots, and skewness and kurtosis coefficients. Where necessary, log transformations were performed on the data before analysis to more closely meet assumptions of normality and homogeneity.

Scheffé's multiple comparison procedure was used in the evaluation of the data. This procedure was employed for tests of all pair-wise comparisons because its relatively low power reduces the risk of Type I errors occurring in the inferences made. An experiment-wise α of 0.05 was used.

RESULTS

Average tree volume differed significantly among tree species ($F = 4.13$; $df = 3, 68$; $p = 0.01$). Red maple trees had the greatest average volume, although their volume was significantly different only from northern red oak trees with Scheffé's multiple comparison procedure (Table 2). Volume was not significantly affected by slope location ($F = 0.60$; $df = 2, 68$; $p = 0.55$) or the interaction of species and slope location ($F = 0.79$; $df = 5, 68$; $p = 0.56$).

Average tree phenology on the first sampling date (13–14 May) was significantly affected by species ($F = 25.07$; $df = 3, 68$; $p = 0.0001$) and slope location ($F = 12.26$; $df = 2, 68$; $p = 0.0001$). Leaf flush of white oak trees was delayed compared to the other tree species (Table 2). White oaks had an

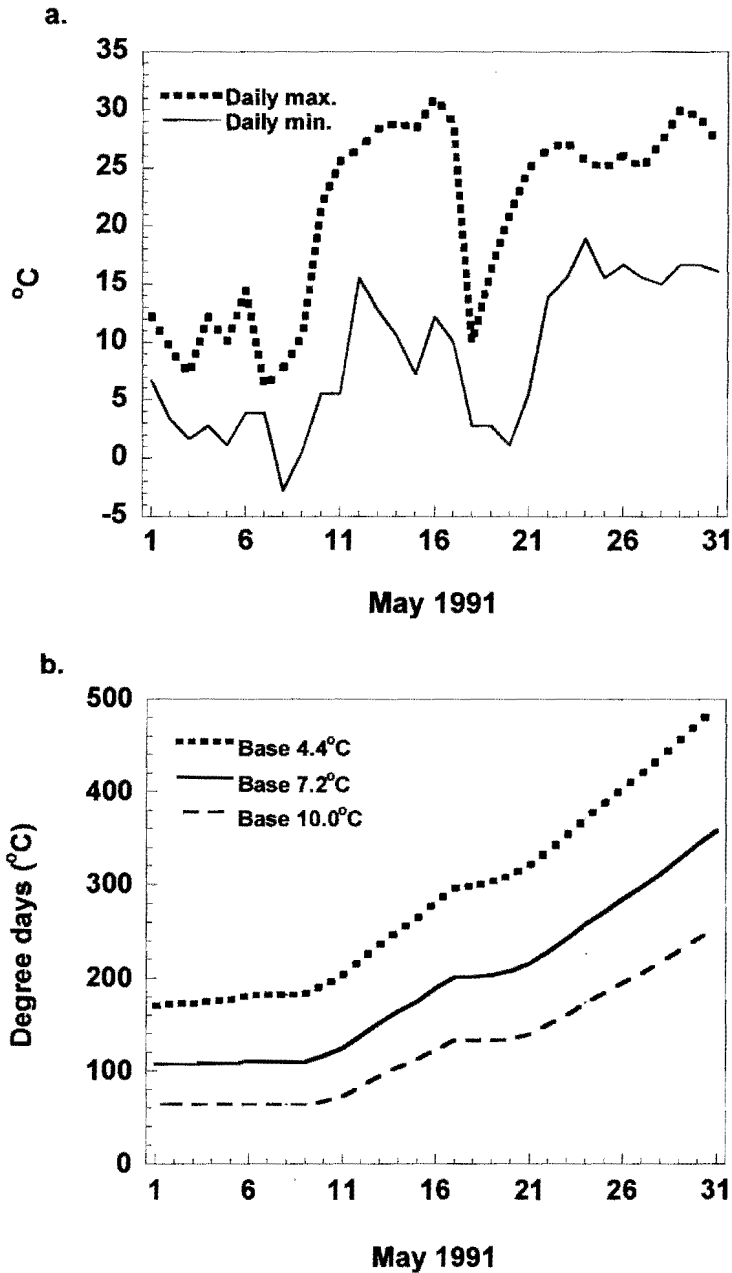


Figure 1. Weather data recorded at the National Oceanic and Atmospheric Administration weather station in Kalkaska, Michigan, USA.

