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Effects of winter temperatures on gypsy moth egg masses in the Great Lakes region of the United States

J.A. Andresen^{a,*}, D.G. McCullough^b, B.E. Potter^c,
C.N. Koller^b, L.S. Bauer^c, D.P. Lusch^a, C.W. Ramm^d

^a Department of Geography, Michigan State University, Room 315, National Science Building, East Lansing, MI 48824, USA

^b Department of Entomology, Michigan State University, Room 241, National Science Building, East Lansing, MI 48824, USA

^c USDA Forest Service, North Central Research Station, 1407 S. Harrison Road, Suite 220, East Lansing, MI 48823, USA

^d Department of Forestry, Michigan State University, Room 315, National Science Building, East Lansing, MI 48824, USA

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Abstract

Accurate prediction of winter survival of gypsy moth (*Lymantria dispar* L.) eggs and phenology of egg hatch in spring are strongly dependent on temperature and are critical aspects of gypsy moth management programs. We monitored internal temperatures of egg masses at three heights aboveground level and at the four cardinal aspects on oak tree stems at two different locations in Michigan during the winter seasons of 1997/1998, 1998/1999 and 1999/2000. Effects of aspect were more strongly associated with observed egg mass temperatures than height above the ground surface. Instantaneous differences between egg mass temperatures on sunny days were as high as 30 °C greater on the southern aspect vs. egg mass temperatures on other aspects, resulting in substantial differences in pre-hatch growing degree accumulations for egg masses on a single tree. Egg masses on southern and western aspects, where solar loading and temperatures were greatest, experienced substantial mortality. Mean survival of eggs averaged across the three seasons was less than 25% on southern and western aspects, compared with averages of 53 and 73% on eastern and northern aspects, respectively. Linear regression of mean monthly egg mass–air temperature differences (between north and south aspects) and mean daily solar flux density resulted in slope coefficient estimates of 0.13 and 0.21 °C MJ m⁻², and correlation coefficients of 0.81 and 0.82 at the two field locations, respectively. Using a simple egg mass hatch phenological model, such dissimilarities in temperature and growing degree day accumulation resulted in differences in estimated egg hatch dates of up to 25 days. Snow cover moderated egg mass temperature, with extreme seasonal minimum winter temperatures under snow cover as much as 7.1 °C warmer than those without snow cover. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

Gypsy moth (*Lymantria dispar* L.) is an important defoliator of oak (*Quercus* spp.), aspen (*Populus*

spp.) and at least 300 other species of forest and shade trees in North America (Elkinton and Leibhold, 1990; Martinat and Barbosa, 1987; Mosher, 1915). This exotic insect pest was introduced from Europe into Massachusetts in 1869 (Montgomery and Wallner, 1988). Despite intensive eradication efforts, populations have continued to expand and are now established as far west as Wisconsin, as far south as

* Corresponding author. Tel.: +1-517-355-0231x107;

fax: +1-517-432-1076.

E-mail address: andresen@msu.edu (J.A. Andresen).

North Carolina, and in areas of Ontario and Quebec (CFIA, 2001; NAPIS, 2001). Gypsy moth larvae feed on tree foliage for roughly 6 weeks in early summer, pupate and adult moths emerge about 10 days later. Each female moth lays a single egg mass on the stem or branches of the host tree or on other nearby objects. Egg masses typically range in size from 4 to 7 cm long, contain 500 to over 1200 eggs and are covered with fine hair from the female's body. Egg masses remain in place for 8–9 months until hatching occurs the following spring.

Counts of egg masses from surveys conducted in autumn are used to identify areas likely to sustain heavy defoliation in the following year and to delineate areas for treatment in suppression programs, typically with the microbial insecticide Btk (*Bacillus thuringiensis* var. *kurstaki*). Between 27 300 and 615 000 ha have been treated with Btk for gypsy moth suppression in the US annually since 1985, with costs ranging from \$ 4.9 million to \$ 22.5 million per year (GMDigest, 2001). Survival of gypsy moth eggs during the winter is a critical factor in accurately predicting the severity and distribution of defoliation. This is particularly a concern in the Great Lakes region of the US where gypsy moth populations are relatively new and climatic conditions can be extreme. Understanding the relationship between weather variables and egg survival is needed to prevent over-spraying and the unnecessary economic and environmental costs that occur if egg mortality is high.

Past studies have examined the links between gypsy moth egg mortality and various environmental factors in laboratory settings where the lethal temperature level ranged from -20 to -29°C (Gray et al., 1991; Waggoner, 1985; Sullivan and Wallace, 1972). Other studies have attempted to correlate changes in gypsy moth density with various winter weather variables (Leonard, 1972; Madrid and Stewart, 1981; Smitley et al., 1998; Summers, 1922) or tested simulation models to predict gypsy moth phenology (Gray et al., 1995; Waggoner, 1984). However, results have not always been consistent. For example, in laboratory tests, Sullivan and Wallace (1972) determined that even after acclimation, uncovered eggs died if air temperatures remained below -30°C for 2 days, but eggs protected by snow cover survived until air temperatures dropped to -80°C . Conversely, field studies suggested that in some cases, egg survival was

greater for egg masses that were laid above the snow line (Leonard, 1972; Madrid and Stewart, 1981). In Ontario, survival of egg masses was greater when they were near the ground and presumably protected by snow cover (Nealis et al., 1999). Higashiura (1989), however, found that snow cover enhanced egg survival only when bird predation of eggs was heavy. Sharov et al. (1999) found that winter temperatures had little effect on the rate of spread of gypsy moth populations through northern Michigan. Weather patterns in autumn before egg diapause or in spring during post-diapause stages may also affect egg survival (Gray et al., 1991; Williams and Leibhold, 1995).

Timing of egg hatch is also a special concern for managers of gypsy moth suppression programs. To be effective, Btk must be applied after larvae hatch and the beginning of feeding but before larval development progresses beyond the instar second stage (Reardon et al., 1994). Process phenological simulation models such as GMPHEN (Sheehan, 1992) are used to predict egg hatch and larval development based on accumulated degree days. However, while most gypsy moth managers recognize that microscale climatic and phenological variability exists, there have been few efforts to assess the source or magnitude of this variability or to incorporate such variability into phenological predictions.

