

Variation in the Suitability of Host Tree Species for Geographically Discrete Populations of Forest Tent Caterpillar

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ABSTRACT The forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), is distributed throughout North American hardwood forests. Although considered polyphagous, regional populations tend to use only a few host species for oviposition, suggesting that *M. disstria* is more oligophagous than commonly thought. We tested this premise using larvae from Manitoba, Canada; Michigan; and Louisiana in a factorial, reciprocal transplant experiment. Pupal mass, development time, and survival were recorded for each population after rearing larvae in Louisiana on three primary hosts used by southern populations (water tupelo, *Nyssa aquatica* L.; sweetgum, *Liquidambar styraciflua* L.; and water oak, *Quercus nigra* L.) and in Michigan on three northern host trees (red oak, *Quercus rubra* L.; trembling aspen, *Populus tremuloides* Michaux; and sugar maple, *Acer saccharum* Marshall). Manitoba, Canada and Michigan populations had the highest pupal mass, best survival, and most rapid development on trembling aspen and red oak, both northern species. Louisiana larvae attained the highest pupal mass on water tupelo, a primary host across the Gulf States. Northern populations grew poorly on water tupelo, whereas Louisiana caterpillars had the smallest pupal mass and poorest survival on sugar maple. Both red and water oaks were acceptable hosts for all three populations. Our results indicate that *M. disstria* is actually a composite of regionally adapted populations rather than an extreme generalist. It is unclear, however, what mechanisms might reduce gene flow, allowing such specialization to evolve and persist. We suggest that varying phenology in adult flight times among populations feeding on different hosts could provide at least a partially isolating mechanism, allowing for the evolution of host adaptation.

KEY WORDS adaptation, specialist, generalist, polyphagy, oviposition

INSECT HERBIVORES OFTEN DIFFER in their ability to use host plant species among sites. Thus, species regarded as polyphagous may actually be a composite of populations with a narrower diet range than the species as a whole (e.g., Fox and Morrow 1981, Thompson 1994, Traxler and Joern 1999). In contrast, other species are true generalists, using a broad array of host plants across the entirety of their range (e.g., Fox and Morrow 1981, Thompson 1994, Wehling and Thompson 1997, Singer and Stireman 2001, Bernays and Singer 2002, Janz 2003). The dichotomy between local specialization and polyphagy is especially difficult to discern in phytophagous insects whose geographic ranges exceed the distribution of any single primary host plant. Such populations may adapt to regional hosts and have greater affinity for and better performance on these locally available species. Most studies have focused on phytophagous species that are locally

monophagous, although it is now recognized that host plants can also drive differentiation in locally polyphagous species (Sword and Dopman 1999).

The number of true generalists varies with insect order, being prevalent in Orthoptera and relatively rare in Lepidoptera (Bernays and Chapman 1994, Chapman and Sword 1997).

One of the most ubiquitous forest insects in North America is the forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae). It occurs from southern Texas ($\approx 29^\circ$ N latitude) to northern Canada ($\approx 62^\circ$ N latitude) and from the Atlantic to the Pacific (Stehr and Cook 1968, Brandt et al. 1996). Across this vast range, *M. disstria* uses a taxonomically diverse array of host species from multiple families of plants (Prentice 1963, Stehr and Cook 1968, Fitzgerald 1995) and occurs in a variety of forest ecosystems, all with no apparent changes to its basic life history. In all regions, wandering late instars can be found feeding on many different host species, lending credence to its status as a generalist. However, oviposition and early-instar feeding occur on only one or a few favored species within a region, suggesting that regional populations may be relatively oligophagous. For example, in the Lake States, the intermountain west, and across much of Canada, the primary ovipositional host is

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trembling aspen, *Populus tremuloides* (Michaux), whereas midwestern and northeastern populations tend to use oaks, *Quercus* spp., and sugar maple, *Acer saccharum* Marshall. Across the Gulf States and into the Carolinas, *M. disstria* uses water tupelo (*Nyssa aquatica* L.), sweetgum (*Liquidambar styraciflua* L.), and various species of oak (Harper and Hyland 1981, Goyer et al. 1987, Leininger and Solomon 1995). To our knowledge, no studies have examined the ability of different populations of *M. disstria* to develop on hosts from other geographic regions.

With respect to several life history attributes, forest tent caterpillar populations do exhibit substantial geographic variation. Among populations, the number of eggs in a clutch is negatively correlated with latitude, and both allocation of resources to individual eggs and the size of neonates are greater in northern populations than in southern populations (Parry et al. 2001). In addition, genetic differences in some enzymes have been found between populations from the southern and northern United States (Lorimer 1979a, b). These studies suggest that populations of *M. disstria* vary regionally, at least for these traits. It is not known if these or any other characteristics found in different populations confer any fitness advantage when feeding on a particular host species.

The objective of this study was to determine whether populations of forest tent caterpillar are regionally adapted to specific ovipositional host plants. To address this question, we conducted a reciprocal transplant experiment using forest tent caterpillar populations from Manitoba, Canada; Michigan; and Louisiana. Caterpillars from each population were reared from egg hatch to pupation on three northern host species (trembling aspen, sugar maple, and northern red oak, *Quercus rubra* L.) in Michigan and on three southern host species (water oak, *Quercus nigra* L., water tupelo, and sweetgum) in Louisiana. Pupal mass, development time, and survival were recorded.