Table 2. Plant characteristics and presence of first instar gypsy moth larvae on four tree species at two sampling times during May 1991.

Variable	Species			
	Red maple	White oak	Witch-hazel	N. red oak
N	20	20	20	19
Mean crown volume (m ³)	1.31 ± 0.14 a	0.96 ± 0.11 ab	0.90 ± 0.09 ab	0.80 ± 0.09 b
Sample 1 (13–14 May 1991):				
Mean phenological rating ^a	6.8 ± 0.1 ab	5.0 ± 0.2 c	6.3 ± 0.2 b	6.8 ± 0.1 a
Mean larvae/tree	51.5 ± 7.7 b	80.7 ± 18.6 b	424.4 ± 50.7 a	643.2 ± 60.1 a
Mean larvae/m ³ of crown	44.6 ± 7.1 c	104.6 ± 33.7 c	536.3 ± 72.9 b	994.8 ± 120.9 a
Sample 2 (16–17 May 1991):				
Mean phenological rating ^a	7.4 ± 0.1 b	6.6 ± 0.2 c	7.7 ± 0.1 ab	8.0 ± 0.03 a
Mean larvae/tree	14.5 ± 2.2 c	207.7 ± 31.4 b	567.1 ± 45.2 a	587.5 ± 70.4 a
Mean larvae/m ³ of crown	13.2 ± 2.6 c	238.6 ± 33.6 b	731.8 ± 94.2 a	901.4 ± 130.5 a
Mean defoliation rating ^b	1.0 ± 0.0 c	1.1 ± 0.1 c	3.1 ± 0.1 b	3.7 ± 0.2 a

Means within each row followed by the same letter do not differ significantly with Scheffé's multiple comparison procedure.

^a1 = Winter condition buds; 2 = Buds swelled, no scale expansion; 3 = Buds and scales expanding; 4 = Scale expansion > 2mm; 5 = Leaf material at tip of bud; 6 = Leaves exposed beyond scales, blades not flat; 7 = Leaves exposed, blades flat; 8 = Leaves expanding and soft; 9 = Leaves expanding and tough; 10 = Leaves fully mature. (Modified from Chilcote (1990).)

^b1 = defoliation < 10%, 2 = 11–25% defoliation, 3 = 26–50% defoliation, 4 = 51–75% defoliation, and 5 = 76–100% defoliation.

average phenology of stage 5 (leaf material just showing at the tip of the bud) as compared to averages of stage 6 (leaves exposed but not flattened) to stage 7 (leaves exposed and flattened) for the other species. In terms of slope location, leaf flush of lower slope trees was significantly delayed compared with midslope and upper slope trees (lower slope = 5.7 ± 0.2 a; midslope = 6.3 ± 0.2 b; upper slope = 6.7 ± 0.1 b; different letters indicate mean values significantly different with Scheffé's multiple comparison procedure). The interaction of tree species and slope location was also significant in relation to tree phenology ($F = 3.45$; $df = 5,68$; $p = 0.01$).

Average number of larvae per tree at the first sampling period also was significantly affected by tree species ($F = 61.58$; $df = 3, 68$; $p = 0.0001$). At that time, northern red oak and witch-hazel trees had significantly more larvae present on them on average than did trees of either white oak or red maple (Table 2). Slope location significantly affected number of larvae present on trees as well ($F = 10.94$; $df = 2,68$; $p = 0.0001$), with an increase in number of larvae per tree as one progressed up the slope (lower slope = 127.6 ± 31.5 larvae/tree a; midslope = 256.0 ± 54.9 larvae/tree b; upper slope = 467.5 ± 59.0 larvae/tree c). The interaction of species and slope location was also significant ($F = 2.97$; $df = 5,68$; $p = 0.02$).

Examining insect presence on the basis of number of larvae per unit volume of tree crown revealed results that were very similar to the results for absolute number of larvae per tree. Average number of larvae per unit volume of tree crown at the first sampling period was significantly affected by tree species ($F = 67.20$; $df = 3, 68$; $p = 0.0001$). Northern red oak had the greatest average number of larvae per unit volume followed by witch-hazel, and the figures were significantly larger on each of these species than on either white oak or red maple, which were not significantly different from one another (Table 2). Slope location also significantly affected average number of larvae per unit volume of tree crown ($F = 6.11$; $df = 2,68$; $p = 0.004$), with increasing values as one progressed up the slope (lower slope = 207.3 ± 71.6 larvae/unit volume a; midslope = 328.4 ± 70.5 larvae/unit volume b; upper slope = 640.6 ± 97.7 larvae/unit volume c). The interaction of species and slope location was significant as well ($F = 3.47$; $df = 5,68$; $p = 0.01$).