Seasonality of vegetation and varying radiative and turbulent fluxes are known to influence microclimatic variability in forests. Wooded areas experience relatively cooler daytime and warmer nighttime air temperatures than open areas because of reductions in incident solar and outgoing long wave radiation, and reduced wind and forced convective heat exchange (Gieger, 1965). The impact of these radiative changes on surface energy balance can be significant. For example, Stoutjesdijk (1977) estimated a net radiative gain of $42\text{--}63\text{ W m}^{-2}$ on a south-facing stand of *Pinus sylvestris* vs. an open field in a wintertime experiment in the Netherlands. In a deciduous forest, distinct seasonal partitioning of sensible and latent heat fluxes occurs, with greatest sensible flux observed in late winter and early spring just before leaf emergence (Fitzjarrald et al., 2001; Wilson and Baldocchi, 2000). Differences in radiative fluxes may in turn lead to significant differences in overall air temperature variability and diurnal temperature range for forested vs. non-forested surfaces (Carlson and Groot, 1997; Chen

et al., 1999; Johnson et al., 1975; Morecroft et al., 1998; Xia et al., 1999). In addition, surface temperatures of various species of forest vegetation, where most gypsy moth egg masses are laid, may differ significantly from ambient air temperature. Mid-day temperatures differed by as much as 20 °C in December between the southern and northern aspects of a 13.5 cm diameter kalopanax (*Kalopanax septemlobus*) tree in Japan and differences were directly associated with levels of incident solar radiation (Sakai, 1966). Similarly, daytime differences in radiative loading due to aspect were directly related to elevated temperatures (relative to air temperatures) in the cambium tissue of lodgepole pine (*P. contorta*) and aspen (*Populus tremuloides*) during the fall and winter months (Derby and Gates, 1966), phloem temperatures of lodgepole pine (Bolstad et al., 1997), wintertime surface temperatures of ant hills and basking reptiles (Stoutjesdijk, 1977), and within spherical insect galls on goldenrod (*Solidago* spp.) during winter days (Layne, 1993).

Given the potential importance of weather and climate in determining the rate of egg mass mortality and egg hatch phenology, and evidence of its variability on small spatial scales, we conducted a study to monitor temperature of gypsy moth egg masses placed at selected locations on trees in two locations in Michigan during three winter seasons. Our objectives were to determine the influence of aspect and height on temperatures experienced by over-wintering egg masses and relate temperatures to egg survival and timing of hatch in spring.

2. Materials and methods

This experiment was conducted at two sites in the Lower Peninsula of Michigan over three winter seasons: 1997/1998, 1998/1999 and 1999/2000. One site was in southwestern Lower Michigan at Michigan State University's W.K. Kellogg Forest near Augusta, MI (hereafter 'KF') in Kalamazoo County (42°21'40"N, 85°21'00"W, elevation 260 m). The second site was in a private woodlot near Roscommon, MI (hereafter 'ROS') in north central Lower Michigan (44°29'50"N, 84°41'42"W, elevation 357 m). The sites are approximately 250 km apart. The KF site was located within a 80-year-old mixed oak shelterwood dominated by white oak (*Quercus alba*) and

northern red oak (*Q. rubra*) with a minor component of black oak (*Q. velutina*) and hickory (*Carya ovata*). Height of dominant/co-dominant trees in the stand was roughly 28 m, mean tree diameter was 56 cm and basal area was 13.5 m²/ha. Understory vegetation was dominated by *Rubus* spp. and multiflora rose (*Rosa* spp.), along with *Viburnum* spp., *Cornus florida*, *C. rasemosa*, *Sassafras albidum*, and *Viburnum* spp. The ROS site was located within a 65-year-old second growth stand that was dominated by white oak, northern red oak, with scattered northern pin oak (*Q. ellipsoidalis*), black oak and oak hybrids. Dominant/co-dominant tree height was 19.8 m, mean diameter was 24.2 cm and basal area was 19.5 m²/ha. Major understory species at ROS included lowbush blueberry (*Vaccinium* spp.), bracken fern (*Pteridium aquilinum*), sweetfern (*Comptonia peregrina*), witch hazel (*Hamamelis virginiana*), white pine (*P. strobus*) and red maple (*Acer rubrum*) seedlings. Climatologically, mean winter (December–February) temperatures and frequency of minimum daily temperatures below –18 °C (days per winter season) at the two sites range from –7.4 °C and 22.1 at ROS to –3.8 °C and 9.1 at KF, respectively (Eichenlaub et al., 1990). Both sites are located in areas of the region frequented by lake effect precipitation (much of it snowfall) during the autumn and winter seasons.

White oak trees, a preferred host of gypsy moth (Mosher, 1915; Martinat and Barbosa, 1987), were selected at both sites for over-winter deployment of the egg masses. At the KF site, we selected a dominant tree, 65 cm in diameter at breast height (1.2 m aboveground). Trees at the ROS site were relatively smaller, and so we selected two adjacent stems (arising originally as stump sprouts), each 28 cm in diameter at breast height, that were separated by 1.2 m at breast height. Lower branches of the selected oaks at KF and ROS were at least 3.5 m aboveground.

In August of each of the three seasons, approximately 1000 freshly laid egg masses were obtained from gypsy moth female adults which were reared and mated in our laboratory. In 1997, gypsy moths were obtained from the USDA Animal and Plant Health Inspection Service, Otis Laboratory (Otis Angora Air Force Base, MA) and in 1998 and 1999, we obtained healthy pupae from wild populations in Michigan. Egg masses were laid on kraft paper backing, which was carefully trimmed to match the shape of each

egg mass. Egg masses were placed in individual $3.8 \times 5 \text{ cm}^2$ pouches fashioned from 20×20 mesh Lumite[®] insect screening to protect eggs from birds and other predators. The enclosed egg masses were placed on the oak trees in early September each year, using 0.5 mm nylon filament that was threaded through the mesh pouches and wrapped around the tree trunk. At the KF site, egg masses were placed in a rectangular 4×8 grid array immediately adjacent to one another at 12 separate locations on the tree trunk: north, south, east and west aspects at heights of 0, 1 and 2 m above-ground level. The procedure was repeated at the ROS site, except smaller 3×6 egg mass arrays were placed on both of the selected adjacent stems. Egg masses remained undisturbed on the trees until the following April, when they were retrieved and returned to the laboratory. Length and width of each egg masses were measured, with three-season average dimensions of 3.6 cm length (0.7 cm standard error of the mean, hereafter s.e.m.) and 1.9 cm wide (0.3 cm s.e.m.). Microscopic examination of all eggs in each egg mass was extremely labor-intensive, so subsamples of eggs from the centers of the egg masses were collected using a No. 7 cork borer. Each subsample typically contained 250–350 eggs. The egg mass subsamples were placed individually into sealed, ventilated Petri dishes and reared in a growth chamber at 24 °C and 60% relative humidity until hatching was completed. Once hatching was completed, larvae were counted and egg masses were dehaired. Eggs were examined under a microscope to quantify parasitized eggs. Parasitism was uniformly low (<1%) in all cases and parasitized eggs were excluded from analyses reported here.