Materials and Methods

Tent Caterpillar Populations. Three populations of tent caterpillar were arbitrarily selected based on their use of taxonomically unrelated ovipositional hosts and wide latitudinal separation. Northern populations were represented by eggs collected from trembling aspen near Flin Flon, Manitoba, Canada (latitude 54° N). Midlatitude eggs were collected from northern red oak and sugar maple in East Lansing, MI (latitude 42° N), while southern egg bands were collected from water tupelo near Sorrento, LA (latitude 30° N). Eggs for experimental work in 1998 and 1999 were collected in the winter of 1997 and 1998, respectively. All egg collections were from low- to moderate-density populations characterized by large, robust egg bands indicative of low stress. Once collected, eggs were returned to the laboratory and held in a refrigerator at 3°C and 70% RH until used in experiments.

To synchronize hatch and adjust all populations to the phenology of bud break at the experimental study sites in Louisiana and Michigan, subsets of the col-

lected egg bands were used to determine the number of days required for hatch to commence in each population. Once thermal requirements were established, egg bands were removed from cold storage at the appropriate time before initiation of the experiment in each location to ensure synchronous emergence among populations. After removal from cold storage, the frothy spumaline covering on each egg band was carefully removed using a razor blade. The eggs were placed in a bleach solution (5% sodium hypochlorite) for 2 min to remove pathogens (particularly nuclear polyhedrosis virus) from the egg surface (modified from Williams et al. 1996).

Northern Host Tree Study (East Lansing, MI). Egg hatch for each population was adjusted to correspond to the phenology of local wild forest tent caterpillars (mean hatch date: 2 April 1998 for 6 in situ egg bands in natural habitats; 9 April 1999 for 13 egg bands). At hatch, larvae from each experimental population (12–30 families) were held in separate containers and allowed to mingle for 24 h to ensure a random sample and maximize genetic diversity. We selected three species of trees commonly used as ovipositional hosts by regional populations of forest tent caterpillar across its northern and central range (trembling aspen, sugar maple, and red oak). Two sets of 65 neonate larvae were randomly allocated to each host by population combination and were placed in screened cages (28 by 28 by 51 cm) held under a 30% shade frame outdoors on the Michigan State University campus.

At bud break in 1998, 10–15 mature trees of each host species growing in a woodlot in East Lansing, MI, were marked and used to provide foliage throughout the larval feeding period. A third of the trees were replaced in 1999 to avoid excessive pruning. Selected trees were exposed to background levels of herbivory, but none suffered to the extent that significant induction was likely. All experimental larvae reared on each host species were fed foliage from the same individual tree on any given feeding day. To minimize stress or induction of any defensive responses, foliage was cut from different individual trees at each feeding date. Sections of branch (30–50 cm) were clipped from each species using pole-pruners, transported from the field in ice chests, and clipped again under water and placed in a water-filled, 500-ml Erlenmeyer flask in each cage. A mesh covering prevented larvae from falling into the flasks. Foliage was changed every third day when the larvae were small and every other day through the final instar. Sufficient foliage was provided so that caterpillars always had an excess of food, and the leaves were changed before they began to desiccate. A polythene sheet was placed on the back and sides of each cage to help maintain humidity. Cages were cleaned at regular intervals to prevent accumulation of frass and greenfall. The position of the cages under the shade frame was initially randomized and subsequently changed weekly until caterpillars had completed their development.

Cocoons were carefully removed from the cages as they were formed. The silk cocoons were cut away from the pupae, which were weighed individually on

Table 1. ANOVA for the effects of year (Y), source population (P), and three species of trees used by northern populations as ovipositional hosts (H) on pupal mass, development time, and survival of forest tent caterpillar

	Source	df	Female			Male		
			MS	F	P	MS	F	P
Pupal mass	Year	1	0.07	58.4	<0.001	0.02	49.0	<0.001
	Population	2	0.12	103.6	<0.001	0.04	117.3	<0.001
	Host	2	0.23	191.2	<0.001	0.06	156.1	<0.001
	P × H	4	0.02	15.2	<0.001	0.01	18.4	<0.001
	Y × P	2	0.01	3.4	0.07	0.00	4.1	<0.04
	Y × H	2	0.01	7.1	<0.007	0.00	2.9	0.09
	Y × P × H	4	0.01	7.9	<0.03	0.00	7.5	<0.03
	Error	16	0.00			0.00		
Development time	Year	1	1130.1	390.6	<0.001	1354.3	312.2	<0.001
	Population	2	657.0	227.1	<0.001	778.7	179.5	<0.001
	Host	2	174.2	60.2	<0.001	180.6	41.6	<0.001
	P × H	4	30.1	10.4	<0.001	47.4	10.0	<0.001
	Y × P	2	106.0	36.6	<0.001	121.5	28.0	<0.001
	Y × H	2	39.7	13.8	<0.001	42.8	9.9	<0.002
	Y × P × H	4	1.1	0.4	0.76	1.8	0.4	0.74
	Error	16	2.9			4.3		
Survival (males and females combined)	Year	1	0.23	14.6	<0.002			
	Population	2	0.35	22.8	<0.001			
	Host	2	0.73	47.1	<0.001			
	P × H	4	0.17	11.3	<0.001			
	Y × P	2	0.19	12.5	<0.001			
	Y × H	2	0.05	3.2	0.07			
	Y × P × H	4	0.04	2.3	0.10			
	Error	18	0.01					

Analyses were conducted using cage means (N = 36). Three cages had no survival; these were treated as missing cells in the ANOVAs for pupal mass and development time. Source populations were from Manitoba, Louisiana, and Michigan. Host trees used were sugar maple, red oak, and trembling aspen.

an electronic balance (to 0.1 mg), and each was placed in a 1-g snap cap plastic cup. Pupae were checked daily for adult emergence. Date of eclosure and sex of the adult was recorded. Representative adult moths from each population were curated and are held in the senior author's personal collection.

