Survival and Development of *Lymantria monacha* (Lepidoptera: Lymantriidae) on North American and Introduced Eurasian Tree Species

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ABSTRACT *Lymantria monacha* (L.) (Lepidoptera: Lymantriidae), the nun moth, is a Eurasian pest of conifers that has potential for accidental introduction into North America. To project the potential host range of this insect if introduced into North America, survival and development of *L. monacha* on 26 North American and eight introduced Eurasian tree species were examined. Seven conifer species (*Abies concolor*, *Picea abies*, *P. glauca*, *P. pungens*, *Pinus sylvestris* with male cones, *P. menziesii* variety *glauca*, and *Tsuga canadensis*) and six broadleaf species (*Betula populifolia*, *Malus x domestica*, *Prunus serotina*, *Quercus lobata*, *Q. rubra*, and *Q. velutina*) were suitable for *L. monacha* survival and development. Eleven of the host species tested were rated as intermediate in suitability, four conifer species (*Larix occidentalis*, *P. nigra*, *P. ponderosa*, *P. strobus*, and *Pseudotsuga menziesii* variety *menziesii*) and six broadleaf species (*Carpinus caroliniana*, *Carya ovata*, *Fagus grandifolia*, *Populus grandidentata*, *Q. alba*, and *Tilia cordata*) and the remaining 10 species tested were rated as poor (*Acer rubrum*, *A. platanoidies*, *A. saccharum*, *F. americana*, *Juniperus virginiana*, *Larix kaempferi*, *Liriodendron tulipfera*, *Morus alba*, *P. taeda*, and *P. deltoides*). The phenological state of the trees had a major impact on establishment, survival, and development of *L. monacha* on many of the tree species tested. Several of the deciduous tree species that are suitable for *L. monacha* also are suitable for *L. dispar* (L.) and *L. mathura* Moore. Establishment of *L. monacha* in North America would be catastrophic because of the large number of economically important tree species on which it can survive and develop, and the ability of mated females to fly and colonize new areas.

KEY WORDS *Lymantria monacha*, host plant suitability, development, survival

Lymantria monacha (L.) (Lepidoptera: Lymantriidae) (nun moth) is a Eurasian pest of conifers that poses an ever-present threat of being introduced into North America. Adults are readily attracted to artificial lights and have been observed in Russian Far East ports (Munson et al. 1995). *L. monacha* has a high potential to be transported via commerce because, although eggs are normally laid in bark crevices, they also could be deposited in crevices on containers, pallets, and ships. *L. monacha* feeds primarily on needles and male cones of conifers (*Picea, Pinus, Abies,* and *Larix* spp.) but also can develop on leaves of deciduous trees and shrubs (*Fagus, Carpinus, Betula,* and *Quercus* spp.) (Sliwa 1987). Its establishment in North America would be disastrous because of its polyphagous feeding habits, ability to colonize new habitats, and capacity to be spread rapidly by flying adult females. Literature on the pheromones, microbial control, and general biology and biological control of *L. monacha* exists (Gries et al. 1996, Glowacka 1989, Švestka 1971, Jensen 1991, Silwa 1987, Grijpma 1989). The best defenses currently used against this potential pest are to monitor its abundance in Eurasian ports (Munson et al. 1995), develop a good pheromone trap to monitor for it (Morewood et al. 1999), and educate people on how to identify it (Keena et al. 1998). However, there is little useful information that addresses the problems that would be encountered should *L. monacha* be introduced into North America. To predict the risk of successful establishment in various North American forest ecosystems and the potential damage to those systems, knowledge of the nun moth's ability to survive and develop on various North American host plants is required.

In Europe, the two species *L. monacha* prefers and most often damages are *Picea abies* (L.) (Norway spruce) and *Pinus sylvestris* L. (Scots pine) (Lipa and Glowacka 1995). Sliwa (1987) provides an extensive list of the intensity of natural feeding of *L. monacha* larvae on trees and shrubs in Poland during the last major outbreak there between 1978–1984. Laboratory investigations of nun moth preferences and utilization of Eurasian host plants provide limited and contradictory information (Bejer 1988). For example, labora-

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tory studies rank the preferred species—spruce, pine, and larch—as intermediate to low in food value (Bejer 1988). Most of the host plant work done on *L. monacha* has concentrated on the relationships between bud burst of the main hosts, *P. abies* and *P. sylvestris*, and hatching of *L. monacha* larvae. This work has shown that host phenology is as important as host preference in determining the survival and successful development of *L. monacha* larvae. For example, when larvae hatch before foliage bud burst the presence of male cones on *Pinus* spp. is critical to larval survival and growth since first and second instar larvae cannot feed on the previous year's foliage because of the toughness of the needles and the secondary compounds they contain (Bejer 1988).