Egg mass temperatures were monitored at both sites with 0.254 mm type E chromel–constantan thermocouples (Omega Engineering, Stamford, CT) inserted into the middle of the egg masses. Temperatures were taken within two separate egg masses at each combination of aspect and height on the experimental trees. Individual thermocouples were also placed in additional “control” egg masses that were not enclosed in the screen pouches and affixed to the bark of the trees at northern and southern exposures to determine any microclimatic influences introduced by the pouches. The thermocouples were monitored by Campbell Scientific, CR10 dataloggers and 16-channel AM416 multiplexers (Campbell Scientific, Logan, UT). Weather instruments monitoring air

temperature and relative humidity (model HMP35C, Vaisala, Woburn, MA), wind speed and direction at 1.5 m height (model 30001, R.M. Young, Traverse City, MI), and total incoming solar and net radiation (model Q6, Radiation Energy Balance Systems, Bellevue, WA) were deployed at the two sites at a 1.5 m height within 3 m of the experimental trees. Sampling frequency of all meteorological data was 60 s with output data averaged over 30 min intervals. Daily measurements of 1.5 m maximum and minimum air temperature, snowfall, and snow depth from reference climatological sites at Gull Lake, MI (3.0 km NW of the KF site) and Houghton Lake, MI (15.1 km SW of the ROS site) were obtained for comparison from the NOAA Climatological Summary of the Day (NOAA, 1997–2001). All sensors used in the experiment were sent out for factory recalibration prior to deployment each season.

3. Results and discussion

Winter conditions during each of the three seasons were unusually mild, with mean monthly air temperatures at nearby reporting stations ranging from 1 to 6 °C above normal and extreme minimum temperatures remaining several degrees above climatological norms (Table 1). Seasonal precipitation and snowfall totals were consistently below normal at the ROS site and in all but one season at the KF site (1997/1998). The number of days with 2.5 cm or more snow cover varied from 70, 55 and 50 days at KF to 97, 89 and 84 days at ROS for the 1997/1998, 1998/1999 and 1999/2000 seasons, respectively. Extreme minimum temperatures at both KF and ROS were above normal in all three seasons and remained above the -29 °C threshold at which winter egg mortality is thought to begin to occur (Giese, 1981; Waggoner, 1985).

The mesh pouches that enclosed the egg masses had negligible effects on temperatures within the egg masses. Mean differences (defined as the enclosed minus the non-enclosed egg mass temperature) for the 30 min readings varied from -0.2 °C at the southern aspect during the month of October to 0.0 °C during December and January. Mean differences were generally negative at the northern aspect and positive at the southern aspect, with a net tendency for the egg masses in the mesh enclosure to be slightly cooler

Table 1

Monthly and seasonal climatological observations and departures from normal for Gull Lake, MI (3 km NW of the KF site) and Houghton Lake (15 km SW of ROS site), 1997/1998, 1998/1999 and 1999/2000 seasons

	Season					
	1997/1998		1998/1999		1999/2000	
	Observation (°C)	Departure (°C)	Observation (°C)	Departure (°C)	Observation (°C)	Departure (°C)
Gull Lake, MI (KF)						
October	11.6	+0.2	13.1	+1.7	11.7	+0.3
November	3.2	-1.7	7.0	+2.2	8.3	+3.5
December	0.1	+2.2	2.2	+4.3	-0.3	+1.8
January	-0.2	+5.0	-4.6	+0.6	-3.5	+1.7
February	2.6	+6.5	1.1	+5.0	1.6	+5.6
March	3.9	+1.9	2.1	+0.1	7.2	+5.2
Ex. min. October–March temperature (°C)	-16.1	+8.4	-23.9	+0.6	-20.6	+3.9
Total October–March precipitation (mm)	416.1	+41.7	358.1	-16.3	326.4	-48.0
Total October–March snowfall (cm)	125.2	-26.9	114.8	-37.3	103.6	-48.5
Houghton Lake, MI (ROS)						
October	7.9	0.0	9.4	+1.4	7.3	-0.7
November	0.3	-1.5	3.4	+1.6	4.4	+2.6
December	-2.0	+2.8	-1.7	+3.1	-3.1	+1.8
January	-4.2	+3.9	-8.1	+0.1	-7.8	+0.4
February	-0.9	+6.6	-3.2	+4.3	-3.8	+3.7
March	-0.3	+1.6	-1.4	+0.5	3.5	+5.4
Ex. min. October–March temperature (°C)	-22.8	+5.9	-23.9	+4.8	-26.1	+2.6
Total October–March precipitation (mm)	254.0	-61.5	282.5	-33.0	202.7	-112.8
Total October–March snowfall (cm)	181.9	-58.7	179.6	-61.0	80.8	-159.8

than non-enclosed egg masses. Mean absolute differences between the enclosed and non-enclosed were less for the northern aspect, ranging from 0.1 °C in December and January to 0.2 °C during the months of October, February and March. Mean absolute differences for the south aspect ranged from 0.3 °C in January to 0.5 °C in October. For all months, the mean and mean absolute errors were less than the 1.0 °C maximum error design specifications associated with the thermocouples and the thermocouple wires. Temperature differences were also examined between the two sample locations at each height/aspect combination. Thirty-minute absolute mean differences were generally less than 0.5 °C at both field sites, but occasionally reached 5 °C or more when radiative loading on the two samples was dissimilar, most likely due to the presence of sun flecks or other differences in shading. For the remainder of the results presented here, we consider readings at each height/aspect combination as averages from the two individual samples.

3.1. Effects of aspect and height

Overall, mean egg mass temperatures were warmer than mean air temperatures for the same time period for all aspects and heights and at both sites during the October–March season in all 3 years (Table 2). Mean differences between mean egg mass and air temperature were slightly greater at the KF site than the ROS site, with height × aspect combination differences ranging from 0.0 to 2.9 °C at KF and 0.1 to 2.3 °C at ROS. Mean temperatures during the 1999/2000 season were relatively cooler than the other two seasons due to an abbreviated data set associated with a computer malfunction and the loss of egg mass temperature data from the KF site prior to 18 November 1999 and from the ROS site prior to 7 January 2000. Greatest overall differences between egg mass and air temperatures occurred in the (abbreviated) 1999/2000 season.

Standard deviations of the 30 min instantaneous temperatures (Table 2), a measure of temperature

Table 2

Seasonal (October–March) mean temperatures (°C) and standard deviations (numbers in parentheses) of 30 min temperatures by year, height and aspect at KF and ROS field sites