Southern Host Tree Study (Baton Rouge, LA). Hatch of the experimental populations was timed to natural tent caterpillar hatch in Sorrento, LA (6 March 1998 and 12 March 1999). Randomization and allocation of larvae to each host species (water oak, sweet gum, and water tupelo) was conducted as in the Northern Host Tree Study. Foliage was collected from 8–12 selected mature trees in the vicinity of Baton Rouge. Approximately one-half of these trees were reused in 1999. In 1998, a large, unheated, and naturally lit room was used for rearing the caterpillars. Windows were left open, and the temperature and photoperiod approximated field conditions. This facility was not available in 1999, so the experiment was conducted on benches in a naturally lit laboratory. We set the temperature at a constant 24°C, which maintained larval growth at a rate similar to that in nearby field populations. Protocols for feeding larvae, cleaning cages, and processing and weighing pupae were the same as in the Northern Host Tree Study.

Statistical Analysis. We used a three-way factorial analysis of variance (ANOVA), with year, population source, and host species as main effects. Northern Host Tree (Michigan) and Southern Host Tree (Louisiana) rearing experiments were treated independently and analyzed separately. Males and females were separated in the analyses for pupal mass and

development time because females usually attain masses twice that of males and require a longer larval development time (Stark and Harper 1982, Robison and Raffa 1994, Parry et al. 2003). Sexes were combined in our analysis of survival because it was not practical to determine the sex of the neonate larvae at the initiation of the experiment. Because those population by host treatment combinations in which no larvae survived to pupation did not provide biological information with respect to pupal mass or development time, but did for survival, we treated these cells as missing in the ANOVAs for the first two response variables and as zeros for the assessment of survival. Type III sums of squares (PROC GLM; SAS Institute 1998) were used for all ANOVAs. We treated the cage as the experimental unit; thus, all analyses were conducted using the mean values for each cage. The PDIF option after the LSMEANS statement was used to make preplanned, pairwise comparisons between populations on individual host species and between host tree species for each population.

Results

Northern Host Tree Study. There were significant main effects of year, tree species, and population source on pupal masses of both male and female forest tent caterpillars (Table 1). There was also a strong interaction between population source and tree species for males and females. Preplanned pairwise comparisons between means indicated that for the Manitoba population, pupal masses in 1998 were largest on aspen, followed by red oak and then sugar maple, a

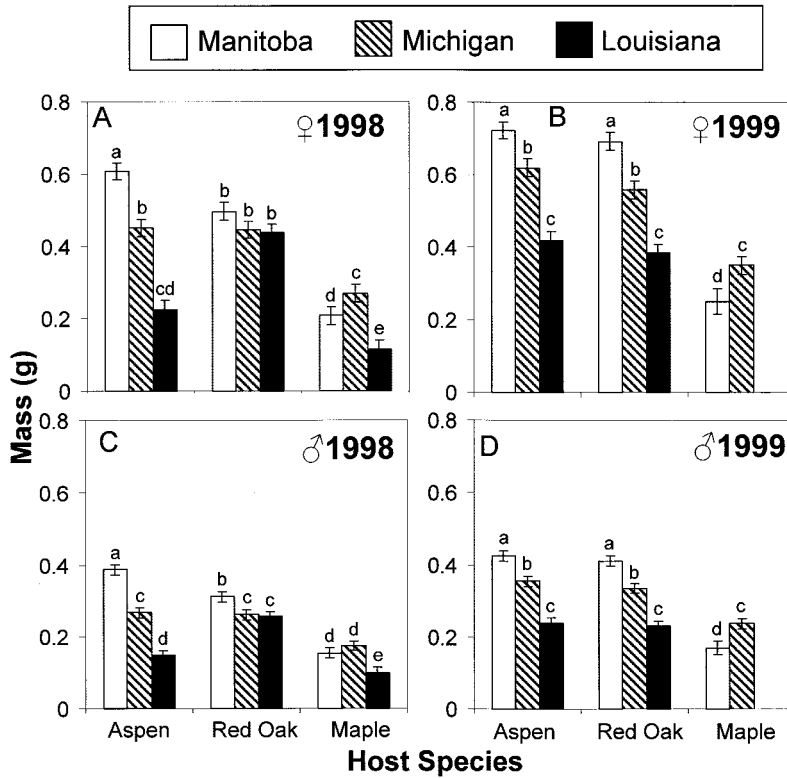


Fig. 1. The effects (LS mean \pm SE) of three northern hosts used for oviposition by forest tent caterpillar on the pupal mass of (A) females in 1998, (B) females in 1999, (C) males in 1998, and (D) males in 1999 for Manitoba, Michigan, and Louisiana populations. The experimental unit was the rearing cage (65 larvae); means represent the two cages in each population by host combination. There was no survival in three cages; these were treated as missing cells in the ANOVA. Preplanned pairwise comparisons (LSD) were between each population on a host and between each hosts for a population. Means with different letters are significantly different at $P < 0.05$.