This study compared the survival and development of *L. monacha* larvae during their first 14 d on 26 North American and 8 introduced Eurasian host plants. Larvae on 11 of the hosts used for the 14-d study were allowed to complete their development on those hosts. The host plants used were from a broad range of tree genera, representing the major forest types present in North America and included many of the major species of economic importance. Species from Eurasia provided a basis for comparison with the results of European research and provided information on exotic hosts commonly grown in urban areas of North America. The risk of successful establishment in various North American forest ecosystems, should *L. monacha* become established, is discussed.

Materials and Methods

Insects. Eggs produced by 200 female *L. monacha* (third laboratory generation) originally from Predin, Czech Republic, were pooled and chilled at 5 ± 1°C and ≈100% RH with L:D of 16:8 for 144 d (first setup) or 151 d (second setup). From the pool of mixed eggs, 16 and eight packets of ≈500 eggs each were made for the first and second setups, respectively. The eggs were surface sterilized to kill potential pathogens by submerging the egg packets in 10% formalin for 15 min, rinsing in lukewarm tap water for 15 min and letting them dry in a hood for no longer than 60 min. The eggs were incubated at 25 ± 1°C and 60% RH a photoperiod of 16:8 (L:H) h for 6–7 d. Date of first hatch of egg packets and total percentage hatch were recorded as quality control checks.

All larvae hatching from incubated eggs were removed every other day with a fine camel hair brush into small, tight fitting preweighed petri dishes. Thirty larvae were placed in each petri dish, the larvae and petri dish were weighed together, and then the weight of the dish was subtracted to determine the weight of the larvae. Average initial weight of the larvae in each set was calculated. To prevent desiccation after weighing, the dishes with larvae were held in a water box at 5 ± 1°C and 100% RH with photoperiod of 16:8 (L:H) h. Additionally, *L. monacha* larvae generally spend a few days resting near the egg mass before searching for food (Lipa and Glowacka 1995). All the dishes of larvae available for setup on a particular day were randomly assigned to each foliage type and any larvae that had died were replaced with extra larvae from the same hatch removal date.

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

Tree Species. Foliage of 1 to 7 trees of 26 North American and 8 Eurasian tree species (Table 1) was obtained, primarily from laboratory property at Ansonia and Hamden (CT), for use in these studies. Larvae were reared to adults on 11 of the host species (*A. rubrum, B. populifolia, F. grandifolia, Q. alba, Q. velutina, L. kaempferi, P. abies, P. glauca, P. strobus, P. sylvestris* (with male cones), and *P. menziesii* variety *glauca*), which represented a range of genera and predicted suitability based on European literature, and served as the basis for developing criteria to predict suitability of all the hosts after only 14 d of rearing. The setup period, 5–13 May, was chosen based on the predicted time of *L. monacha* hatch and bud break of trees at 41.3° N latitude. Because of the large number of hosts that were to be tested, hosts on which the larvae were to be reared to adults and 12 of the 14-d hosts were set up on 5 May (conifers) and 6 May (deciduous) (Table 1). The remaining 12 of the 14-d hosts were set up on 12 May (conifers) and 13 May (deciduous) (Table 1). The only hosts included in both set up times were *P. glauca* and *P. sylvestris* (first setup without males cones and second setup with them); in both cases, the two sets are reported separately in the results section.

Initial Setup. Short branch tips (15–25 cm long) with foliage were clipped from the trees. Clippings from conifers included both the current and previous year's foliage, and flower buds/cones if available. Clippings from deciduous trees included both foliage and flowers, if available (see Table 1 for flowering times relative to the setup for each species). For initial setup, all branch tips came from the same tree and had foliage/flowers of similar size and age present on them. For subsequent foliage changes, foliage was collected from the other individual trees being used in a sequential rotation. The trees used varied in their phenology within each host species. The ends of the branches that were clipped were kept in de-ionized water until used later in the day. Insects and debris found on the foliage were removed or washed off with de-ionized water. If the leaves were washed, they were allowed to dry before being used.

