Comparison of the Hatch of *Lymantria dispar* (Lepidoptera: Lymantriidae) Eggs from Russia and the United States After Exposure to Different Temperatures and Durations of Low Temperature

MELODY A. KEENA

Northeastern Center for Forest Health Research, USDA–Forest Service, Hamden, CT 06514

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ABSTRACT Comparisons are made of the effects of temperature and duration of low temperature on egg hatch of North American and Russian gypsy moth, *Lymantria dispar* (L.), under controlled laboratory conditions. Percentage of hatch of embryonated eggs, days to 1st hatch after incubation at warm temperature and temporal distribution of hatch are used to compare hatch of different strains under various conditions. Eggs from 2 Russian gypsy moth strains required less exposure to low temperature to be able to hatch than did eggs from a North American strain. Hatch took longer to begin and proceeded more slowly in eggs held at constant 15 and 20°C. Hatch did not occur for >99% of North American and Russian eggs held at a constant 25°C. Substantial variation in hatch in response to low temperature exists both within and between gypsy moth strains, making adaptation to a wide range of climates possible. Variation in diapause requirements within a strain and between strains can be assessed and compared by holding eggs for 60 d at 5°C followed by incubation at 25°C.

KEY WORDS *Lymantria dispar*, temperature, diapause, gypsy moth, eggs

THE GYPSY MOTH, *Lymantria dispar* (L.), has become a major tree pest in the United States since its initial introduction from France in the mid-nineteenth century (Forbush and Fernald 1896). Defoliation by gypsy moth larvae can cause shifts in tree species composition (Campbell and Sloan 1977) and seedling mortality (Gottschalk 1990) and can threaten human health and result in costly suppression programs (USDA 1995). More recently, Asian strains of gypsy moth have been accidentally introduced into North America on commercial and military vessels and their cargo (Anonymous 1992, Garcia 1994). Gypsy moths from Asia differ from those already in the United States in many ways; most notably, female Asian gypsy moths can fly up to 100 km (Rozkhov and Vasilyeva 1982), and larvae feed on a broader range of hosts including conifers (Baranchikov 1988, Turova 1992). Because of these and other characteristics, Asian gypsy moths may pose a more serious threat to North American forest ecosystems than those already present and could increase the speed with which the gypsy moth range expands.

The gypsy moth appears to be a univoltine species wherever it occurs in the world (Goldschmidt 1934). Diapause of the mature embryonic larva within the egg is a lengthy (8–9 mo/yr) and critical portion of the life cycle of the gypsy moth (Goldschmidt 1934, Leonard 1968). Diapause enhances survival during the winter and synchronizes hatch with bud burst of preferred host plants in the spring. Strains of gypsy moth from different geographic areas have heritable differences in requirements for completing diapause and hatching (Goldschmidt 1932, 1934). Goldschmidt (1934) hypothesized that these strain differences were adaptational to the natural environments where the strains were found. Therefore, it is very likely that the gypsy moths introduced from Asia will have different requirements for diapause completion and hatch than do the moths already present in the United States.

Several predictive models of gypsy moth egg hatch already exist (Johnson et al. 1983, Waggoner 1984, Lyons and Lysyk 1988, Sawyer et al. 1993, Gray et al. 1995). The ability to forecast egg hatch is critical to scheduling control programs. Therefore, knowledge of the temperature requirements for egg hatch of the Asian strain is required to parameterize correctly predictive models. Many researchers have looked at the effects of temperature on the diapause process in strains of gypsy moth from various geographical areas (including Asia) by measuring time to hatch, distribution of hatch, and hatch success (e.g., Masaki 1956, Pantyukhov 1962, Lyons and Lysyk 1988, Tauber et al. 1990). Eggs used in most of these studies had been

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collected from the field after exposure to ambient conditions of unknown character for varying lengths of time. This makes the comparison and interpretation of results difficult, because the state of diapause of the eggs at the start of the experiment is not known (Gray et al. 1991). This article documents differences in thermal requirements for egg hatch between gypsy moths from North America and Russia. The possibility of using these differences in requirements for hatch as a way to differentiate populations is discussed. Percentage of hatch of embryonated eggs, days to 1st hatch after incubation at warm temperature, and temporal distribution of hatch are used to compare hatch of the different strains under various controlled laboratory conditions. Exposure of eggs to constant temperature treatments in the laboratory does not approximate nature, but will allow direct comparisons between strains to be made.

Materials and Methods

Gypsy Moth Strains. The source of the Russian gypsy moth used in experiment 1 was the Russian grain ship Allalinhorn which docked in Vancouver, BC, on 14 September 1991. The ship had just arrived from the Far East Russian port of Nakhodka. More than 100 egg masses were scraped from the super-structure of the ship by the crew and brought, at ambient temperature, to the United States Department of Agriculture (USDA) Animal Plant Health Inspection Service (APHIS) quarantine facility Otis Methods Development Center, Otis Air National Guard Base, MA. The strain was reared for 1 generation at Otis then brought to the USDA Forest Service Quarantine Laboratory, Ansonia, CT, and reared for 1 additional generation before the experiment was conducted. This strain will be referred to as the "AA" strain.