pattern consistent for both males and females (Fig. 1). However, in 1999, aspen and oak were equivalent hosts for both sexes. Michigan males and females performed equally as well on aspen and oak in both years. In 1998, females and males from Louisiana attained highest pupal masses on red oak, followed by aspen and then sugar maple. However, in 1999, pupal masses for females as well as males were equivalent on oak and aspen. No Louisiana larvae completed development on sugar maple in 1999.

When pupal masses were compared between populations on a single host, large differences were apparent. On aspen, the Manitoba population produced the largest pupal masses, followed by Michigan and then Louisiana, a pattern that held for males and females in both years (Fig. 1). When feeding on a diet of red oak, there was no difference in female pupal masses for the three populations in 1998. However for males in 1998, the Manitoba population attained greater pupal masses. In contrast, females from Manitoba had the greatest pupal mass in 1999 on red oak, followed by Michigan and then Louisiana. This pattern held for males in 1999 as well. On sugar maple in both years, pupal mass was highest for Michigan females on sugar maple followed by those from Mani-

toba. Louisiana pupae were the smallest on this host in 1998, and none pupated in 1999. There was no difference between Michigan and Manitoba males on sugar maple in 1999.

Development time from egg hatch to adult emergence for both sexes was significantly affected by the main effects of year, population source, and host tree (Table 1). In addition there was a significant population by host tree interaction for both males and females. In pairwise comparisons, Manitoba females had shorter development times than those from Michigan, which in turn, developed more rapidly than Louisiana females on aspen (Fig. 2). This pattern was consistent between years. For males, development on aspen was equally as fast for the Manitoba and Michigan populations, with Louisiana significantly slower in both years. In 1998 and 1999, populations from Manitoba and Michigan developed equally as rapidly when feeding on red oak, a pattern that held for both sexes. Once again, development of the Louisiana population was retarded relative to the other populations, a pattern that held for both sexes. On sugar maple in 1998, Michigan females developed most rapidly, followed by Manitoba and then Louisiana. In 1998, there was no difference between males from Michigan and Mani-

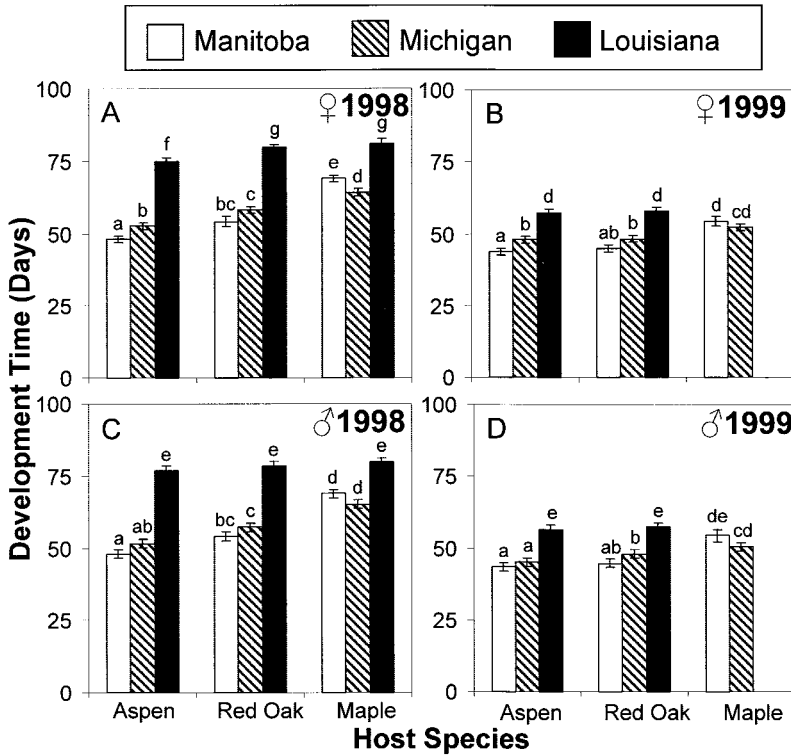


Fig. 2. The effects (LS mean \pm SE) of three northern hosts used for oviposition by forest tent caterpillar on the development from egg hatch to adult for (A) females in 1998, (B) females in 1999, (C) males in 1998, and (D) males in 1999 for Manitoba, Michigan, and Louisiana populations. The experimental unit was the rearing cage (65 larvae); means represent the two cages in each population by host combination. There was no survival in three cages; these were treated as missing cells in the ANOVA. Preplanned pairwise comparisons (LSD) were between each population on a host and between each host for a population. Means with different letters are significantly different at $P < 0.05$.

toba. In 1999, no Louisiana caterpillars completed development. There was no significant difference between the development of either males or females from Manitoba and Michigan on sugar maple in 1999.