The ends of each branch tip were inserted through a hole in a plastic lid of a 256-ml plastic cup that served as a de-ionized water reservoir and the tip recut underwater before the lid was snapped onto the cup. One or more branch tips were placed in each plastic cup depending on the amount of foliage the larvae required. All plastic cups for a given tree species received the same number of branch tips at each foliage change. One plastic cup containing foliage and 30 larvae was placed in each 3.8-liter rolled paper-rearing container. A piece of clear plastic wrap was used to replace the lid, allowing light to enter the container. Three containers were set up (a total of 90 larvae) for

Table 1. Tree species tested as potential hosts for *L. monacha* in the spring of 1998

Scientific name	Common name	# Trees and type[a]	Leaf bud break[b]	Setup date	Native region
Aceraceae					
A. rubrum L.	Red maple	7 large trees	13 April	6 May	E North America
A. platanoides L.	Norway maple	1 large tree	20 April	13 May	Europe
A. saccharum Marshall	Sugar maple	7 large trees	13 April	6 May	E North America
Betulaceae					
B. populifolia Marshall	Gray birch	6 large trees	3 April	6 May	NE North America
C. caroliniana Walter	American hornbeam	3 large trees	13 April	13 May	E North America
Fagaceae					
F. grandifolia Ehrhart	American beech	1 large tree	5 May	6 May	E North America
Q. alba L.	White oak	2 large trees	2 May	6 May	E North America
Q. lobata Née	California white oak	3, 1.5 m potted trees	20 April	13 May	California, USA
Q. rubra L.	Northern red oak	5, 2.1 m potted trees	20 April	6 May	E North America
Q. velutina Lamarck	Black oak	7 large trees	20 April	6 May	E North America
Juglandaceae					
C. ovata (Miller) K. Koch	Shagbark hickory	3 large trees	4 May	13 May	E North America
Magnoliaceae					
L. tulipifera L.	Yellow poplar	3 large trees	3 April	13 May	E North America
Moraceae					
M. alba L.	White mulberry	1 large tree	13 April	13 May	China
Oleaceae					
F. americana L.	White ash	3 large trees	20 April	13 May	E North America
Rosaceae					
P. serotina Ehrhart	Wild cherry	5 large trees	3 April	13 May	North America
M. domestica (no author)	Apple	2 large trees	3 April	13 May	Eurasia
Salicaceae					
P. deltoides Bartram	Eastern cottonwood	3 large trees	20 April	6 May	E. North America
P. grandidentata Michaux	Bigtooth aspen	2 large trees	3 April	6 May	NE North America
Tiliaceae					
T. cordata Miller	Littleleaf linden	3, 1.5 m potted trees	3 April	13 May	Europe
Cupressaceae					
J. virginiana L.	Eastern red cedar	2 large trees	1 May	12 May	E North America
Pinaceae					
A. concolor (Gordon) Lindley	White fir	1, 1.5 m tree	8 May	5 May	Western North America
L. kaempferi (Lambert) Carrière	Japanese larch	3 large trees	25 March	6 May	Central Japan
L. occidentalis Nuttall	Western larch	3, 0.9 m potted trees	25 March	6 May	W North America
P. abies Karsten	Norway spruce	3 large trees	30 April	5 May	Europe
P. glauca (Moench) Voss	White spruce	4 large trees	30 April	5 May 12 May	N North America
P. pungens Engelman	Colorado spruce	1 large tree	8 May	5 May	Western U.S., North America
P. nigra Arnold	Black pine	4 large trees	15 May	5 May	Europe
P. ponderosa Lawson	Ponderosa pine	3, 1.5 m potted trees	8 May	5 May	W North America
P. strobus L.	Eastern white pine	7 large trees	5 May	5 May	NE North America
P. sylvestris L.	Scots pine	3, 1.8 m potted trees 2 large trees	15 May	5 May 12 May[c]	Eurasia
P. taeda L.	Loblolly pine	3, 1.5 m potted trees	30 April	5 May	SE North America
P. menziesii var. glauca (Beissner) Franco	Rocky Mountain Douglas Fir	1 large tree	30 April	5 May	Rocky Mountains, North America
P. menziesii var. menziesii (Mirbel) Franco	Coast Douglas Fir	1 large tree	8 May	5 May	Pacific Coast, North America
T. canadensis (L.) Carrière	Eastern hemlock	4 large trees	8 May	12 May	NE North America