Aspect	KF height (cm)			ROS height (cm)		
	0	100	200	0	100	200
1997/1998						
North	2.6 (6.6)	2.6 (6.7)	2.8 (6.8)	0.3 (6.1)	0.4 (6.4)	0.5 (6.5)
East	3.0 (6.9)	3.0 (7.0)	3.1 (7.1)	0.6 (6.4)	0.7 (6.6)	0.8 (6.6)
South	4.1 (8.5)	3.7 (7.9)	3.9 (8.1)	1.3 (7.2)	1.5 (7.4)	1.4 (7.5)
West	3.5 (7.2)	3.3 (7.4)	3.3 (7.5)	0.8 (6.7)	0.9 (6.8)	0.8 (6.8)
Air ^a		2.6 (6.9)			0.2 (6.8)	
1998/1999						
North	4.3 (6.4)	2.7 (7.8)	2.6 (8.0)	0.6 (6.9)	0.4 (7.6)	0.5 (7.6)
East	3.4 (6.9)	3.1 (8.1)	3.0 (8.2)	1.0 (7.9)	1.0 (7.9)	1.0 (7.9)
South	5.2 (9.0)	4.6 (9.8)	4.3 (9.5)	2.1 (7.8)	2.0 (8.9)	1.8 (8.6)
West	4.3 (7.7)	3.6 (8.9)	3.6 (9.1)	1.3 (7.9)	1.0 (8.5)	1.1 (8.2)
Air		2.3 (8.3)			0.0 (8.0)	
1999/2000 ^b						
North	0.3 (5.8)	0.2 (6.8)	0.3 (6.9)	-2.1 (7.1)	-1.9 (7.8)	-2.0 (7.8)
East	0.8 (6.2)	0.5 (7.1)	0.7 (7.1)	-1.0 (7.7)	-1.2 (8.6)	-1.1 (8.3)
South	2.2 (8.5)	1.7 (8.1)	1.5 (7.6)	-0.1 (8.6)	-0.2 (9.6)	-0.4 (9.5)
West	1.4 (6.4)	0.7 (7.2)	0.8 (7.3)	-1.3 (8.2)	-1.4 (8.6)	-1.6 (8.3)
Air		0.1 (7.5)			-2.4 (8.0)	

^a Air temperatures were taken at a height of 150 cm.

^b During the 1999/2000 season, data were not available prior to 18 November at the KF site and prior to 7 January at the ROS site.

variability, were consistently highest at southern and western aspects and least at the northern aspects across all heights at both sites, which is not surprising given the highest observed temperatures on southern and western egg masses. Values at individual height × aspect combinations generally ranged from 6.0 to 9.0 °C, with a range from 5.8 °C at the 0 cm height north aspect egg mass at KF to 9.8 °C at the 100 cm southern aspect at the KF site. Variability tended to be greater at the KF site vs. the ROS site, except during the 1999/2000 season, in which the data series at ROS was significantly shorter than that at the KF site and the 1997/1998 and 1998/1999 seasons.

The effect of aspect and resulting influence of incident solar radiation is readily apparent, with warmest temperatures during all three seasons occurring at southern exposures, followed by western, eastern and northern aspects. The link between solar radiation intensity and egg mass–air temperature differences is illustrated at the 100 cm height for mean differences at each aspect by month in Table 3. Observed mean daily solar flux densities taken at a 1.5 m level within

3 m of the trees are listed for comparison. The differences are generally positive, especially during the late fall and early spring months, and were slightly greater at ROS than at the KF site. The magnitude of the differences was generally greatest at the southern aspect (up to 4.4 °C at ROS during March 1999) and least at the northern aspect (0.0 °C at both sites during several months). The magnitude of the difference was seasonally dependent and positively correlated with total solar flux density. A simple linear regression of mean monthly egg mass–air temperature differences (between north and south aspects) and mean daily solar flux density resulted in slope coefficient estimates of 0.13 and 0.21 °C MJ m⁻² and correlation coefficients of 0.81 and 0.82 at KF and ROS, respectively (statistically significant at $P < 0.001$).

The influence of height above the ground surface on egg mass temperatures was relatively minor. There was a tendency for egg mass temperatures at the lowest level (0 cm) at the KF site to be warmer than egg mass temperatures at 100 cm (nine of 12 height/aspect combinations) and 200 cm (nine of 12 height/aspect

Table 3

Mean monthly egg mass–air temperature differences ($^{\circ}\text{C}$) by year and aspect at 100 cm height and mean total daily solar flux density (denoted as ‘SR’ in MJ m^{-2}) at KF and ROS field sites

Aspect	KF						ROS					
	October	November	December	January	February	March	October	November	December	January	February	March
1997/1998												
North	0.1	0.1	0.0	0.2	−0.4	0.2	0.3	0.1	0.2	0.5	0.3	0.6
East	0.9	0.3	0.3	0.3	0.0	0.9	0.5	0.2	0.1	0.4	1.0	1.6
South	2.2	1.1	1.0	0.4	0.7	1.5	1.1	0.5	0.5	0.5	1.8	2.7
West	1.0	0.4	0.6	0.6	0.6	1.2	0.5	0.2	0.5	0.8	0.5	0.9
SR	6.1	2.6	2.5	2.4	5.2	7.7	4.2	1.9	1.9	0.8	3.9	6.7
1998/1999												
North	0.7	−0.1	0.1	0.2	0.4	0.5	0.4	0.0	−0.1	0.9	0.6	1.1
East	1.1	0.3	0.4	0.5	0.7	1.5	0.8	0.2	0.2	1.2	1.2	2.6
South	2.2	1.8	1.9	1.8	2.1	3.9	1.5	0.7	1.2	2.0	2.3	4.4
West	1.6	0.8	0.8	1.0	1.1	2.3	0.8	0.2	0.3	1.2	1.1	2.5
SR	6.2	1.5	4.2	3.3	6.9	12.4	4.5	2.7	2.2	1.1	4.2	9.2
1999/2000												
North	^a	−0.1	0.1	0.2	0.1	0.2	^a	^a	^a	0.3	0.3	0.7
East	^a	0.1	0.3	0.5	0.5	0.9	^a	^a	^a	0.7	0.9	2.0
South	^a	0.7	1.2	1.8	1.8	2.7	^a	^a	^a	1.7	1.7	3.2
West	^a	0.0	0.5	0.8	0.9	1.2	^a	^a	^a	0.6	0.7	1.6
SR		3.4	2.8	2.4	5.7	9.6				1.8	3.4	8.6

^a During the 1999/2000 season, data were not available prior to 18 November at the KF site and prior to 7 January at the ROS site.

combinations), while no trends were apparent at the ROS site. Differences between 100 and 200 cm temperatures at both sites were small and variable in sign. This may be a result of the 0 cm height egg masses being attached on the buttresses of the trees, with solar radiation striking at a more direct angle. It may also have been due to the temperature-moderating effect of occasional snow cover at the 0 cm level. None of the differences between monthly means grouped by height were found to be statistically significant at the $P = 0.05$ level.

3.2. Diurnal patterns

Diurnal differences in solar loading and the variable effects of canopy shading on the tree trunks led to large instantaneous differences between egg mass temperatures at different aspects and between egg masses and ambient air temperature. Thus, while overall mean air and egg mass temperatures were within a few degree Celsius of one another (Table 2), diurnal temperature patterns for a given day were frequently quite dissimilar, especially for eastern,

southern and western aspects during daylight hours. When averaged diurnally across the 6-month October–March period at KF and ROS sites, egg mass temperatures at the east, south, west and north aspects and ambient air temperature peaked at times of 13:30, 13:30, 15:00, 13:30 and 15:00 LST, respectively. A secondary average diurnal maximum was present for the east aspect at 10:30 LST, which was associated with greater incident levels of solar radiation at that time. Average diurnal minimum temperatures for both sites at all aspects and for the air occurred at 7:00 LST.