Among each of the host trees, females from Manitoba had the shortest development time on aspen, followed by oak and then maple, a pattern that held for both years (Fig. 2). In 1998, Manitoba males developed fastest on aspen, but in 1999, their development on aspen and oak was equally as rapid. Development on sugar maple was slower than either oak or aspen for Manitoba males and females in both years. Michigan females developed more rapidly on aspen than on oak or sugar maple in 1998, but development time was the same on aspen and oak in 1999. For males from Michigan, development time on aspen was shortest in both years. For the Louisiana population in 1998, development time of females was most rapid on aspen. In 1999, development for Louisiana females was equal on aspen and oak. There was no difference in development time among the hosts for Louisiana males in either year.

Year, population source, and host tree species all had significant effects on survival (Table 1). Manitoba and Michigan had high survival on aspen in 1998, and all three populations had good survival on aspen in

1999 (Fig. 3). In 1998, both Manitoba and Louisiana survived poorly on sugar maple. Maple was initially palatable to both Manitoba and Louisiana larvae, although their growth clearly lagged relative to Michigan larvae on the same host. Once maple leaves had fully expanded, caterpillars from Manitoba and especially Louisiana spent increasing amounts of time wandering rather than feeding. Mortality for these two populations increased after the first few instars. In fact, no Louisiana caterpillars survived past the fourth instar on sugar maple in 1999. Many of the Manitoba larvae that did complete development on sugar maple underwent an additional molt, completing six instars instead of the usual five.

Southern Host Tree Study. As with the northern study, host tree species had large effects on forest tent caterpillar pupal mass. There were significant main effects of host trees on both male and female pupal mass and a significant interaction between host species and source population for both sexes (Table 2). The main effect of population source on pupal mass was significant only for males. When populations were compared on a single host, Manitoba and Michigan females had the highest pupal mass on water oak in both years (Fig. 4). In contrast, Louisiana females grew largest on water tupelo in both 1998 and 1999.

Table 2. ANOVA for the effects of year (Y), source population (P), and three species of trees used by southern populations as ovipositional hosts (H) on pupal mass, development time, and survival of forest tent caterpillar

	Source	df	Female			Male		
			MS	F	P	MS	F	P
Pupal mass	Year	1	0.009	11.0	<0.005	0.001	6.5	<0.03
	Population	2	0.000	0.18	0.85	0.001	7.1	<0.007
	Host	2	0.019	22.8	<0.001	0.005	31.4	<0.001
	P × H	4	0.026	30.8	<0.001	0.006	29.4	<0.001
	Y × P	2	0.006	7.7	<0.005	0.001	5.5	<0.02
	Y × H	2	0.011	12.7	<0.001	0.004	22.5	<0.001
	Y × P × H	4	0.004	4.3	<0.03	0.000	2.2	0.13
	Error	16	0.001			0.0002		
Development time	Year	1	123.9	24.1	<0.001	91.0	19.8	<0.001
	Population	2	369.6	71.9	<0.001	405.7	88.2	<0.001
	Host	2	292.6	56.9	<0.001	320.5	69.7	<0.008
	P × H	4	38.4	7.5	<0.02	42.9	9.3	<0.001
	Y × P	2	1.1	1.1	0.80	3.4	0.7	0.50
	Y × H	2	61.5	11.9	<0.001	71.4	15.5	<0.001
	Y × P × H	4	9.3	1.8	0.19	8.7	1.9	0.18
	Error	16	5.1			4.5		
Survival (males and females combined)	Year	1	0.21	8.9	<0.008			
	Population	2	0.68	28.3	<0.001			
	Host	2	0.24	10.0	<0.002			
	P × H	4	0.07	2.9	<0.05			
	Y × P	2	0.01	0.5	0.65			
	Y × H	2	0.13	5.4	<0.02			
	Y × P × H	4	0.02	0.9	0.47			
	Error	18	0.02					

Analyses were conducted using cage means (N = 36). Three cages had no survival; these were treated as missing cells in the ANOVAs for pupal mass and development time. Source populations were from Manitoba, Louisiana, and Michigan. Host trees used were water oak, sweetgum, and water tupelo.

Results were less consistent for sweetgum, with Michigan females largest in 1998 and smallest in 1999. The magnitude of the effects was generally less for males, although trends were similar to those of females. On water oak, Manitoba males were largest, followed by Michigan. On water tupelo, males from Louisiana attained the greatest mass in 1998, but in 1999, Michigan males were as large.

There were significant main effects of year, population and host species on development time of both

males and females (Table 2). In addition, the interaction between population and host was significant for both sexes. As with the northern tree species above, both Louisiana females and males consistently required more days to complete development on each of the southern host species, although the difference was not significantly greater than for Michigan females on water tupelo in 1999 and females from Manitoba on sweetgum in 1999 (Fig. 5). Both male and female Manitoba and Michigan caterpillars developed most