The Russian strain used in experiment 2 was 20 egg masses from Mineralni, Russia, and 4 egg masses from Krasnoyarsk, Russia, collected in July and August of 1992. The egg masses were brought to the USDA Forest Service Quarantine Laboratory in Ansonia, CT, for rearing. The 2 populations were allowed to mate randomly in the 1st generation and reared for 2 additional generations preceding the experiment. This Russian strain will be referred to as the "RR" strain.

The North American gypsy moths used for comparison with the Russian strains were from Wrentham (Norfolk County), MA. More than 200 egg masses were collected here on 13 February 1992, and were reared through 1 generation before use in experiment 1, and 4 generations before use in experiment 2. The Massachusetts strain will be referred to as the "MA" strain.

Voucher specimens have been deposited at the Entomology Division, Yale Peabody Museum of Natural History, New Haven, CT.

Egg Mass Production and Preparation. All rearings to produce the egg masses used in the experiments were conducted in walk-in environmental chambers maintained at 25°C, 60% RH, a photoperiod of 16:8 (L:D) h, and air movement of ≈2–3 cfm. Larvae were reared, in cohorts of 10, in 236.5-ml clear plastic cups (Sweetheart, Chicago, IL) with unwaxed paper lids for 35 or 40 d. Each cup contained 90 ml of high wheat germ diet (Bell et al. 1981). Pupae were harvested, sexed, and stored by sex, egg mass (family), and strain in 473.2- or 236.6-ml unwaxed squat paper cups (James River Corporation, James River, VA) with clear plastic lids (Sweetheart) until adult eclosion. Adults were removed daily and held for 24 h before mating. Individual pair matings were made in 473.2-ml paper cups. Matings were random within strain except that sibling matings were avoided.

Ten days after mating, egg masses were harvested by scraping each egg mass from the inside of the paper cup. Thirty egg masses were chosen randomly from each strain for use in each experiment. The eggs from an individual egg mass were then mixed and divided into 6 or 8 samples (experiments 2 and 1, respectively,) of 50–100 eggs each. Each of the egg samples for an egg mass were put in separate petri dishes: experiment 1, plastic petri dishes (60 by 15 mm) with loose fitting lids (Falcon); and experiment 2, plastic petri dishes (50 by 9 mm) with tightly fitting lids (Falcon). Egg samples in petri dishes were then placed by treatment in covered, clear plastic boxes (30 by 15.5 by 9 cm, Wilson, Sunbury, PA) and held an additional 32 d in the rearing chamber to ensure prediapause was completed (Gray et al. 1991) before the experiments began. Relative humidity in the box was maintained at ≈90–95% by placing water in the box; petri dishes with egg samples were placed on a wire screen (0.63-cm gauge) above the water.

Experiment 1. One egg sample from each egg mass of the AA and MA strains was subjected to 0, 30, 60, 90, 120, 150, 180, or 210 d at 5°C, followed by incubation at 25°C. A photoperiod of 16:8 (L:D) h was maintained at both temperatures. Egg hatch was counted and larvae were removed from each petri dish 3 times per week (0- to 120-d treatments) or daily (150- to 210-d treatments) following transfer to 25°C. Egg hatch was recorded for each egg mass-treatment combination for a minimum of 30 d after the last nonzero observation. The experiment was terminated on day 225.

Experiment 2. One egg sample from each egg mass of the RR and MA strains was subjected to 60 d at 5, 10, or 15°C, followed by 25°C until termination of the experiment. One egg sample from each egg mass of these strains was subjected to constant 15, 20, or 25°C until termination of the experiment. A photoperiod of 16:8 (L:D) h was maintained for all temperatures. Egg hatch was counted and larvae were removed from each petri disk 3 times per week (constant temperature treatment) or daily (alternated temperature treatment). Egg hatch was recorded for each egg mass–treatment combination for a minimum of 30 d after the

last nonzero observation. The experiment was terminated on day 275.

Following termination of each experiment, eggs were dehaired and examined to determine embryonation. Unembryonated eggs appeared yellow (often concave); embryonated eggs were dark. The number of each type of egg was recorded and percent hatch of embryonated eggs was calculated. The number of days from incubation at 15, 20, or 25°C to 1st hatch and the duration of hatch also was determined for each egg sample.

Statistical Analysis. The summary statistics computed for each strain and treatment combination were the mean, standard deviation, and 95% CI of days to 1st hatch and of arcsine (square root of percentage of hatch of embryonated eggs) using each egg sample (30 different egg masses) as observations. The Minitab version 5.1.3 (AOS/VS version) (Ryan et al. 1985) TWOSAMPLE-T command was used to compare means of treatments between strains because variances were found to be unequal; this statistic has an approximation *t*-distribution and variances are not pooled. Bonferoni protection against multiple testing problems was used to avoid considering means to be different when they were not (Neter and Wasserman 1974). Means in experiment 1 were considered to be different if the P value was <0.003125, and <0.04167 for experiment 2.