An example of egg mass temperatures at differing aspects at the 100 cm height on a clear, relatively calm day at the ROS site is given in Fig. 1. For the dark and twilight hours of the 24 h period, egg mass temperatures are generally within 2°C of the air temperatures. During the daylight hours between 08:00 and 18:50 LST, however, egg mass temperatures diverge rapidly, beginning with the eastern and southern aspects between 09:00 and 12:00 LST and between 13:00 and 18:00 LST on the western aspect. Maximum diurnal temperatures of 4.0°C at the eastern aspect and

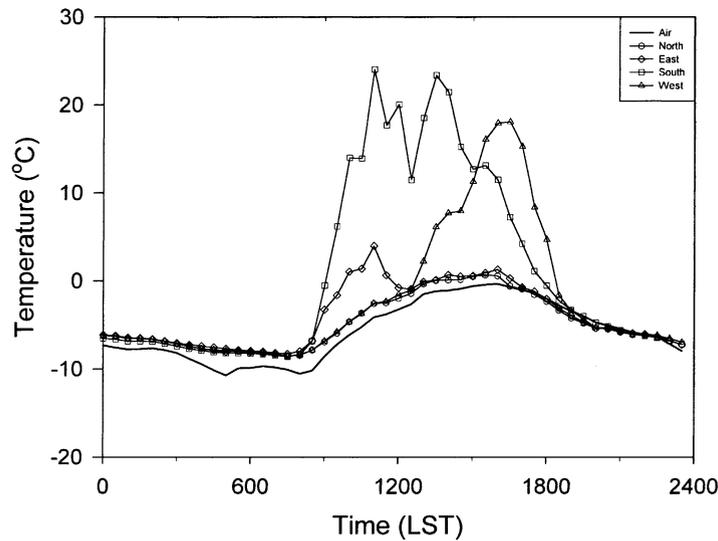


Fig. 1. Thirty-minute 100 cm egg mass temperatures at various aspects and 150 cm air temperatures ($^{\circ}\text{C}$) on a sunny day, ROS site, 9 December 1998.

24.1°C at the southern aspect are reached at 11:00 LST, followed by 0.7 and 18.1°C at northern and western aspects, respectively. Because they occurred at the same time each day, we believe the relatively early time of maximum temperature and sharp drop of the southern aspect egg temperature between 11:00 and 13:00 LST are due to shading by large tree limbs to the south of the instrumented oak tree. Similar to the nighttime pattern, egg mass temperatures on the northern aspect (and the eastern and western aspects when not exposed to incident solar radiation) closely follow the air temperatures. The patterns and magnitude of the differences between egg mass and air temperature we recorded are consistent with patterns observed by Derby and Gates (1966) in the cambium tissue of lodgepole pine and aspen during the fall and winter months, as well as temperatures of vegetative and non-vegetative surfaces in a pine forest warmed by exposure to direct sunshine (Stoutjesdijk, 1977). The magnitude of the warming under relatively high levels of incident solar radiation (greater than 400 W m^{-2} on a horizontal surface) at both sites was striking, with egg mass temperatures sometimes reaching levels above 50°C (30°C greater than ambient air temperatures) on southern and western aspects (data not shown).

3.3. Effect of snow cover

The presence of snow cover may have a significant moderating influence on surface or near surface temperatures due to its insulating properties which are the result of trapped air of relatively low thermal conductivity within the snow matrix and from the high reflectance of incident radiation on a snow-covered surface. An illustration of this moderating influence is given in Fig. 2, which depicts egg mass temperatures at north and south aspects at the 0 and 100 cm levels during a 48 h period at the ROS site on 10 and 11 January 1999. During this period, a cold frontal passage occurred at the site during the middle of the day on 10 January 1999 with light to occasionally moderate snow showers resulting in accumulations of 5 cm from 18:00 to 24:00 LST on 10 January 1999. A trace amount of snowfall was recorded on 11 January 1999. Snow depth at the site was 25 cm at 08:00 LST on the morning of 10 January 1999 and 30 cm at 08:00 LST on the morning of 11 January 1999. Average winds at the site were in excess of 1 m s^{-1} on 10 January 1999, decreasing to $0.5\text{--}0.75\text{ m s}^{-1}$ on 11 January 1999. Skies during the period were generally cloudy, with the exception of the afternoon of 10 January 1999, when the clouds broke briefly and led to a temporary

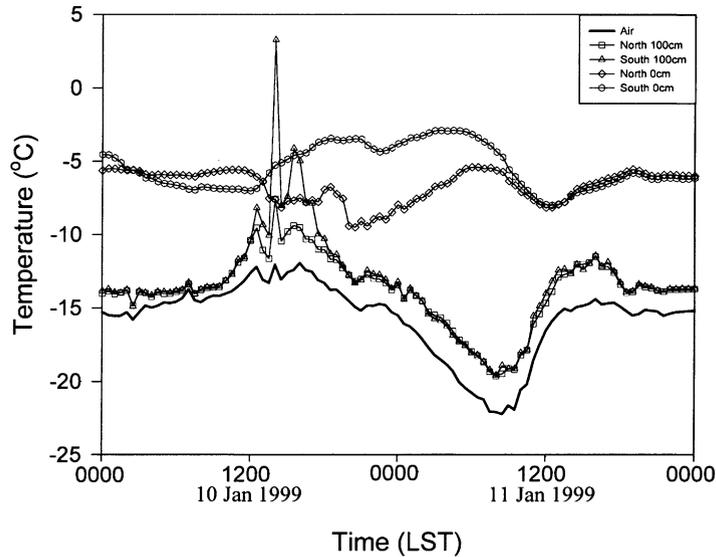


Fig. 2. Thirty-minute egg mass and air temperatures at north and south aspects at 0 and 100 cm heights, ROS site, 12:00 LST 10 January 1999 to 12:00 LST 12 January 1999.

increase of solar radiation flux (horizontal surface) from less than 50 W m^{-2} at 11:00 LST to 200 W m^{-2} at 12:30 LST. Rapid temperature increases associated with the increases in solar flux were recorded at both of the 100 cm height egg masses (up to 15°C) and for the air temperature, but not at the southern aspect at 0 cm under the snow cover. There was a minor 1°C increase in temperature at the northern aspect at 0 cm approximately 3 h after the last air temperature peak. Egg mass temperature differences between the 0 cm north and south aspects on 10 January 1999 are likely due to cavitation of the snow on the northern and western side of the tree resulting in a slightly lesser snow cover above the northern aspect egg masses. These differences were reduced with the new snowfall late in the day. The damping effect of the snow cover on 0 cm temperatures can be seen in the temperature traces on 11 January 1999. The diurnal temperature increase for the 0 cm egg masses during the daytime hours on 11 January 1999 is approximately 2.5°C , which lags approximately 4 h behind the 8.1°C increase at 100 cm height.