[a] Large trees were either landscape or forest trees. Shorter trees that were not in pots were at a tree farm planted in the ground.
[b] Before the study started, leaf bud break was checked weekly and the date given was the first week that buds were open. After the study started bud break was checked three times a week.
[c] The second setup of *P. sylvestris* had male cones and foliage but the first setup had only foliage.

each tree species with larvae that were assessed for only the first 14 d of development, and six containers were set up (a total of 180 larvae) for each tree species with larvae that went through their entire development. There was one exception to this; six containers were set up for *P. sylvestris* without cones because larvae initially were to be allowed to complete development on it, but because of high mortality, this treatment was terminated at 14 d. The additional larvae were set up on hosts on which the larvae were reared to adults in an attempt to have ≥30 individuals of each sex survive to adult. All rearing containers for each host species were set up on the same day with the exception of those for *P. glauca.* A perfume and dye free facial tissue was draped over the plastic cup to ensure that larvae that fell to the bottom could easily climb back up to the branch. The containers were held at 25 ± 2°C and 60 ± 5% RH with a photoperiod of 16:8 (L:D) h.

Because only three potted trees of *P. ponderosa* with few leaders were available, cutting tips was not possible. Instead, 30 larvae were placed in a mesh bag on each tree and the trees were held at the same environmental conditions as the rearing containers. At 7 d, the bags were opened, all larvae removed, data collected as described for the other tree species, and the larvae put back in the bags on the trees.

Foliage Changes. Deciduous foliage (which included the *Larix* spp.) was changed every Monday, Wednesday, and Friday. Conifer foliage was changed every Tuesday and Friday. The timing of foliage change was based on previous experience indicating that conifer foliage is more stable under these conditions than is deciduous foliage. For all foliage changes the plastic cup with old foliage was removed and placed on the rearing container lid in a safety hood. All frass and other debris in the rearing container also were emptied onto the lid. The rearing container, old leaves, and debris were searched for live and dead larvae and their numbers recorded. Observations of what host tissues the larvae fed on were made at day 2 and at all subsequent foliage changes. If diseased larvae were found, all surfaces of the rearing container were cleaned with a weak Zephiran chloride solution before a new, clean cup containing fresh foliage was placed in the container and all live larvae placed onto the foliage.

Larval Development (14 d). After the larvae had been on the foliage for 14 d, the number of live larvae and the weight and instar of each larva were recorded, and the average initial larval weight was subtracted to determine weight gain over the first 14 d. Percentage survival was calculated as the number of live larvae per rearing container minus the number of larvae that were lost or damaged, divided by the initial number of larvae.

For tree species on which the larvae were to continue their development to adult, the number of larvae per rearing container was reduced to a maximum of 15 by increasing the number of containers used and combining larvae from different containers as needed. This was done to prevent the larvae from consuming all of the foliage before the foliage was to be changed. The number of branches of foliage added was determined by the amount being consumed. All containers with the same host foliage received the same number of branches at each foliage change. At each subsequent foliage change, the larvae that had not pupated on each foliage type were consolidated to maintain ≈15 larvae per rearing container.

Pupal and Adult Development. Pupae were removed every Monday, Wednesday, Friday, and Sunday from deciduous foliage and every Tuesday, Thursday, Friday, and Sunday from conifer foliage. Pupae that were newly formed were removed from each rearing container (if possible) and kept with their webbing intact in a labeled 473-ml paper container and weighed the next day. All other pupae were weighed individually the day they were found then grouped by tree species, setup date, and sex in 473-ml paper containers with clear plastic lids. Any pupal deformities observed were recorded along with the weight, sex, and pupation date. Because the pupae were grouped, a correlation between pupal and adult weights could not be obtained.

Pupae were checked daily, adults removed, and eclosion recorded. Adult females were individually placed in 473-ml paper containers labeled with tree species, setup date, and eclosion date. Males that eclosed on the same day were placed in groups (maximum of 10) in 473-ml paper containers labeled with the same information as the females. Adults of both sexes were individually weighed and wing color was recorded. One male from the same tree species was placed in a 473-ml container with a female. The male was chosen arbitrarily from those that had eclosed from that tree species; males that eclosed >2 d previously generally were not used. The mating pairs were held for 2 d in a dark, quiet container because previous tests have shown that *L. monacha* mates better in a dark, quiet environment.