At the second sampling period (16–17 May), average tree phenology was once again significantly affected by tree species ($F = 21.73$; $df = 3,68$; $p = 0.0001$), with white oak trees still significantly behind the others in terms of average phenological stage (Table 2). Biologically, however, the average phenological condition of the white oak trees indicated that they were beginning to be more suitable as food for the caterpillars at this point. White oak trees now had an average phenology of stage 6 to 7 (leaves fully exposed beyond bud scales with leaf blades not yet flat to blades exposed and flattening), as compared to the average white oak phenology at the first sampling period of a stage 5 (leaf material just showing at the tip of the bud). Slope location also significantly affected average phenology at the second sample date ($F = 12.75$; $df = 2, 68$; $p = 0.0001$). Mean phenological stage, averaged across all trees in the study, increased as one progressed up the slope (lower slope = 7.0 ± 0.1 a; midslope = 7.4 ± 0.1 b; upper slope = 7.8 ± 0.1 c). The interaction of species and slope location was also significant ($F = 2.34$; $df = 5, 68$; $p = 0.05$).

Average absolute number of larvae present on the study trees at the second sampling period was significantly affected by tree species ($F = 128.60$; $df = 3, 68$; $p = 0.0001$). Northern red oak and witch-hazel trees had the greatest numbers of larvae per tree on average, and the numbers on these species were significantly greater than the numbers on white oak (Table 2). Numbers of larvae on red maple were significantly lower than numbers of larvae on any other tree species. At this second sampling period, average numbers

of larvae per tree were not significantly affected by slope location ($F = 2.25$; $df = 2, 68$; $p = 0.11$) or an interaction of species and slope location ($F = 1.87$; $df = 5, 68$; $p = 0.11$).

Results based on number of larvae per unit volume of tree crown at the second sampling period were once again very similar to the results for absolute numbers of larvae per tree. Average number of larvae per unit volume of tree crown was significantly affected by tree species ($F = 156.92$; $df = 3, 68$; $p = 0.0001$), with values being greatest on northern red oak and witch-hazel, which were not significantly different from each other (Table 2). These were followed by the significantly lower figure on white oak and finally the average number of larvae per unit volume of tree crown on red maple, which was significantly lowest of all species. Average number of larvae per unit volume of tree crown was not significantly affected by slope location ($F = 0.75$; $df = 2, 68$; $p = 0.48$) but was affected by the interaction of species and slope location ($F = 2.80$; $df = 5, 68$; $p = 0.02$).

Average defoliation levels were significantly affected by tree species ($F = 124.67$; $df = 3, 68$; $p = 0.0001$) and ranged from $<10\%$ to $>50\%$ (Table 2). High defoliation levels were due to the large number of gypsy moth caterpillars per tree on certain species and the small size of leaves early in the season. Slope location also significantly affected defoliation levels ($F = 10.27$; $df = 2, 68$; $p = 0.0001$). Effects of slope location on defoliation followed the general pattern seen for tree phenological development and numbers of larvae present, with lower defoliation occurring on the lower slope and increasing defoliation as one moved up the slope (lower slope = 1.5 ± 0.1 a; midslope = 2.0 ± 0.3 b; upper slope = 2.9 ± 0.2 c; where class 1 = defoliation $< 10\%$, class 2 = 11–25% defoliation, class 3 = 26–50% defoliation, as described above). Tree species and slope location significantly interacted to affect defoliation as well ($F = 3.18$; $df = 5, 68$; $p = 0.01$).