One major objective of this study was to observe the magnitude and frequency of extreme cold temperature events inside an over-wintering gypsy moth egg mass, which can be directly influenced by snow cover (Gray et al., 1991; Nealis et al., 1999; Sullivan and Wallace,

1972; Waggoner, 1985). Because winter temperatures during the three seasons were abnormally mild, however, we did not observe instantaneous air or egg mass temperatures below the -29°C temperature threshold at which high rates of egg mortality is thought to occur (Giese, 1981; Waggoner, 1985). The coldest egg mass temperature at the KF site was -24.0°C at 200 cm height and southern aspect during the 1998/1999 season and -21.8°C at the eastern and southern aspects at the ROS site during the 1999/2000 season (Table 4). Similar to the pattern with mean temperatures, egg mass extreme readings were generally $1\text{--}3^\circ\text{C}$ warmer than the air temperatures. In contrast, extreme minima at the 0 cm height during the 1998/1999 season were from 5.1 to 7.1°C and 2.0 to 5.3°C warmer than air and 100 and 200 cm egg mass temperatures at KF and ROS sites, respectively. Closer investigation of the data revealed 23 and 8 cm of snow cover at KF and ROS sites, respectively, coincident with the dates of extreme minimum temperature occurrence (14 January 1998 and 16 March 1998, respectively). This cover provided some insulation from the colder air temperatures that led to colder readings at the higher heights. Timewise, the majority of the extreme minima occurred during early morning hours. With little or no incoming solar radiation at these hours, there was

Table 4
Extreme minimum egg mass and air temperatures (°C) by year, aspect and height at KF and ROS field sites

Aspect	KF height (cm)			ROS height (cm)		
	0	100	200	0	100	200
1997/1998						
North	-15.9	-15.4	-15.1	-17.2	-17.9	-18.0
East	-14.9	-15.5	-15.0	-17.9	-18.0	-17.8
South	-14.5	-16.4	-15.6	-17.6	-17.7	-17.8
West	-12.9	-14.8	-15.1	-17.4	-17.7	-17.6
Air ^a		-16.2			-18.8	
1998/1999						
North	-18.0	-23.6	-23.4	-17.1	-19.7	-19.8
East	-19.2	-23.4	-23.1	-20.2	-19.6	-19.6
South	-17.6	-23.4	-24.0	-16.9	-19.7	-19.4
West	-19.6	-23.3	-23.9	-19.4	-20.4	-19.4
Air		-24.7			-22.2	
1999/2000 ^b						
North	-18.0	-19.8	-20.1	-20.3	-21.4	-21.1
East	-19.2	-19.8	-19.5	-19.3	-21.8	-21.3
South	-17.6	-19.1	-18.7	-19.3	-21.8	-21.6
West	-19.6	-20.0	-19.0	-19.7	-21.7	-21.4
Air		-19.4			-21.3	

^a Air temperatures were taken at a height of 150 cm.

^b During the 1999/2000 season, data were not available prior to 18 November at the KF site and prior to 7 January at the ROS site.

Table 5
Mean percentage (\pm s.e.m) of gypsy moth eggs that hatched by year, height and aspect at KF and ROS field sites

Aspect	KF height (cm)			ROS height (cm)		
	0	100	200	0	100	200
1997/1998 ^a						
North	68.7 \pm 4.1	81.9 \pm 7.6	74.4 \pm 9.7	82.4 \pm 4.2	81.6 \pm 4.8	64.1 \pm 9.2
East	19.1 \pm 9.1	66.2 \pm 10.2	84.3 \pm 5.5	53.8 \pm 12.0	79.9 \pm 5.3	75.9 \pm 3.0
South	0.0	27.8 \pm 10.9	43.3 \pm 9.2	3.8 \pm 3.4	34.8 \pm 10.4	41.7 \pm 10.4
West	8.1 \pm 5.7	62.9 \pm 7.7	62.1 \pm 8.5	42.8 \pm 11.2	72.3 \pm 7.6	82.7 \pm 4.2
1998/1999 ^a						
North	11.3 \pm 11.3	85.8 \pm 1.2	53.2 \pm 15.6	82.5 \pm 11.8	70.5 \pm 15.4	92.8 \pm 1.0
East	8.7 \pm 5.8	70.6 \pm 10.3	77.2 \pm 5.2	11.8 \pm 11.8	44.1 \pm 16.4	85.0 \pm 3.7
South	0.0	0.0	17.4 \pm 10.9	0.0	0.0	21.9 \pm 13.3
West	0.0	4.7 \pm 4.7	0.0	0.0	37.9 \pm 17.7	64.6 \pm 14.5
1999/2000 ^b						
North	73.8 ^c \pm 6.1/73.5 ^d \pm 6.3		77.8 \pm 4.6/64.0 \pm 10.6			
East	14.1 \pm 7.4/72.0 \pm 5.1		72.9 \pm 6.9/76.8 \pm 2.9			
South	0.0/20.9 \pm 12.8		11.3 \pm 4.6/72.9 \pm 7.7			
West	0.0/71.2 \pm 4.9		0.0/71.9 \pm 8.9			

^a Eight egg masses were deployed at each aspect \times height combination.

^b Fifteen egg masses were deployed at each aspect \times height combination in 1999/2000.

^c Mean percentage hatch (\pm S.E.) for egg masses exposed from 3 September 1999 to 4 November, 1999.

^d Mean percentage hatch (\pm S.E.) for egg masses exposed from 4 November 1999 until April 2000.

little evidence of any effect of aspect. This is in agreement with the observations of Blennow (1998), who found microclimatic variability of minimum temperatures at a 25 cm height aboveground level in forests to be more closely related to canopy skyview factor.

Overall, while snowfall during the three seasons of the project was below normal climatologically, its influence was still discernible in the magnitude of extreme minimum temperatures at both sites and in the monthly average egg mass temperatures during months when snow cover was present (Table 2). Thus, while limited in extent, there was some evidence suggesting snow cover can alter temperature patterns on a diurnal basis and moderate the effect of extreme low temperatures by several degrees.

3.4. Egg Survival

Mean egg mass hatch rates (expressed as sample percentage of egg masses brought in from the field and reared in a climate-controlled laboratory setting) for the three seasons are given in Table 5. During the last season, 1999/2000, egg hatch counts was quantified at the KF site only and only at heights of 0 and 200 cm. These egg masses were deployed in two

groups, the first deployed in early September and retrieved in early November, and the second batch deployed after removal of the first batch in November and then retrieved in early April.

Previous research in Ontario and in laboratory settings indicated that gypsy moth eggs protected by snow cover could withstand substantially colder temperatures than unprotected egg masses located higher on a tree (Nealis et al., 1999; Sullivan and Wallace, 1972). Contrary to our expectations, however, egg masses at the base of trees generally had the poorest survival and survival of eggs at both sites was profoundly influenced by the aspect of exposure.