Results

Experiment 1. When eggs of either strain (AA or MA) were incubated at 25°C without exposure to low temperature, only 6 out of 6,496 eggs hatched within 6 mo or longer. Only 1 AA and 2 MA egg masses had hatch with no exposure to low temperature. Exposure to 5°C for 30 d apparently did not satisfy requirements for hatch of the majority of eggs of either the AA or MA strains, producing only 44 larvae total when incubated at 25°C. Only 10 AA and 7 MA egg masses had hatch after 30 d at 5°C. However, a substantial number of larvae hatched at 25°C after 60 d or longer at 5°C (Fig. 1). All egg masses of both strains had some hatch when exposure to 5°C exceeded 60 d except for 8 MA strain egg masses at 60 d. The form of the hatch curve varied with the length of exposure to 5°C (Fig. 1). When exposure to 5°C was brief, hatching of the eggs was delayed, fewer eggs hatched, and the duration of hatch was greater than when eggs were exposed longer to 5°C. There was no fundamental difference in the general pattern of response of the AA and MA strains to increasing the duration of exposure to 5°C; synchrony of hatch increased and days to 1st hatch decreased. However, the AA strain generally took fewer days to begin hatching (Fig. 1).

Mean percentage of hatch of embryonated eggs increases from near 0 to >80% with increasing exposure to 5°C followed by incubation at 25°C (Fig. 2). Mean percentage hatch of embryonated AA eggs was significantly greater than that of MA eggs after 60 d and 90 d at 5°C (Table 1, Fig. 2). Mean percentage of hatch of embryonated MA eggs was significantly greater than that of AA eggs after 210 d at 5°C (Fig. 2). The greatest separation of means for the 2 strains occurred at the 60 d treatment (Fig. 2).

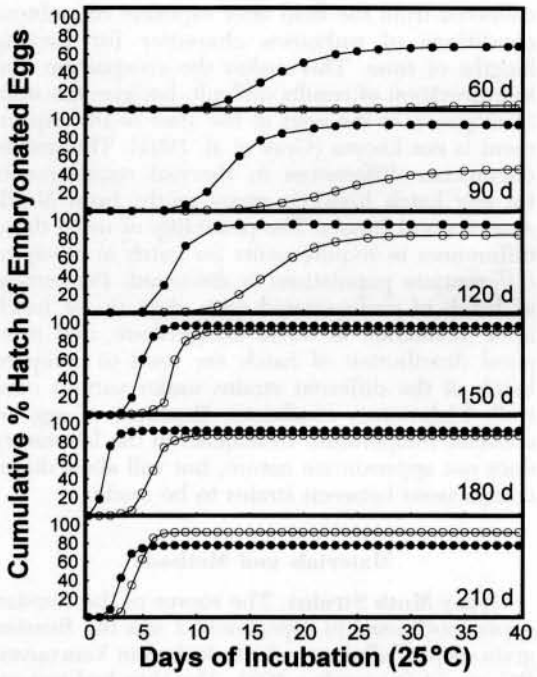

Fig. 1. Cumulative percentage of hatch of embryonated eggs for gypsy moth strains from far eastern Russia (AA, solid circles), left, and Massachusetts (MA, open circles), right, after different numbers of days at 5°C (60–120 d), followed by incubation at 25°C. No results for the treatments of <60 d at 5°C are presented because <1% hatch occurred.

The mean number of days to 1st hatch after incubation at 25°C decreased with increasing exposure to 5°C (Fig. 3). Mean number of days to 1st hatch of AA eggs was significantly less than that of MA eggs after 60, 90, 120, 150, 180, and 210 d at 5°C (Table 1; Fig. 3). The greatest separation in significantly different means between the 2 strains occurred at the 60 d treatment (Fig. 3). Substantial between-egg mass within-strain variation exists for both percentage hatch of embryonated eggs and days to 1st hatch. The wider the 95% CI for a strain the greater the between egg mass variation (Figs. 2 and 3). Variation between egg masses in days to 1st hatch decreases as the number of days at 5°C increases (Fig. 3). Variation between egg masses in percentage hatch of embryonated eggs is greater when minimal requirements for hatch of all egg masses are met, 60 d for AA eggs and 90 d for MA eggs (Fig. 2). Variation between egg masses in percentage of hatch of embryonated eggs also