DISCUSSION

Work by others has shown that oaks are highly favored host plants of the gypsy moth, but maples are not very acceptable or suitable hosts, which is perhaps due to the presence of toxic/deterrent chemicals in maple foliage (Barbosa et al. 1990, Martinat and Barbosa 1987, Lance 1983, Barbosa and Greenblatt 1979, Barbosa et al. 1979, Barbosa 1978a, 1978b). However, red maples often tend to be among the earlier flushing tree species in the Great Lakes region and in our study ranked highest in terms of average volume. Large-volume trees that flush early and have relatively large leaves should provide an excellent surface area for catching insects that are randomly dispersed by the wind, and one might expect to find high numbers of larvae on such trees. Despite this, the number of larvae present on red maple trees in our study was very low at both sampling times, both in terms of absolute numbers and on the basis of mean larvae per m^3 of crown. A qualitative examination revealed that red maple buds and branch tips were often covered with more insect silk than was true for trees of other species except for white oaks with very delayed phenology, on which the amount of silk appeared similar to that seen on red maple. The large amount of silk observed on red maple trees indicates that they were probably encountered by many larvae. However, since we found very few larvae remaining on the trees it is likely that larvae may have re-dispersed in search of different host material. Because few larvae were located on this species, it suffered very little defoliation on average during the study period. Research by others has demonstrated that young gypsy moth larvae do disperse rapidly and with high

frequency from unacceptable substrates (Martinat and Barbosa 1987, Lance 1983, Capinera and Barbosa 1976, van der Linde 1971, Leonard 1967).

While there are other factors that also come into play when insects choose among relatively favored host species, match of optimal host phenology to insect activity is one important factor. An appropriate level of phenological development means that adequate leaf material in suitable condition for feeding is available (Stoyenoff et al. 1994a, Raupp et al. 1988). Level of phenological development is also related to other important characteristics of the foliage, such as nutrient and water content, toughness, and levels of defensive compounds (Hunter and Lechowicz 1992, Hough and Pimentel 1978, Feeny 1976). Many workers have found that plant phenology is a major factor affecting insect host use (Parry et al. 1998, Kolb and Teulon 1992, Crawley and Akhteruzzaman 1988, Larsson and Ohmart 1988, Raupp and Denno 1983, Mitter et al. 1979, Schweitzer 1979, Witter and Waisanen 1978, Holliday 1977, Feeny 1970, Greenbank 1956).

For those species that are acceptable hosts of the gypsy moth, average level of phenological development seen on a given tree, species, or forest stand at the time of larval dispersal may be one important predictor of plant or stand susceptibility to insect establishment and subsequent defoliation. We found that numbers of insects present on acceptable host species tended to strongly follow patterns seen in plant phenology, with more insects occurring on tree species that had advanced leaf development. For instance, at the first sampling period, northern red oaks had on average leaf material free of the bud scales and flattening out, witch-hazels had leaf material free of the bud scales but on average more folded, and white oaks had much leaf material still surrounded by bud scales with only some tightly folded leaf material showing at the tips of the buds. Northern red oaks at this sample had a high number of larvae present on them on average, witch-hazels had a slightly lower number, and white oaks had a much lower number. This was true both in terms of absolute numbers of larvae per tree and number of larvae per unit of crown volume.

In the case of the significant increase in insect numbers on white oak between the first and second sampling times, the phenological changes that took place over this time period greatly altered the usefulness of these plants to young gypsy moth caterpillars. However, while this phenological change may be very important, it is inadequate to elevate numbers of insects found on white oak to the level found on the other acceptable host species. At stage 6, white oak leaves are still covered by many dense trichomes, and the presence of trichomes has been shown to inhibit feeding in some cases of plant-insect interactions (Agrawal 1999, Zvereva et al. 1998, Dix et al. 1996, Kanno 1996, Oghiakhe 1995, Wright and Giliomee 1992, Gross and Price 1988, Khan et al. 1986, Hardin 1979, Johnson 1975, Levin 1973). This factor may be coming into play here. By contrast, northern red oak trees at the second sample date were about 1.5 stages more advanced than white oak on average and had expanding, soft, young leaves that had shed any trichome covering. While it is possible that insect numbers were higher on northern red oak because the more phenologically advanced northern red oak leaves had larger flattened leaf surfaces available for catching larvae than did white oak, we repeatedly observed that the lower-phenology white oak trees were covered with more caterpillar silk than were the northern red oak trees, indicating that large numbers of larvae were also encountering the white oak trees but some were leaving in search of more highly acceptable food sources.