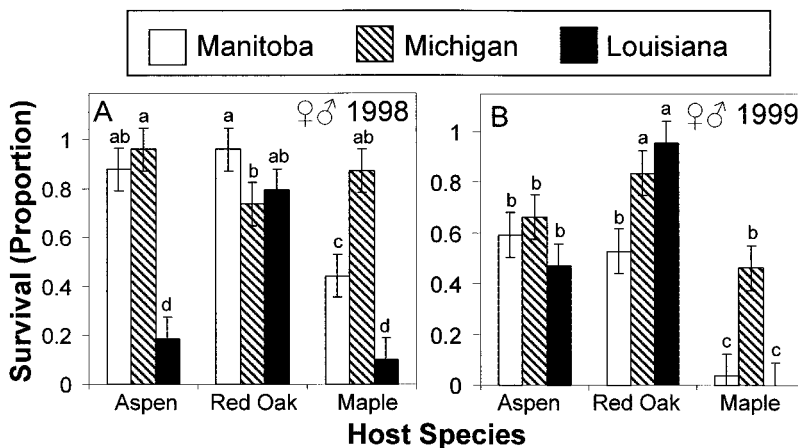


Fig. 3. The effects (LS mean ± SE) of three northern hosts used for oviposition by forest tent caterpillar on the survival of (A) combined sexes in 1998 and (B) combined sexes in 1999 for Manitoba, Michigan, and Louisiana populations. The experimental unit was the rearing cage (65 larvae); means represent the two cages in each population by host combination. Preplanned pairwise comparisons (LSD) were between each population on a host and between each host for a population. Means with different letters are significantly different at P < 0.05.

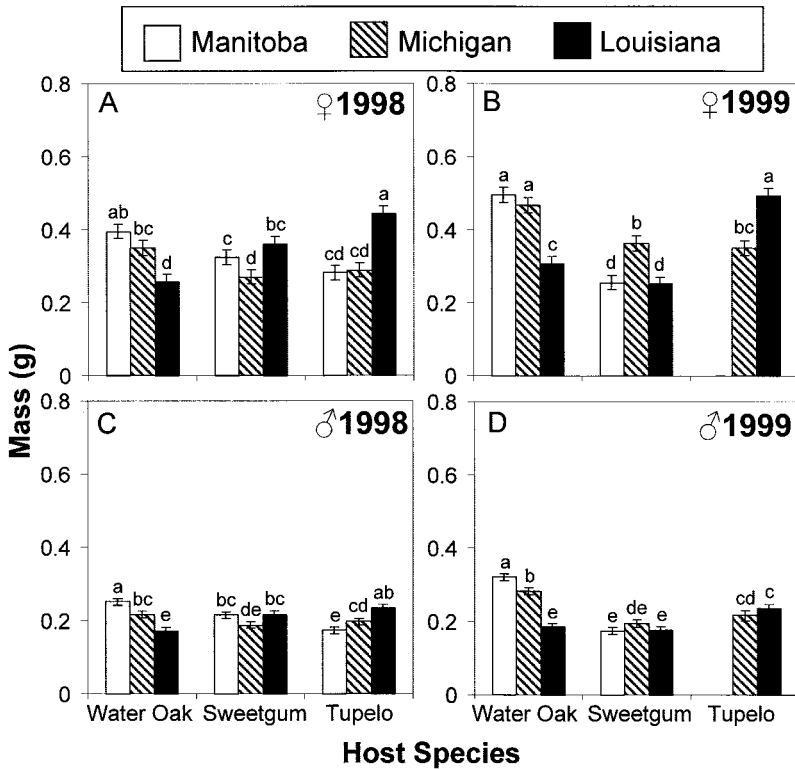


Fig. 4. The effects of three southern host trees on the pupal mass (LS mean \pm SE) from egg hatch to adult for (A) females in 1998, (B) females in 1999, (C) males in 1998, and (D) males in 1999. Forest tent caterpillar populations from Manitoba, Michigan, and Louisiana were reared on each host species. Means were calculated from two replicate cages in each population by host combination. There was no survival in three cages; these were treated as missing cells in the ANOVA. Preplanned pairwise comparisons (LSD) were between each population on a host and between each host for a population. Means with different letters are significantly different at $P < 0.05$.

rapidly on oak in each year. In contrast, Louisiana females developed equally as rapidly on water oak and water tupelo in 1998 and on water oak and sweetgum in 1999. In 1998, Louisiana males developed equally as rapidly on oak and tupelo, whereas in 1999, tupelo and sweetgum provided the fastest development.

There were strong main effects of year, host, and source population on survival in the southern rearing experiment (Table 2). There was also a significant population by host interaction. Louisiana caterpillars survived well on all three southern hosts in each year (Fig. 6). Survival was dramatically reduced for Manitoba larvae on water tupelo, with 23% surviving in 1998 and none surviving in 1999. This population also fared poorly on sweetgum (14 and 26% survival in 1998 and 1999, respectively). Survival of Michigan larvae was intermediate and did not exhibit a consistent pattern between years.

Discussion

Our study strongly supported the hypothesis that the forest tent caterpillar is a composite of regional populations adapted to specific host trees. In both the northern and southern host experiments, populations

of *M. disstria* varied significantly in their ability to use host trees favored by other regional populations. Performance was especially variable on sugar maple, a primary host used by some midwestern and north-eastern populations (Connola et al. 1957, Eggen 1987), and water tupelo, favored by populations in south-eastern states and along the Gulf coast (Stark and Harper 1982, Goyer et al. 1987). The range of sugar maple does not extend to either Louisiana or Manitoba, and water tupelo is restricted to the southeast and Gulf States (Burns and Honkala 1990). However, a strong geographical relationship was not evident between forest tent caterpillar and oaks, even though the Manitoba population was far north of the range of any North American *Quercus*. Trees in this genus may be good hosts for forest tent caterpillar populations, irrespective of their geographical origin.