In both 1997/1998 and 1998/1999, egg survival at the ROS site was associated with height on all but the northern aspect (Table 5). For example, when 1998/1999 ROS data from all aspects were combined, egg survival at the 200, 100 and 0 cm heights averaged 66.1% (± 6.7 s.e.m.), 38.1% (± 8.1 s.e.m.) and 23.6% (± 7.3 s.e.m.), respectively. Survival of eggs at the base of the trees was especially poor on the southern aspect, where less than 4% of eggs survived in 1997/1998 and no eggs survived in 1998/1999. Height of egg masses was perhaps even more important at KF than at the ROS site, where neighboring trees may have provided some shade to the lowest egg masses. Egg masses placed at the base of the KF tree, where the buttress of the tree flared out, consistently had lower survival in 1997/1998 and 1998/1999 than egg masses that were placed higher on the tree trunk, regardless of aspect. For example, average survival of egg masses on all aspects in 1998/1999 was 36.0% (± 7.1 s.e.m.) and 40.3% (± 7.4 s.e.m.) at 200 and 100 cm, respectively, but only 5.0% (± 3.2 s.e.m.) at the base of the tree.

Effects of aspect on egg survival were even more pronounced than height. Egg survival at the ROS site was consistently highest on the northern aspect and lowest on the southern aspect, while survival was intermediate on the western and eastern aspects (Table 5). In 1998/1999, overall egg survival at the ROS site averaged 81.9% (± 6.5 s.e.m.), 47.0% (± 9.1 s.e.m.), 34.0% (± 9.1 s.e.m.) and only 7.3% (± 4.7 s.e.m.) on the northern, eastern, western and southern aspects, respectively. Differences among aspects at KF were similar to those at the ROS site, although eggs on the western aspect at KF experienced mortality as high as those on the southern aspect. In 1998/1999, survival by aspect at KF averaged 50.1% (± 8.8 s.e.m.) and

52.2% (± 7.6 s.e.m.) for the northern and eastern aspects, respectively, but only 5.8% (± 3.9 s.e.m.) and 1.6% (± 1.6 s.e.m.) for the southern and western aspects, respectively.

Results from the experiment conducted at KF in 1999/2000 appear to confirm our notion that solar loading and high temperatures in autumn were largely responsible for the variation among aspects and heights in gypsy moth egg survival. The first set of egg masses at KF, exposed from 3 September to 4 November 1999, had high survival on the northern aspect, regardless of height. Few eggs survived on the southern and western aspects, where solar loading was most intense (Table 5). Survival of eggs on the eastern aspect was low at the base but relatively high when eggs were at 200 cm, consistent with results from the previous 2 years. Effects of aspect and height on egg survival were much less apparent in the second set of egg masses, which were deployed at KF from early November to mid-April (Table 5). Survival of these egg masses, which experienced only winter and spring conditions, was generally high at all locations on the tree, with the exception of egg masses at the base of the tree on the southern aspect.

We originally hypothesized that the insulative effects of snow cover would result in greater survival of eggs placed at the base of the trees compared with egg masses placed higher on the tree trunk. Instead, diurnal patterns of solar loading in autumn, combined with the relatively mild winters that occurred during the 3 years of this study, led to unexpectedly poor survival of eggs on the southern and western aspects, particularly at the base of the trees. The diurnal pattern of egg mass temperatures exemplified in Fig. 2 illustrates the degree of variation in solar radiation among aspects. Maximum diurnal temperatures of the egg masses on the southern aspect were often more than 20 °C warmer than maximum temperatures experienced by egg masses on the northern and eastern aspects. Although we could find no reports of a maximum lethal temperature for gypsy moth eggs, egg mass temperatures that exceeded 50 °C on the southern and western aspects of the tree would almost assuredly be lethal to the developing embryos.

After oviposition in late summer, gypsy moth eggs go through a period of embryogenesis, as well as an acclimation process that enables them to survive winter conditions. Gray et al. (1991) suggested that gypsy moth eggs could be vulnerable to temperature

extremes during this period, but most previous studies focused primarily on survival during cold periods. Nealis et al. (1999) did attempt to differentiate between gypsy moth mortality that occurred above and below snow line in autumn vs. over the winter. They found that egg mortality was much greater above snow line than below, where egg masses were presumably protected by snow. However, to assess survival below the snow line, they placed egg masses on the underside of wooden stakes that leaned against a tree, thereby protecting those eggs from any exposure to solar radiation and associated high temperatures.

Given that gypsy moth egg survival can be strongly affected by solar loading and high temperatures in autumn, as well as cold winter temperatures, the distribution of egg masses in wild gypsy moth populations becomes an important question. Sullivan and Wallace (1972) found no differences in the ability of gypsy moth eggs from different populations to supercool or survive cold regimes, indicating that ovipositional behavior by female moths may be more important than egg physiology. There is evidence that choice of oviposition sites by female moths may vary among populations and could be related to microclimatic conditions. For example, Nealis et al. (1999) noted the abundance of gypsy moth egg masses on rocks on the surface of the ground in eastern Ontario, while anecdotal observations in Michigan indicate that relatively few egg masses occur in such locations. Higashiura (1989) found average height of egg mass deposition varied among three gypsy moth populations in Japan, and suggested that such variation may function as a means to cope with variability in weather and bird predation. In Ontario, Lyons and Liebhold (1991) found that egg masses were relatively scarce on the western aspect of trees in a dense gypsy moth population, while egg masses were most abundant on the eastern aspects of trees in sparse and dense populations.

Obviously, a more thorough understanding of factors that influence egg mass distribution, as well as egg survival, is needed.

3.5. Differences in thermal time accumulation

Accurate assessment of gypsy moth phenology is important in insect suppression activities, as commonly used pesticides are effective for relatively short periods during the insect's larval stages. Results of our study indicate that microclimatic factors, particularly aspect, can lead to substantial variability in timing of egg hatch at a single location. For example, we calculated base 3 °C growing degree day totals, which serve as the basis of the egg hatch algorithm from the GMPHEN gypsy moth phenological model (Sheehan, 1992, based on Masaki, 1956) using egg mass temperatures at each of the aspects at the 100 cm height. According to the Sheehan model, a GDD total of 282 is assumed to be associated with beginning of hatch. Seasonal base 3 °C growing degree day accumulations based on air and egg mass temperatures between 1 January and 31 March of each season from both field sites are given in Table 6. Differences in maximum accumulation in a given season averaged 111.9 GDDs at the KF site and 96.5 GDDs at the ROS site. Totals were greatest at southern aspect and least at northern aspect in all three seasons at both sites.