Average defoliation levels observed for the various tree species in this study indicate that northern red oak and witch-hazel were very acceptable food sources to the larvae, and they ate large fractions of the leaf material on

these species. Since white oak leaves were on average less developed and smaller than leaves of northern red oak and witch-hazel by the date defoliation was evaluated, it would have been possible for the white oaks to score higher in terms of defoliation rating even if they were fed on less, due to the fact that white oak trees had less expanded foliage available to begin with (Valentine 1983). Such was not the case, however. Despite larger amounts of foliage present, northern red oaks and witch-hazels scored significantly higher in terms of average defoliation rating than did white oaks in this study. Both white oaks and red maples escaped significant defoliation early on in the season due to various characteristics that led to these plants being less acceptable to young gypsy moth larvae.

Foliage of preferred host species has been shown by others to generally retain higher numbers of gypsy moth larvae than foliage of less preferred species (Lance 1983, Lance and Barbosa 1981, Barbosa 1978a). Based on average number of insects present and average defoliation levels seen in the field in this study, witch-hazel appears to be a very acceptable host species for young gypsy moth larvae, almost as much so as northern red oak. Larvae may use species such as witch-hazel and northern red oak at a time when other species such as white oak or aspens are phenologically behind and are not as acceptable to the insects. The insects can later move on to aspens and white oak as their leaves flush and their acceptability increases (Stoyenoff et al. 1994b, 1994c). Presence of acceptable hosts that are phenologically well timed with caterpillar hatch and early dispersal can therefore increase overall defoliation potential of a stand throughout the season and heighten performance of the gypsy moth in an area.

ACKNOWLEDGMENTS

This work was supported in part with funds provided to the University of Michigan by the USDA McIntire-Stennis Program. We thank the Michigan DNR, Forest Management Division, for providing research housing. Anonymous reviewers provided helpful comments and insight.

LITERATURE CITED

- Agrawal, A. A. 1999. Induced responses to herbivory in wild radish: Effects on several herbivores and plant fitness. *Ecology* 80: 1713–1723.
- Barbosa, P. 1978a. Distribution of an endemic larval gypsy moth population among various tree species. *Environ. Entomol.* 7: 526–527.
- Barbosa, P. 1978b. Host plant exploitation by the gypsy moth, *Lymantria dispar*. *Entomol. Exp. Appl.* 24: 28–37.
- Barbosa, P. and J. Greenblatt. 1979. Suitability, digestibility and assimilation of various host plants of the gypsy moth *Lymantria dispar* L. *Oecologia* 43: 111–119.
- Barbosa, P., J. Greenblatt, W. Withers, W. Cranshaw and E. A. Harrington. 1979. Host-plant preferences and their induction in larvae of the gypsy moth, *Lymantria dispar*. *Entomol. Exp. Appl.* 26: 180–188.
- Barbosa, P., P. Gross, G. J. Provan, D. Y. Pacheco and F. R. Stermitz. 1990. Allelochemicals in foliage of unfavored tree hosts of the gypsy moth, *Lymantria dispar* L. I. Alkaloids and other components of *Liriodendron tulipifera* L. (Magnoliaceae), *Acer rubrum* L. (Aceraceae), and *Cornus florida* L. (Cornaceae). *J. Chem. Ecol.* 16: 1719–1730.
- Capinera, J. L. and P. Barbosa. 1976. Dispersal of first-instar gypsy moth larvae in relation to population quality. *Oecologia* 26: 53–64.