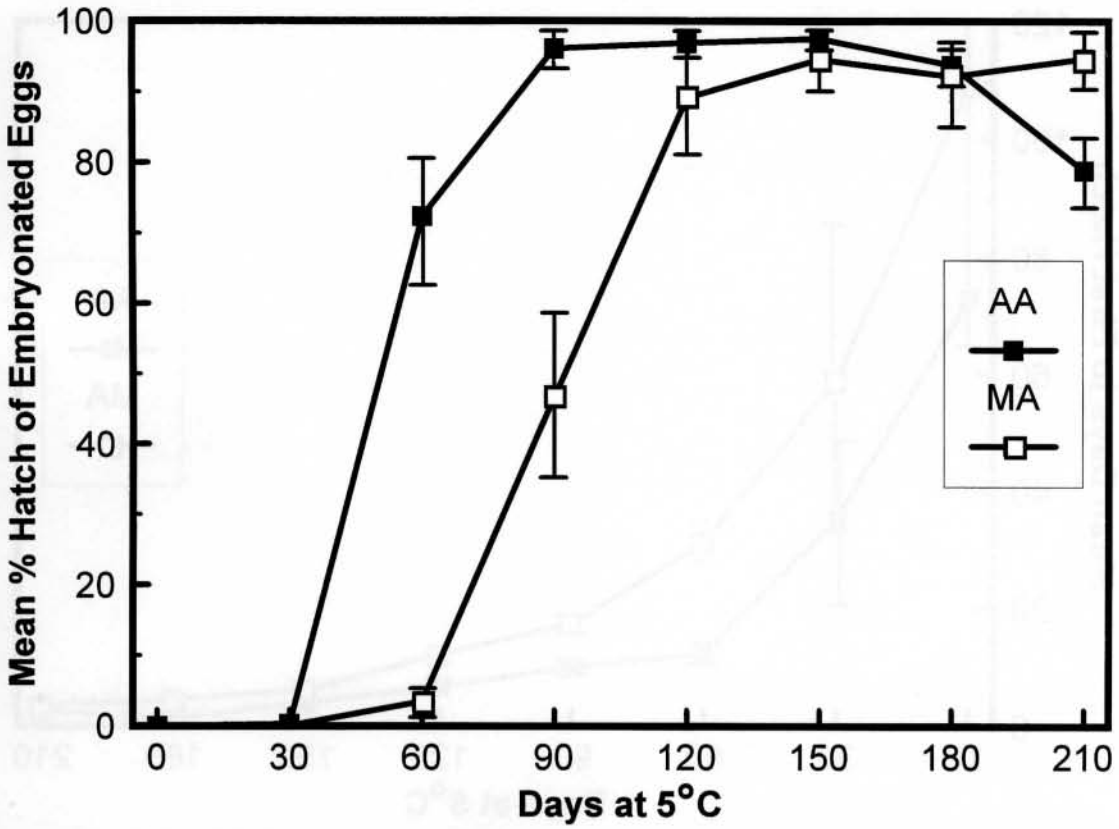

Fig. 2. Comparison of the effects of different durations at 5°C, followed by incubation at 25°C, on mean percentage of hatch of embryonated eggs for gypsy moth strains from far eastern Russia (AA) and Massachusetts (MA). Bars = 95% CI.

increases when AA eggs are exposed to 5°C for 210 d (Fig. 2).

Experiment 2. When the low temperature used for the 60-d exposure increased, the number of days to 1st hatch after incubation at 25°C increased, but not significantly for both strains (Figs. 4 and 5). The RR strain began hatching significantly faster than the MA strain when incubated at 25°C after either 60 d at 5°C or 10°C (Table 2). Percentage of hatch of embryonated eggs was similar for the RR strain after 60 d at either 5° or 10°C, but significantly decreased when 15°C was used as the low temperature (Figs. 4 and 5). Mean percentage of hatch of the MA strain was similar after 60 d at 5, 10, or 15°C followed by incubation at 25°C (Figs. 4 and 5). The RR strain had significantly greater percentage hatch of embryonated eggs than the MA strain when incubated at 25°C

Table 1. Mean comparison statistics for hatch of ship Asian (AA) and Massachusetts (MA) eggs in response to different lengths (days) of exposure to 5°C followed by incubation at 25°C

Days at 5°C	AA (*n*)	MA (*n*)	% hatch embryonated eggs[a]			AA (*n*)	MA (*n*)	Days to 1st hatch		
			t	df	*P*			*t*	df	*P*
0	30	30	−0.92	35.9	0.3600	1	1	—	—	—
30	30	30	1.51	48.1	0.1400	7	10	1.94	9.9	0.0850
60	30	30	14.32	46.4	<0.00005	22	30	7.18	22.6	<0.00005
90	30	30	9.20	42.6	<0.00005	30	30	7.61	38.9	<0.00005
120	30	30	2.65	37.8	0.0120	30	30	12.86	38.6	<0.00005
150	30	30	1.58	38.7	0.1200	30	30	8.36	41.7	<0.00005
180	30	30	0.51	41.8	0.6100	30	30	14.38	39.5	<0.00005
210	30	30	5.05	54.2	<0.00005	30	30	5.83	53.1	<0.00005

Mean separation used was TWOSAMPLE-T command in Minitab (Ryan et al. 1985). *P* values <0.0031 are considered to be significant.

[a] Mean separation test on arcsine $\sqrt{x}$ transformed data.