Louisiana caterpillars developed more slowly on all hosts in both the northern and southern studies even though their pupal masses varied by five-fold among the different hosts, and they grew larger than any other population on water tupelo. This suggests that the rate of larval development has a strong genetic component and is much less plastic than pupal mass. The protracted development in the Louisiana popu-

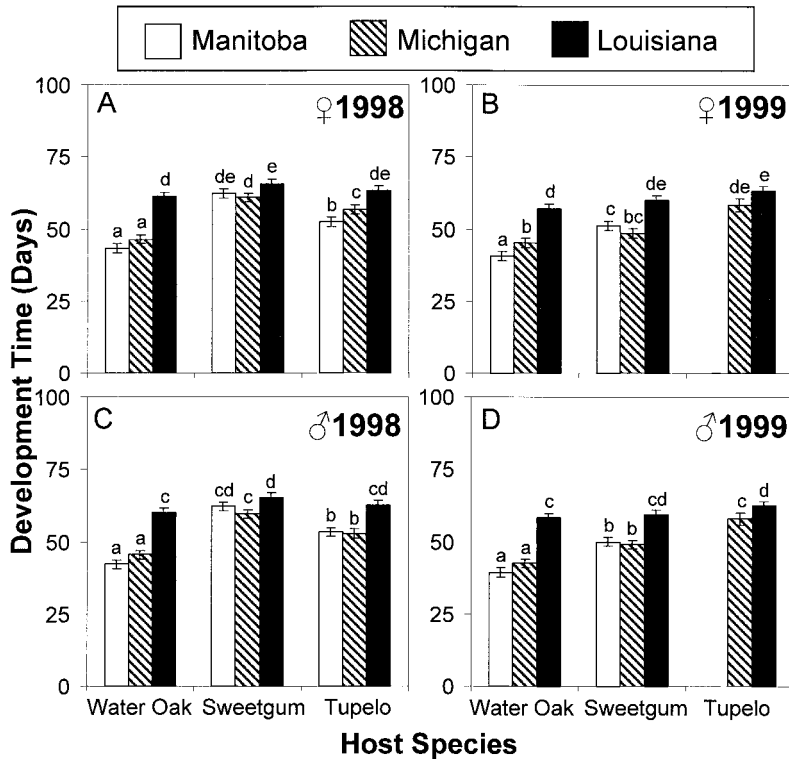


Fig. 5. The effects of three southern host trees on the development time (LS mean \pm SE) from egg hatch to adult for (A) females in 1998, (B) females in 1999, (C) males in 1998, and (D) males in 1999. Forest tent caterpillar populations from Manitoba, Michigan, and Louisiana were reared on each host species. Means were calculated from two replicate cages in each population by host combination. There was no survival in three cages; these were treated as missing cells in the ANOVA. Preplanned pairwise comparisons (LSD) were between each population on a host and between each host for a population. Means with different letters are significantly different at $P < 0.05$.

lation may be the result of the significantly smaller size of hatching neonates, as was shown by Parry et al. (2001). They speculated that smaller initial size may lengthen the larval period because adults attain similar mass in both northern and southern populations.

There were significant effects of year in both the northern and southern experiments. Because the population sources were the same in each year and the experimental protocol was very similar, variation in tree quality is the most likely source of this variation. Not all the host trees used in the experiment were the same in each year, and phytochemistry can vary substantively between trees (e.g., Osier et al. 2000, Tikkanen and Julkunen-Tiitto 2003). In addition, phenology among individual trees was variable. This was especially apparent for red oak in the northern host tree study and sweetgum in the southern host tree study. We minimized the potential effect of individual trees by using a different tree on each feeding date and allocating the foliage collected on each date evenly among all cages receiving that treatment. Development times were generally shorter and pupal masses were larger on most host by population combinations in 1999 relative to the same combinations in 1998 in the northern host tree study. While there was year to year

variation among the different southern hosts, there was not a consistent pattern.

A paradoxical result of our study was the relatively poor performance of Michigan larvae on sugar maple, an ovipositional host used frequently by this population. The Michigan population performed much better on red oak and trembling aspen. In natural populations in Michigan, we occasionally have found large egg masses on sugar maple, but the progeny of these egg masses perform no better than any other larvae reared on sugar maple (D. Parry, unpublished observation), suggesting that the parents likely fed on other tree species before oviposition on maple. Other studies indicate that forest tent caterpillar performance on sugar maple is only moderate, at least in Quebec, with female pupal masses ranging from 210 to 400 mg (Fortin and Maufette 2001, 2002), similar to our Michigan population. Perhaps sugar maple confers other benefits such as reduced parasitism or susceptibility to disease, although one study showed that susceptibility to the pathogen *Bacillus thuringiensis* Berliner is 100-fold greater on sugar maple than on aspen (Kouassi et al. 2001). Another possibility is that maple is phenologically better matched with the early hatch of forest tent caterpillar than some other hosts. On numerous