- Chilcote, C. A. 1990. The effects of host phenology and site interactions on the gypsy moth, *Lymantria dispar*. Ph.D. dissertation, University of Michigan, Ann Arbor.
- Chilcote, C. A., J. A. Witter, M. E. Montgomery and J. L. Stoyenoff. 1992. Intra- and interclonal variation in gypsy moth larval performance on bigtooth and trembling aspen. *Can. J. For. Res.* 22: 1676–1683.
- Crawley, M. J. and M. Akhteruzzaman. 1988. Individual variation in the phenology of oak trees and its consequences for herbivorous insects. *Func. Ecol.* 2: 409–415.
- Dix, M. E., R. A. Cunningham and R. M. King. 1996. Evaluating spring cankerworm (Lepidoptera: Geometridae) preference for Siberian elm clones. *Environ. Entomol.* 25: 58–62.
- Eggen, D. A. and L. P. Abrahamson. 1983. Estimating gypsy moth egg mass densities. State University of New York, Syracuse, Sch. of Forestry Misc. Publ. No. 1, ESF 83-002.
- Feeny, P. 1976. Plant apparency and chemical defense, pp. 1–40. *In: J. W. Wallace and R. L. Mansell (eds.), Recent advances in phytochemistry*, vol. 10: Biochemical interaction between plants and insects. Plenum Press, New York.
- Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51: 565–581.
- Fosberg, M. A. and M. Peterson. 1986. Modeling airborne transport of gypsy moth *Lymantria dispar* (Lepidoptera: Lymantriidae) larvae. *Agric. For. Meteorol.* 38: 1–8.
- Greenbank, D. O. 1956. The role of climate and dispersal in the initiation of outbreaks of the spruce budworm in New Brunswick. *Can. J. Zool.* 34: 453–476.
- Gross, P. and P. W. Price. 1988. Plant influences on parasitism of two leafminers: A test of enemy-free space. *Ecology* 69: 1506–1516.
- Hardin, J. W. 1979. Patterns of variation in foliar trichomes of eastern North American *Quercus*. *Amer. J. Bot.* 66: 576–585.
- Holliday, N. J. 1977. Population ecology of winter moth (*Operophtera brumata*) on apple in relation to larval dispersal and time of bud burst. *J. Appl. Ecol.* 14: 803–813.
- Hough, J. A. and D. Pimentel. 1978. Influence of host foliage on development, survival, and fecundity of the gypsy moth. *Environ. Entomol.* 7: 97–102.
- Hunter, A. F. and M. J. Lechowicz. 1992. Foliage quality changes during canopy development of some northern hardwood trees. *Oecologia* 89: 316–323.
- Johnson, H. B. 1975. Plant pubescence: An ecological perspective. *Bot. Rev.* 41: 233–258.
- Kanno, H. 1996. Role of leaf pubescence in soybean resistance to the false melon beetle, *Atrachya menetriesi* Faldermann (Coleoptera: Chrysomelidae). *Appl. Entomol. Zool.* 31: 597–603.
- Khan, Z. R., J. T. Ward and D. M. Norris. 1986. Role of trichomes in soybean *Glycine max* resistance to cabbage looper *Trichoplusia ni*. *Entomol. Exp. Appl.* 42: 109–118.
- Kolb, T. E. and D. A. J. Teulon. 1992. Effects of temperature during bud burst on pear thrips damage to sugar maple. *Can. J. For. Res.* 22: 1147–1150.
- Lance, D. R. 1983. Host-seeking behavior of the gypsy moth: The influence of polyphagy and highly apparent host plants, pp. 201–224. *In: S. Ahmad (ed.), Herbivorous insects: Host-seeking behavior and mechanisms*. Academic Press, New York.
- Lance, D. and P. Barbosa. 1981. Host tree influences on the dispersal of first instar gypsy moths, *Lymantria dispar* (L.). *Ecol. Entomol.* 6: 411–416.
- Larsson, S. and C. P. Ohmart. 1988. Leaf age and larval performance of the leaf beetle, *Paropsis atomaria*. *Ecol. Entomol.* 13: 19–24.
- Leonard, D. E. 1981. Bioecology of the gypsy moth, pp. 8–29. *In: C. C. Doane and M. L. McManus (eds.), The gypsy moth: Research toward integrated pest management*. Forest Service Tech. Bull. 1584, USDA, Washington, D. C.
- Leonard, D. E. 1967. Silking behavior of the gypsy moth, *Porthetria dispar*. *Can. Entomol.* 99: 1145–1149.
- Levin, D. A. 1973. The role of trichomes in plant defense. *Quart. Rev. Biol.* 48: 3–15.