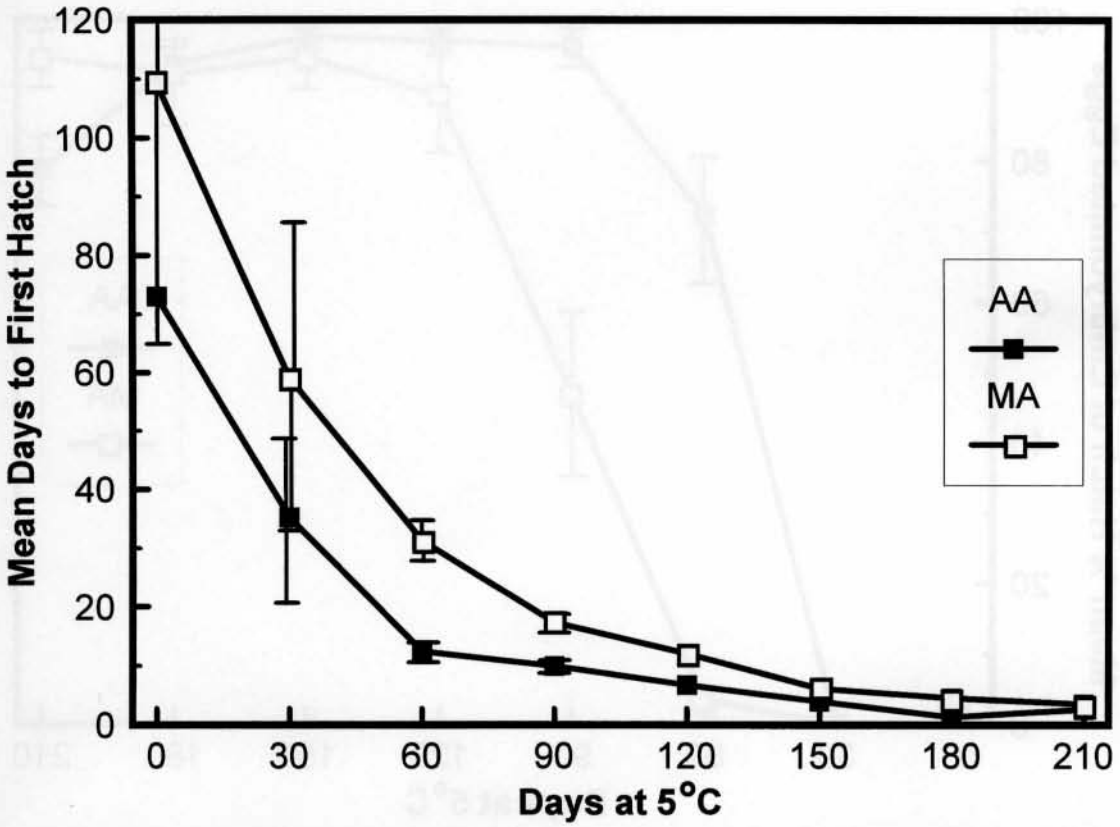

Fig. 3. Comparison of the effects of different durations at 5°C, followed by incubation at 25°C, on mean days to 1st hatch of eggs from gypsy moth strains from far eastern Russia (AA) and Massachusetts (MA). When confidence intervals are smaller than the marker width they do not show up in the graph. Bars = 95% CI.

after 60 d at 5, 10, or 15°C (Table 2). The number of egg masses with hatch for each strain in the different 60 d low temperature treatments varied (see *n* for each strain in Table 2).

When eggs of both strains (RR and MA) were incubated at 25°C without exposure to low temperature, only 2 out of 4,058 eggs hatched in 275 d. Only 1 RR egg mass had hatch with no exposure to low temperature. As the constant holding temperature decreased hatch increased, but there were no significant differences between strains in percentage of hatch of embryonated eggs for the constant holding temperatures tested (Figs. 4 and 6). However, it took the MA strain longer to reach its maximal percentage of hatch than it did the RR strain (Fig. 6). Days to 1st hatch was significantly less for the RR eggs than the MA eggs in either the constant 15°C or the constant 20°C treatment (Table 2; Fig. 4). Almost all of the egg masses of each strain had some eggs hatch when held at 15

Table 2. Mean comparison statistics for hatch of Russian (RR) and Massachusetts (MA) eggs exposed to different temperature treatments

Temp, °C treatment[a]	RR (*n*)	MA (*n*)	% hatch embryonated eggs[b]			RR (*n*)	MA (*n*)	Days to 1st hatch		
			t^2	df	*P*			*t*	df	*P*
5/25	30	30	9.70	41.7	<0.00005	30	16	−6.66	18.1	<0.00005
10/25	30	30	10.98	52.9	<0.00005	29	17	−5.54	28.3	<0.00005
15/25	30	30	4.77	41.9	<0.00005	25	13	−2.66	17.2	0.0170
15	30	30	−1.42	57.5	0.1600	29	29	−6.56	52.5	<0.00005
20	30	30	0.72	52.8	0.4700	27	30	−7.39	46.3	<0.00005
25	30	30	1.00	29.0	0.3300	1	0	—	—	—

Mean separation used was TWOSAMPLE-T command in Minitab (Ryan et al. 1985). *P* values <0.04167 are considered to be significant.

[a] Eggs were exposed to lower temperature for 60 d then incubated at 25°C for the remainder of the experiment in the first 3 treatments, and held at constant temperature in the last 3.