Approximately 2 wk after mating, all eggs laid by each female were harvested, weighed, and embryonation evaluated. This length of time allowed embryonation to proceed to the point that a color change could be observed; embryonated eggs turn dark brown, while unembryonated eggs are blue-green and flattened as a result of dehydration. The percentage of successful matings for each tree species was calculated as the number of matings that produced >10 embryonated eggs divided by the total number of attempted matings.

All eggs from an individual female were placed in a separate tared glassine envelope and weighed. The envelope was then labeled with tree species, setup date, and egg mass number. Egg masses with >10 embryonated eggs after a minimum of 22 d were placed at 5 ± 1°C, ≈100% RH with a photoperiod of 16:8 (L:D) h for 130 d. After incubation at 25 ± 2°C and 60 ± 5% RH with a photoperiod of 16:8 (L:D) h, the percentage hatch of embryonated eggs was calculated and days to first hatch was recorded for each egg mass.

Host Suitability Ratings and Analyses. The 11 hosts that larvae were allowed to complete development on were assigned a host suitability rating based on completion of larval development. A host species was considered poor if <10% of the larvae were able to complete development, intermediate if ≥10% but <60% of the larvae completed development, and suitable if >60% completed development and produced viable eggs. To develop a host suitability rating for all species, it was assumed that the 14 d survival and weight gain data for larvae that completed development on 11 hosts was similar to that for all hosts. The 14-d survival and weight gain data were analyzed for larvae that were allowed to complete development, by host suitability class, and thresholds were developed for each poor, intermediate and suitable class. Using the thresholds for 14 d percent survival and weight gain, all species were assigned a host suitability rating.

To check for container effects on the 14-d weight gain data, the data were ranked and an analysis of variance (ANOVA) of the ranks was carried out to

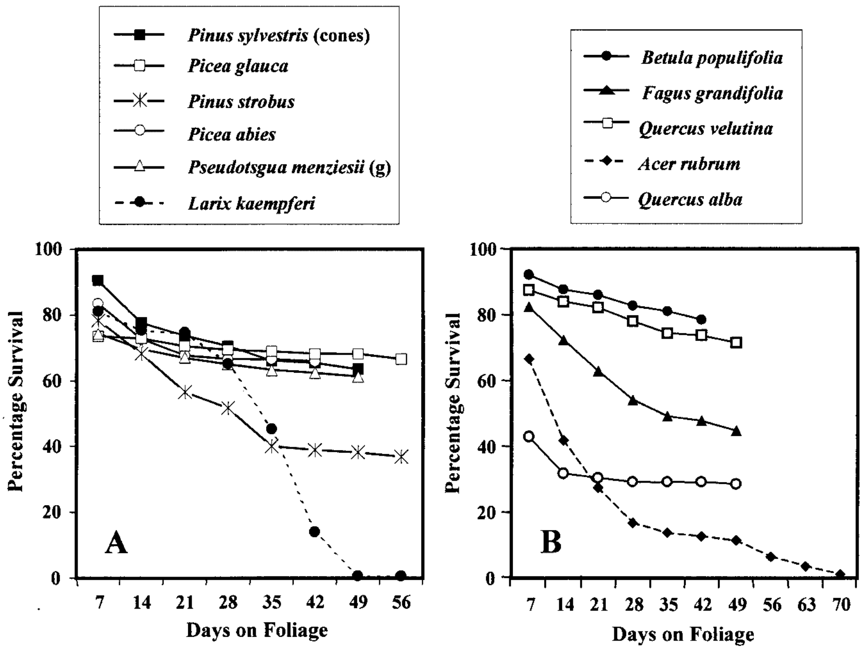

Fig. 1. Percentage survival of *L. monacha* larvae on coniferous (A) and deciduous (B) tree species over the entire larval developmental period. g, *P. menziesii* variety *glauca*, and cones, males cones present with foliage.

approximate a Kruskal–Wallis two-way, nonparametric analysis with container nested within host species (SAS Institute 1989). The nonparameteric test was necessary because of heteroscedasticity in the data and no useful data transformations. A Kruskal–Wallis two-way, nonparametric ANOVA followed by a z test for comparison of groups (Statistix 1998) was run for each sex separately for days to adult and to compare weigh gain for suitability rating groups between the 14d hosts and the hosts that larvae were reared to adult. One-way ANOVA followed by Bonferroni comparison of means (Statistix 1998) were run for each sex separately, on pupal weight, days to pupation, adult weight, days to adult, and fecundity to determine if there were significant differences between suitability rating groups. One-way ANOVA followed by Bonferroni comparison of means (Statistix 1998) was also run to assess sex differences in pupal weight. Linear regression was used to examine relationships between female adult weight and fecundity and total egg weight and fecundity.