Time series of daily accumulated base 3 °C GDD for egg mass and air temperatures from 1 January to 10 April (date of egg mass removal) of the 1999/2000 season are given in Fig. 3 for the KF site. The GDD total at the southern aspect was greatest (353.1), followed by west (301.3), east (284.6) and north (247.0) aspects. This supports previous observations of first egg hatch on southern sections of tree trunks in the wild (Lyons and Liebhold, 1991). The GDD total for the air temperatures, 250.2, is between the totals at northern and

Table 6

Base 3 °C growing degree day accumulations from 100 cm egg masses and air temperatures vs. aspect for 1 January to 31 March during the three seasons of the study at KF and ROS field sites

Year	KF location					ROS location				
	Air	North	East	South	West	Air	North	East	South	West
1998	160.6	153.9	175.1	247.9	190.6	79.0	73.0	76.8	142.6	110.3
1999	99.2	97.9	140.2	251.4	186.2	54.7	60.2	77.7	179.0	113.0
2000	139.3	118.2	137.5	206.5	149.0	112.5	113.9	154.0	208.1	178.6

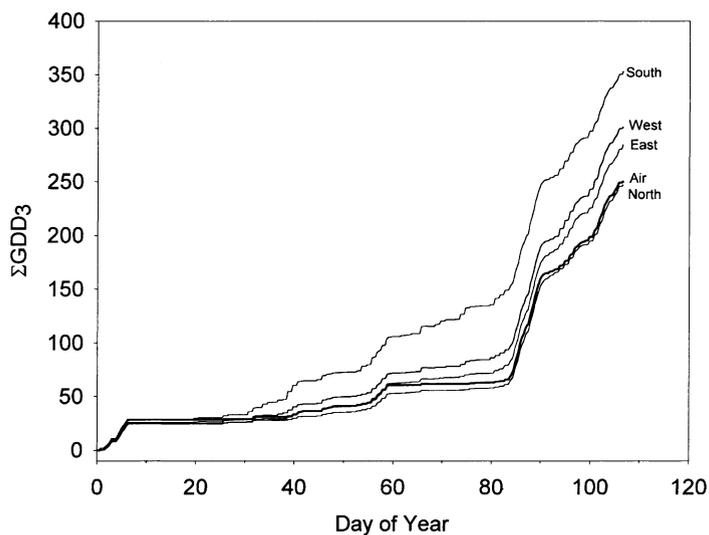


Fig. 3. Base 3°C growing degree day unit accumulations at various aspects vs. DOY, 100 cm height, KF site, 1997/1998 winter season.

eastern aspects. Divergence of the accumulations begins around day of year (DOY) 30 and increases to as much as 106.1 GDDs (south vs. north aspect) by DOY 100. According to NOAA (1997–2001), the climatic normal temperatures for the first half of April at Gull Lake yield 4.2 GDDs (base 3°C) per day. Using this figure, we converted the observed GDD differences between aspects to calendar days. For the 1999/2000 KF data, differences between location ranged from 0.8 days (air vs. north aspect) to 25.3 days (south vs. north aspect). While more variable, and without comparable information on the number of days the eggs were in cold storage (which can affect the rate of hatch (Masaki, 1956)), these numbers and the differences in Table 6 are comparable with the 2–3.5-week range of egg hatch times observed in eastern deciduous forests of North America by Lyons and Liebhold (1991). They are also generally larger than the natural/genetic variability of larval development rates, estimated by Casagrande et al. (1987) at a time period on the order of several days. Thus, microclimatic differences introduced primarily by differences in aspect and solar radiation loading could be a significant source of variability in the time of hatch at a single location. These differences may also help explain the results of Russo et al. (1993), whose model-simulated egg hatch dates were similar to but still statistically different from observed hatch dates in the eastern US

after spatially downscaling temperature data to a 1 km spatial resolution. Further, the observed differences among aspects in egg hatch timing are great enough to potentially play a role in gypsy moth population dynamics. A 4-week difference in the timing of egg hatch can be associated with differences in mortality attributable to natural enemies and substantial differences in the quality of oak foliage, potentially affecting female fecundity (Hunter and Elkinton, 1999).

4. Conclusions

A study to monitor internal egg mass temperatures at three heights aboveground level and at the four cardinal aspects was carried out on oak tree stems at two different locations in Michigan during the winter seasons of 1997/1998, 1998/1999 and 1999/2000. Aspect of the egg mass was more important than height as an environmental factor influencing internal egg mass temperatures.

Egg survival was dramatically affected by high temperatures resulting and varied among aspects due to differences in solar loading. Few egg masses on southern and western aspects survived, while more than 60% of the eggs on the eastern and northern aspects survived (averaged over time). Based on projected GDD accumulations, our data indicate that variability

in egg hatch among the egg masses on a single tree could be similar to the magnitude of differences in GDD accumulation that would occur between the KF site and the ROS site, 250 km to the north.

Snow cover, which has often been assumed to insulate egg masses from cold temperatures, did provide some protection, but differences were not as great as we expected. Extreme minimum temperatures of egg masses at the base of trees where they were protected by snow cover remained roughly 2–7 °C warmer than air temperature.

Our results suggest that consideration of aspect may improve the simulation of temporal variability of phenological stages found in the wild, and could perhaps be used to further refine local and regional pest suppression activities. In this regard, an accurate estimate of the spatial distribution of egg masses in wild gypsy moth populations is needed. We recognize that while gypsy moth egg masses are commonly found on tree stems, the grids of egg masses we placed on the tree stems for this experiment represent a somewhat artificial situation. The poor survival of eggs on southern and western aspects suggests, however, that there should be strong selection for ovipositional behavior that leads to deposition of egg masses in locations protected from intense solar radiation. Lyons and Liebhold (1991) reported that egg masses on Ontario and Pennsylvania tended to be found most often on the eastern sides of tree boles. In our study, egg masses on the eastern aspect were not exposed to intense solar radiation, and GDD accumulations on the eastern and northern aspects were most similar to air temperatures. More information about the spatial distribution and location of egg masses in the wild and the potential influence of population density or site factors on egg mass distribution would likely improve phenological modeling capabilities.

In addition, our data were collected in two sites, one consisting of a mature oak shelterwood stand and the other a well-stocked, pole-sized oak stand. The degree of solar loading and associated microclimatic factors in other locations will likely be influenced by stand-related factors including canopy architecture characteristics and tree density or size. Additional study may be needed to assess microclimatic influence in other situations such as urban forests.

Increased understanding of the magnitude and source of microclimatic variability in forests may have

implications for organisms other than gypsy moth. Localized distribution of arthropods inhabiting tree stems, e.g., may be determined by the capability of those groups to access optimal heat or humidity conditions (Prinzing, 2001). In addition, introduction and establishment of new exotic insects, weeds and other pests will likely continue as economic globalization and international trade increase. Accurate assessment of the potential geographic range of new exotic species is a critical aspect of predicting the potential impact of the organism and developing appropriate regulatory or management programs (Mack et al., 2000). Our results suggest that microclimatic variability will need to be considered when efforts are made to estimate the potential range of a new exotic organism.

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