[b] Mean separation test on arcsine $\sqrt{x}$ transformed data.

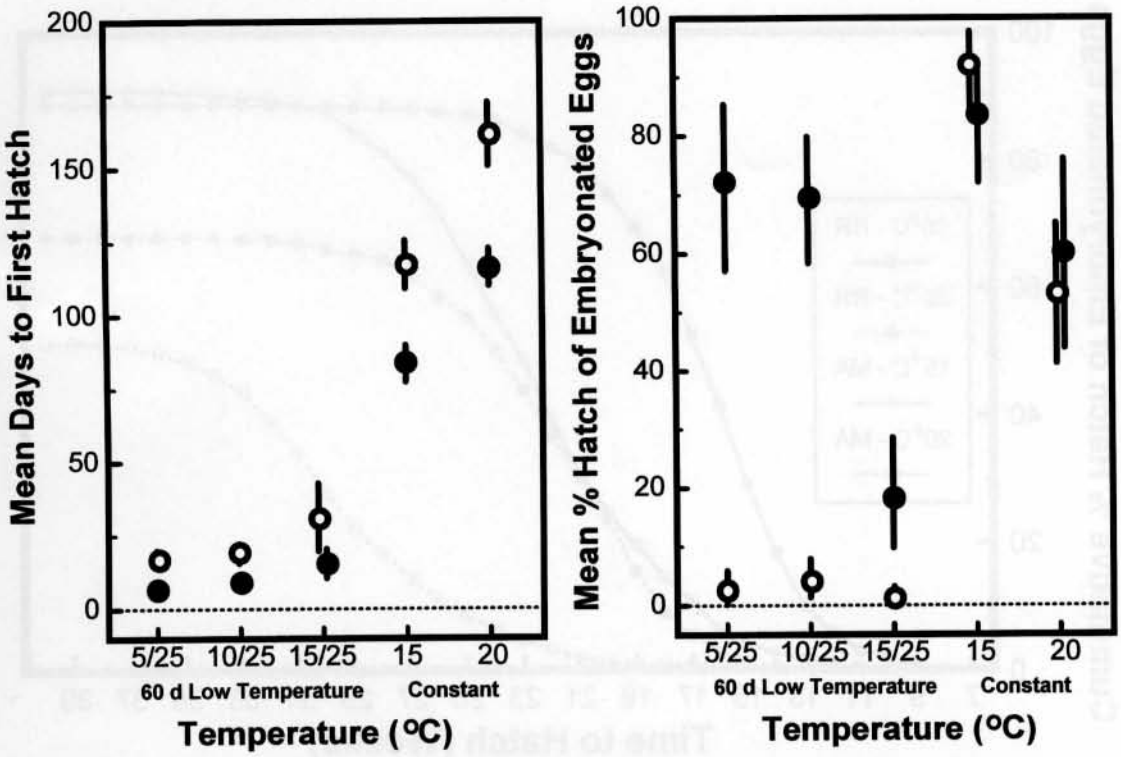

Fig. 4. Comparison of days to 1st hatch, left, and mean percentage of hatch of embryonated eggs, right, for gypsy moth strains from Russia (RR, solid circles), and Massachusetts (MA, open circles) exposed to 5 different temperature regimes. Sixty days at 3 different low temperatures followed by incubation at 25°C, and 2 constant temperatures. No results for the 25°C constant temperature are presented because <1% hatch occurred. Bars = 95% CI.

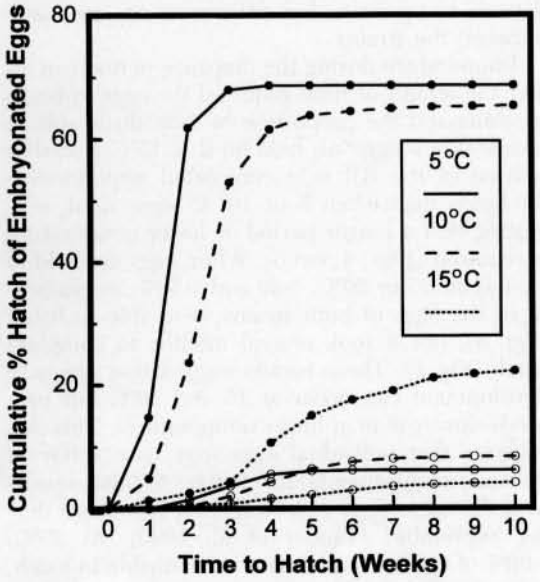

Fig. 5. Cumulative percentage of hatch of embryonated eggs for gypsy moth strains from Russia strain (RR, solid circles), Massachusetts (MA, open circles) for 60 d at 3 different low temperatures followed by incubation at 25°C.

or 20°C. It took significantly longer for hatch to begin and reach its maximum for eggs in the constant temperature treatments than when eggs received 60 d of lower temperature followed by incubation at 25°C (Figs. 4–6).