Results

Host Suitability Ratings for Larval Development (14 d). Of the 11 host species where *L. monacha* larvae were reared to adult, *B. populifolia, Q. velutina, P. abies, P. glauca, P. sylvestris* (with male cones), and *P. menziesii* variety *glauca* were suitable, *F. grandifolia, Q. alba,* and *P. strobus* were of intermediate suitability and *A. rubrum* and *L. kaempferi* were poor in suitability (Fig. 1). There was little mortality after the first 14 d on suitable hosts while mortality on the other hosts was either high early then leveled off or occurred at varying rates over the whole time period to adults (Fig. 1). Representatives from each rating level were chosen: *P. abies* for suitable, *P. strobus* for intermediate, and *A. rubrum* for poor. *P. abies* was chosen to represent the suitable level because it is a primary host in Europe that does not depend on the presence of male cones for larvae to establish. The latter two species were chosen because larvae on the other host species in their rating level had suitable development and/or survival during part of their developmental period while larvae on *P. strobus* and *A. rubrum* consistently fit the rating level throughout their developmental period.

When the number of individuals in each 14d weight gain group were analyzed for the three representative host species it was found that >90% of the larvae weighing <10 mg at 14 d ultimately died (all three hosts), the majority of larvae from poor host weighed <10 mg, all larvae from intermediate host weighed <50 mg, and larvae reared on the suitable host weighted >50 mg (Fig. 2). Based on this information, 14d suitability criteria for weight gain were developed (poor, weight gain averaging ≤10 mg; intermediate, weight gain averaging >10 mg and ≤50 mg; and suitable, weight gain averaging >50 mg) and applied (Figs. 3 and 4). These weight gain categories also have developmental significance; larvae that are still first instars have gained <10 mg (5.7 ± 1.1 mg [average ± SE] on suitable hosts), second instars gain <50 mg (30.9 ± 1.6 mg on suitable hosts) before they molt, and third instars on suitable hosts gain just over 50 mg (55.7 ± 1.3 mg) before they molt. Third instars on

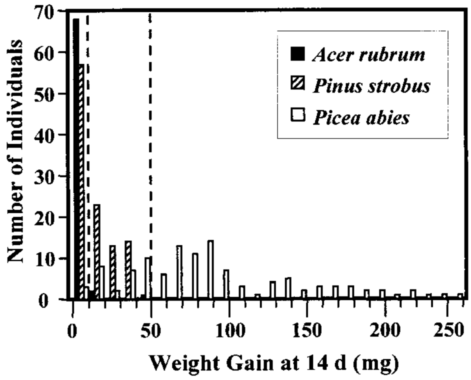

Fig. 2. Number of individuals by weight gain at 14 d for a suitable (*P. abies*), intermediate (*P. strobus*), and poor (*A. rubrum*) host.

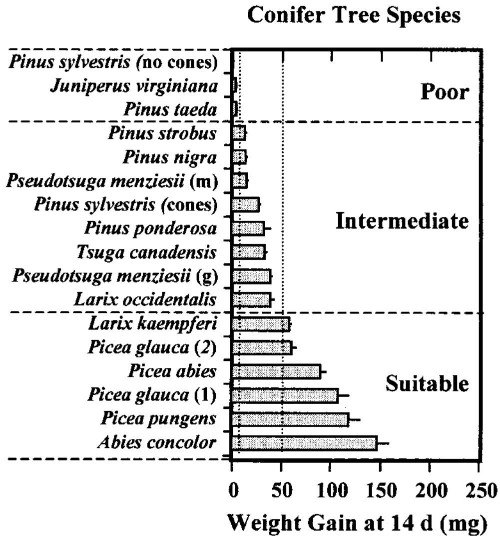

Fig. 4. Conifer host species suitability ratings for *Lymantria monacha* based on mean larval weight gain (±SE) at 14 d. Ratings: poor, mean weight gain <10 mg; intermediate, mean weight gain ≥10 mg and <50 mg; suitable, mean weight gain ≥50 mg. g, *P. menziesii* variety *glauca*; m, variety *menziesii*; cones, males cones present with foliage; no cones, no males cones present with the foliage; 1 and two refer to the first and second setups on this host.