- Martinat, P. J. and P. Barbosa. 1987. Relationship between host-plant acceptability and suitability in newly eclosed first-instar gypsy moths, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae). Ann. Entomol. Soc. Am. 80: 141-147.
- Mason, C. J. and M. L. McManus. 1981. Larval dispersal of the gypsy moth, pp. 161-202. In: C. C. Doane and M. L. McManus (eds.), The gypsy moth: Research toward integrated pest management. Forest Service Tech. Bull. 1584, USDA, Washington, D.C.
- McManus, M. L. 1973. The role of behavior in the dispersal of newly hatched gypsy moth larvae. USDA Forest Service, Res. Paper NE-267.
- Mitter, C., D. J. Futuyma, J. C. Schneider and J. D. Hare. 1979. Genetic variation and host plant relationships in a parthenogenetic moth. Evolution 33: 777-790.
- Naidoo, R. and M. J. Lechowicz. 1998. Foliage suitability of saplings grown under contrasting water regimes to the gypsy moth, *Lymantria dispar*. Can. Entomol. 130: 853-857.
- Oghiakhe, S. 1995. Effect of pubescence in cowpea resistance to the legume pod borer *Maruca testulalis* (Lepidoptera: Pyralidae). Crop Protec. 14: 379-387.
- Parry, D., J. R. Spence and W. J. A. Volney. 1998. Budbreak phenology and natural enemies mediate survival of first-instar forest tent caterpillar (Lepidoptera: Lasiocampidae). Environ. Entomol. 27: 1368-1374.
- Raupp, M. J., J. H. Werren and C. S. Sadof. 1988. Effects of short-term phenological changes in leaf suitability on the survivorship, growth and development of gypsy moth (Lepidoptera: Lymantriidae) larvae. Environ. Entomol. 17: 316-319.
- Raupp, M. J. and R. F. Denno. 1983. Leaf age as a predictor of herbivore abundance, pp. 91-124. In: R. F. Denno and M. S. McClure (eds.), Variable plants and herbivores in natural and managed systems. Academic Press, New York.
- SAS Institute. 1996. SAS System for Windows, ver. 6.12. SAS Institute, Cary, North Carolina.
- Schweitzer, D. F. 1979. Effects of foliage age on body weight and survival of larvae of the tribe Lithophanini (Lepidoptera: Noctuidae). Oikos 32: 403-408.
- Stanton, M. L. 1983. Spatial patterns in the plant community and their effects upon insect search, pp. 125-157. In: S. Ahmad (ed.), Herbivorous insects: Host-seeking behavior and mechanisms. Academic Press, New York.
- Stoyenoff, J. L., J. A. Witter and M. E. Montgomery. 1994a. Gypsy moth (Lepidoptera: Lymantriidae) performance in relation to egg hatch and feeding initiation times. Environ. Entomol. 23: 1450-1458.
- Stoyenoff, J. L., J. A. Witter and M. E. Montgomery. 1994b. Nutritional indices in the gypsy moth (*Lymantria dispar* (L.)) under field conditions and host switching situations. Oecologia 97: 158-170.
- Stoyenoff, J. L., J. A. Witter, M. E. Montgomery and C. A. Chilcote. 1994c. Effects of host switching on gypsy moth (*Lymantria dispar* (L.)) under field conditions. Oecologia 97: 143-157.
- Taylor, R. A. J. and D. Relling. 1986. Density-height profile and long-range dispersal of first-instar gypsy moth *Lymantria dispar* (Lepidoptera: Lymantriidae). Environ. Entomol. 15: 431-435.
- Ticehurst, M. and W. Yendol. 1989. Distribution and abundance of early instar gypsy moth (Lepidoptera: Lymantriidae) in forests during day and night. Environ. Entomol. 18: 459-464.
- Valentine, H. T. 1983. Budbreak and leaf growth functions for modeling herbivory in some gypsy moth hosts. For. Sci. 29: 607-617.
- van der Linde, V. R. J. 1971. The sailing flight of the gypsy moth (*Lymantria dispar* L.) and the effect of the food plant on this phenomenon. Z. Ang. Entomol. 67: 316-324.
- Weseloh, R. M. 1998. Modeling the influence of forest characteristics and ant (Formicidae: Hymenoptera) predation on dispersal and survival of neonate gypsy moths (Lymantriidae: Lepidoptera). Environ. Entomol. 27: 288-296.
- Witter, J. A. and L. A. Waisanen. 1978. The effect of differential flushing times among

- trembling aspen clones on tortricid caterpillar populations. *Environ. Entomol.* 7: 139–143.
- Wright, M. G. and J. H. Giliomee. 1992. Insect herbivory and putative defence mechanisms of *Protea magnifica* and *Protea laurifolia* Proteaceae. *Afr. J. Ecol.* 30: 157–168.
- Zlotina, M. A., V. C. Mastro, J. S. Elkinton and D. E. Leonard. 1999. Dispersal tendencies of neonate larvae of *Lymantria mathura* and the Asian form of *Lymantria dispar* (Lepidoptera: Lymantriidae). *Environ. Entomol.* 28: 240–245.
- Zvereva, E. L., M. V. Kozlov and P. Niemela. 1998. Effects of leaf pubescence in *Salix borealis* on host-plant choice and feeding behaviour of the leaf beetle, *Melasoma lapponica*. *Entomol. Exp. Appl.* 89: 297–303.