Discussion

The thermal requirements for egg hatch were met with shorter exposure to low temperature for the AA and RR strains than for the MA strain. The percentage of individuals whose hatch requirements were met increased from 0 to >90% as days at 5°C increased from 0 to 90 d for the AA strain and 0 to 120 d for the MA strain (Fig. 2). Exposing eggs to 5°C for >120 d only increased synchrony of hatch and decreased time to 1st hatch, indicating that more individuals have completed diapause and have begun postdiapause development before incubation at 25°C (Gray et al. 1995). Additionally, AA eggs began hatching significantly earlier than MA eggs when held for between 60 and 210 d at 5°C (Fig. 3). The results for duration at low temperature are similar to those for other strains (Masaki 1956, Maksimovic 1958, Tauber et al. 1990). Reduced hatch and a slight increase in the number of days to 1st hatch of AA eggs after 210 d at 5°C could be caused by death of larvae before hatch

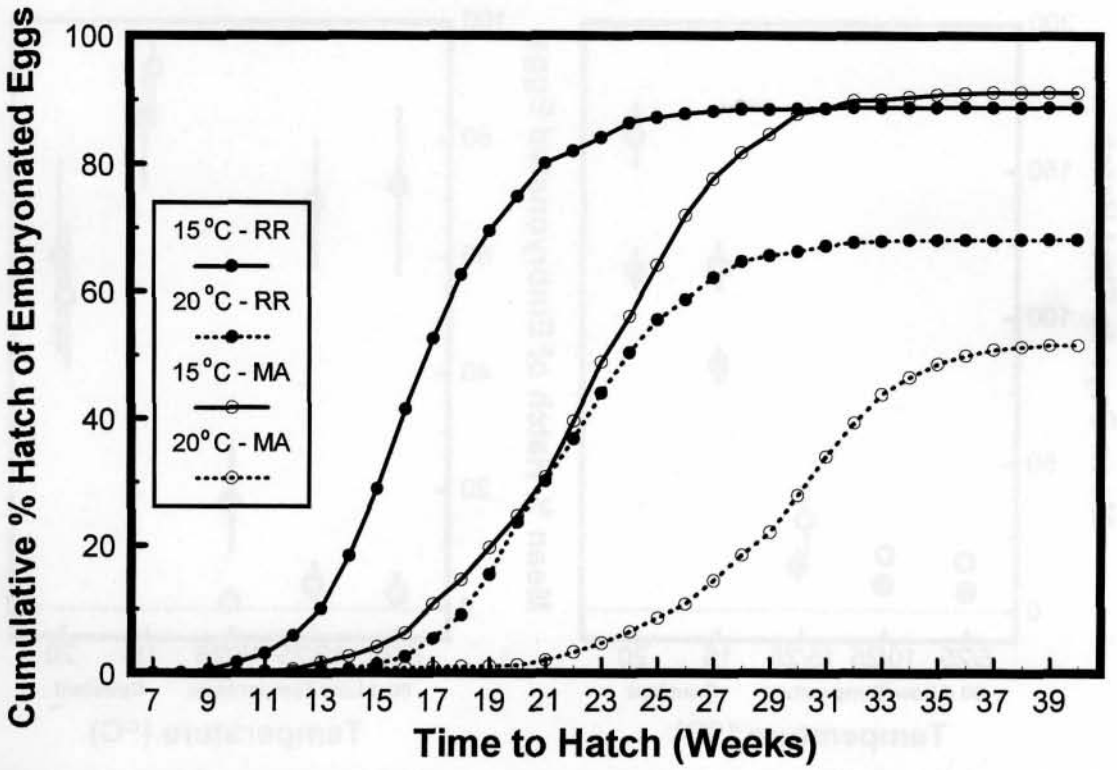

Fig. 6. Cumulative percentage of hatch for embryonated eggs for gypsy moth strains from Russia (RR) and Massachusetts (MA) for 2 different constant temperatures.

(Figs. 1 and 2). Because diapause is completed earlier in AA eggs, the increased metabolic activity during postdiapause (Gray et al. 1995) during subsequent holding periods could reduce resources required for hatch. The New Jersey standard laboratory strain (NJSS) responds in a similar way after 180 d chill at 5–7°C (Bell 1989). The NJSS has apparently adapted to the laboratory rearing system and requires shorter exposure to low temperature for eggs to hatch, making its response to increased duration at 5°C similar to that of the AA strain (Bell 1989).

These results suggest that 60 d at 5°C followed by incubation at 25°C could be used to bioassay populations for relative thermal requirements for hatch. Sixty days at 5°C gave the widest separation in significantly different means for both days to 1st hatch and percentage of hatch of embryonated eggs between the AA and MA strains (Figs. 2 and 3). If the individual egg mass values for percentage of hatch of embryonated eggs are plotted against days to 1st hatch for 60 d at 5°C, the within-strain variation and between strain differences can be seen (Fig. 7). Although substantial within-strain variation existed, there was very little overlap in range between the 2 strains, indicating that this bioassay could be used to differentiate between strains with different thermal requirements for hatch. A 2nd assay of 150 d at 5°C should also be used to determine the percentage of eggs that hatch given sufficient chill and to adjust the 60 d data to compensate for differences in egg hatch between the strains.