intermediate and poor hosts tend to molt before they have gained 50 mg (34.0 + 6.1 for poor hosts and 37.0 + 1.5 for intermediate hosts). When 14 d hosts and hosts that larvae were reared to adult were compared significant differences in 14 d weight gain between but not within each suitability-rating group were found ($F = 421$, $P = 0.0000$, df = 5, 2077, z = 2.94). Rearing container had a significant effect on larval weight gain ($F = 2.93$; df 98, 1949; $P < 0.0001$) during the first 14 d, but this did not appear to affect the suitability ratings for any of the hosts.

Criteria for percentage survival after 14 d of larvae with 14d weight gain of >10 mg also were assigned (poor, ≤10% of surviving larvae with weight gain >10 mg; intermediate, >10% but ≤60% of surviving larvae with weight gain >10 mg and suitable >60% of surviving larvae with weight gain >10 mg) and applied (Figs. 5 and 6). All but three host species classify the same using 14 d weight gain and 14 d percent survival: *P. sylvestris* with males cones, *T. canadensis,* and *P. serotina* classify as suitable using the percentage survival criteria and as intermediate using the weight gain criteria (Figs. 3–6). Two species on which the larvae were reared to adult were misclassified using the 14-d criteria–*L. kaempferi* and *F. grandifolia* (Figs. 3–6). Larvae on both of these host species initially developed and survived well but experienced difficulties later. When larvae on *L. kaempferi* reached the late third to early fourth instar they refused to feed on the foliage, began wandering, and chewing the clear plastic cover, and ultimately died. At 12 d on *F. grandifolia,* the larvae (about the fourth instar) began producing stringy, watery frass, signs of difficulty in digesting the leaves.

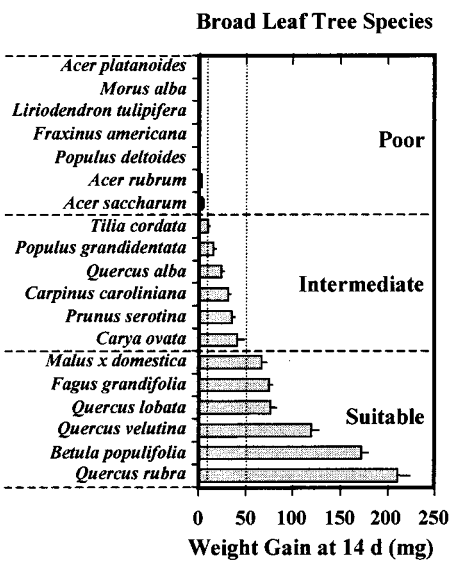

Fig. 3. Broadleaf host species suitability ratings for *Lymantria monacha* based on mean larval weight gain (±SE) at 14 d. Ratings: poor, mean weight gain <10 mg; intermediate, mean weight gain ≥10 mg and <50 mg; suitable, mean weight gain ≥50 mg.

Feeding Observations. *Lymantria monacha* initiated feeding on all conifers tested (Table 2). On *J. virginiana* and *P. sylvestris* without male cones or newly expanded foliage the larvae fed little and spent most of their time off the host wandering and producing silk. On *T. canadensis,* larvae fed only on newly expanded foliage, and on *P. strobus* larval feeding was light on both previous year's and newly expanded foliage. In both *P. sylvestris* and *P. nigra,* the larvae fed exclusively on male cones for the first 2 wk until the new foliage appeared, covering themselves completely in the yellow pollen. For most conifer species tested, the order of tissue preference of first and sec-