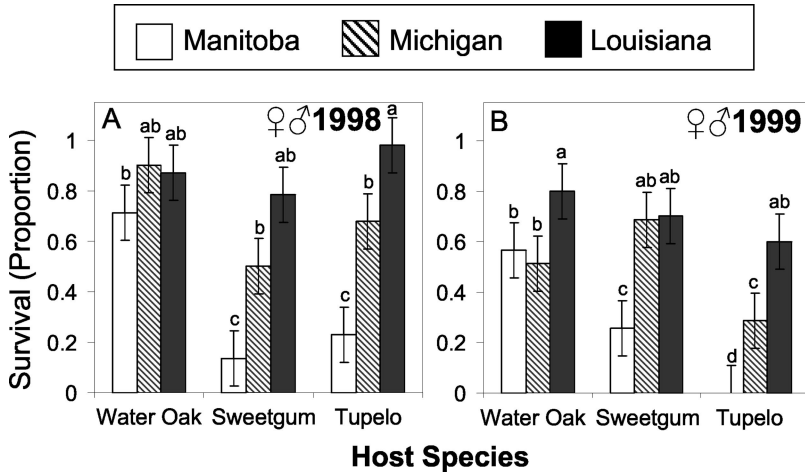


Fig. 6. The effects of three southern host trees on the survival (LS mean \pm SE) from egg hatch to adult for three populations of forest tent caterpillar. (A) Pooled males and females in 1998 and (B) pooled males and females in 1999. Forest tent caterpillar populations from Manitoba, Michigan, and Louisiana were reared on each host species. Means were calculated from two replicate cages in each population by host combination. Preplanned pairwise comparisons (LSD) were between each population on a host and between each host for a population. Means with different letters are significantly different at $P < 0.05$.

occasions, we observed that *M. disstria* hatches too early relative to bud break, and the neonates starve to death on individual late flushing red oak trees (D. Parry, personal observation). In some areas of its range, such as northern New York, however, sugar maple is an important primary host and supports expansive outbreaks (Connola et al. 1957, Eggen 1987), suggesting that mediocre performance on sugar maple is not universal.

We did not condition our populations to the hosts before conducting our experiment. Some herbivorous insects have been shown to have different responses to hosts after they have completed a generation on them (e.g., Jermy 1987, Ting et al. 2002, Ikonen et al. 2003). While conditioning could change the outcome of laboratory experiments, interaction between less plastic traits such as development time and the phenology of egg hatch may negate these changes in the field. In an attempt to address this aspect of host use, Louisiana, Michigan, and Manitoba females reared on red oak and aspen in this study were allowed to oviposit on each of these hosts in Michigan, and the resulting egg bands were left in situ over winter. All egg bands survived and successfully hatched the following spring. However, Manitoba larvae emerged 10–14 d before bud break and starved, whereas Louisiana caterpillars emerged 12–16 d after bud break and could not complete development on the maturing foliage of either host (D. Parry and W. J. Mattson, unpublished data). This suggests that large genetically fixed differences in hatch phenology may have a much greater effect on performance than small improvements in feeding efficiency because of conditioning. Forest tent caterpillars have previously been shown to be very sensitive to phenological asynchrony (Robison and Raffa 1994, Parry et al. 1998), and changes of

the magnitude described above were sufficient to eliminate the nonsynchronized populations.

There are genetically based differences among regional populations of forest tent caterpillar for a number of traits, including enzymes (Lorimer 1979a, b) and several reproductive parameters, such as the number of eggs, mass of individual eggs, and neonate size (Parry et al. 2001). Our study showed that there are also differences in host suitability for different populations. However, the origin and maintenance of the geographic adaptations shown in this and the aforementioned studies are puzzling, given that forest tent caterpillar adults seem to have strong dispersal capabilities, and the species occurs continuously throughout most of its range. Thus, possible isolating factors are not obvious from the ecology and distribution of the species. Furthermore, in a related species, the eastern tent caterpillar, *M. americanum* (F.), little genetic variation was found over a wide area of eastern North America, which was attributed to high levels of gene flow among different populations (Costa and Ross 1994). However, the diet of eastern tent caterpillar is much narrower than that of the forest tent caterpillar; it feeds on only a few species of *Prunus* and *Malus* across the entirety of its range.

Host plant specialization can occur through changes to an insect's phenology. Phenological differences among populations have been implicated in the development of host races and even speciation in some phytophagous insects. These differences can be maintained despite continued gene flow (Feder and Filchak 1999, Dres and Mallet 2002). We suggest that variable phenology is a plausible explanation for geographic differences among populations of forest tent caterpillar. Larvae feeding on different host species may develop at different rates, leading to phenological

differences in adult emergence times. Because adults live for only a few days, they may not encounter adults originating from other host species. If adults show some fidelity to their larval host, specialization could develop. Full phenological separation is unlikely because adult flight periods are likely to overlap among several different hosts. In addition, final instars leave their natal tree, wandering extensively while feeding on a broad array of secondary host species, which would tend to counteract any effects of primary host species on earlier stage caterpillars. Nonetheless, at least at the regional scale used in our study, some host specialization has occurred, suggesting that impediments to gene flow may exist.

In conclusion, our study showed that there are strong regional differences in the ability of forest tent caterpillar to use different primary host species. Understanding driving mechanisms underlying regional differences in host utilization, preferences, and other geographically variable traits in forest tent caterpillar populations would be an interesting area of future research.

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