Temperature during the diapause period can affect the length of time required for eggs to begin hatching and the proportion of individuals able to hatch. When eggs are held 60 d at 15°C a smaller portion of the RR eggs completed requirements for hatch than when 5 or 10° C were used, suggesting that a longer period or lower temperature is required (Figs. 4 and 5). When eggs are held at a constant 15 or 20°C, >80 and >50%, respectively, of the eggs of both strains were able to hatch (Fig. 4), but it took several months to complete hatch (Fig. 6). These results suggest that diapause development can occur at 15 and 20°C but proceeds slower than at lower temperatures. This also suggests that individual eggs may have different thermal requirements for hatch. Similar results were found in eggs collected from New York during September (Tauber et al. 1990). At 25°C, >99% of eggs of both strains were unable to hatch, indicating that lower temperatures are required for hatch requirements to be met. This result is consistent with the findings of Masaki (1956) for Japanese strains held at 26°C and Leonard (1968) for Connecticut and Quebec, at 28°C.

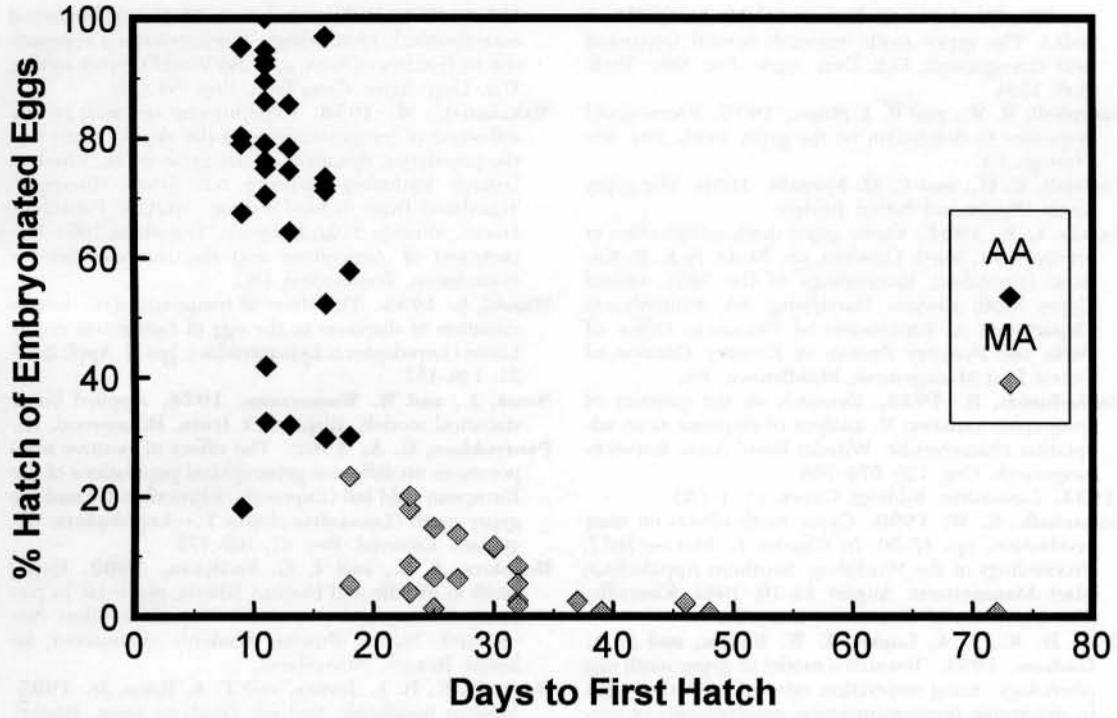

Fig. 7. Individual egg mass values for percentage of hatch of embryonated eggs and days to 1st hatch for gypsy moth strains from far eastern Russia (AA) and Massachusetts (MA) after 60 d at 5°C when incubated at 25°C.

Substantial within- and between-strain differences in requirements for hatch, the adaptation of the NJSS to hatch with less exposure to low temperature (Keena et al. 1994), and rapid selection for a nondiapausing strain that requires no exposure to low temperature to hatch (Hoy 1977) indicate that gypsy moths should be able to adapt requirements for hatch, given sufficient time and availability of suitable host plants, to survive in areas with climates that have winter temperatures that go below a mean of 20°C for only a few days. Additionally, Russian strains are likely to be able to hatch earlier than the North American strains in most climates, especially where the number of days of low temperature are few. Earlier hatch could be beneficial or detrimental depending on host plant availability. If suitable host plants are available at the time of hatch, the Russian strains could begin growing and reduce the quality of food available to the later-hatching North American strains. If however, no suitable host plants were available when the Russian larvae hatch, substantial death of 1st instars would occur. This emphasizes the possible added threat posed by the introductions of gypsy moths from Russia into North America. Should gypsy moths from Russia become established in North America, the resulting increase in the variability in hatch requirements could allow the gypsy moth to expand its range to cover more of the United States.

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