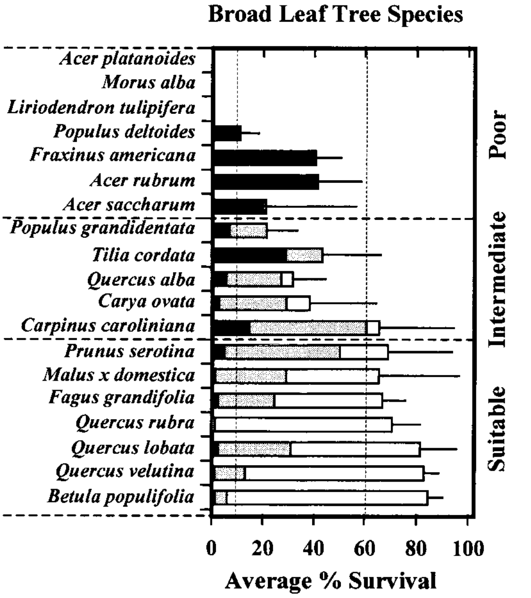

Fig. 5. Broadleaf host species suitability ratings for *Lymantria monacha* based on percentage survival of larvae with 14-d weight gain >10 mg (shaded plus open bars). Ratings: poor, ≤10% survival; intermediate, >10% but ≤60% survival and suitable >60% survival. Weight classes: black bars, ≤10 mg; shaded bars, >10 and ≤50 mg; and open bars, >50 mg.

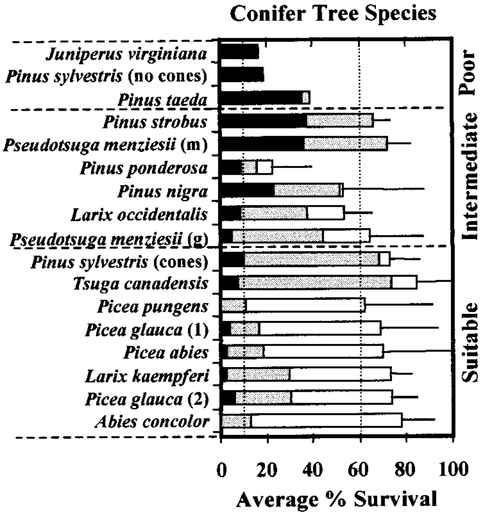

Fig. 6. Conifer host species suitability ratings for *Lymantria monacha* based on percentage survival of larvae with 14-d weight gain >10 mg (shaded plus open bars). Ratings: poor, ≤10% survival; intermediate, >10% but ≤60% survival and suitable >60% survival. Weight classes: black bars, ≤10 mg; shaded bars, >10 and ≤50 mg; and open bars, >50 mg. g, *P. menziesii* variety *glauca*; m, variety *menziesii*; cones, males cones present with foliage; no cones, no males cones present with the foliage; 1 and two refer to the first and second setups on this host.

ond instars was new needles, male cones or bud scales, and old foliage. In all cases where the larvae grew well, they began feeding on older foliage at about the third molt.

There was no observable feeding on three of the deciduous tree species, *L. tulipifera*, *A. platanoides*, and *M. alba*. There were sporadic signs of feeding (pin holes in leaves, chewed spots on petioles, and frass) during the first 2 wk on *A. rubrum*, *A. saccharum*, *C. ovata*, *F. americana*, *P. deltoides*, *P. grandidentata*, and *T. cordata*. Larvae fed only on the green stems of *Q. alba* for the first week while the new, unexpanded leaves were red in color; once green, expanded leaves were provided they ate them voraciously. *L. monacha* larvae on *P. serotina* left leaves to feed on the flowers when they became available. After the first week, larvae on *B. populifolia*, *F. gandifolia*, *Q. velutina*, *Q. rubra*, *Q. lobata*, and *P. malus* consumed >50% of the leaf surface area provided before the next foliage change, even with increasing amounts of foliage being added.

Larval ability to use different foliage types and host species changed over the developmental period. In addition to the difficulties that larvae had with *L. kaempferi* and *F. grandifolia* foliage when they reached fourth and higher instars that already have been mentioned, larvae did not use the old foliage of most of the species tested in the Pinceae family until they reached the fourth instar. The exception to this was major utilization of old foliage of *P. strobus*, even by newly hatched larvae (Table 2).

Pupal and Adult Development. On average, female pupae (770 mg) weighed significantly more than male pupae (414 mg, $F = 1667$, $P < 0.0000$, df = 1, 854, $t = 1.96$). Pupae of both sexes reared on suitable hosts weighted significantly more than those reared on intermediate hosts, which weighed significantly more than those reared on poor hosts (Table 3). Adult

Table 2. Conifer tissues utilized by *L. monacha* larvae during the first 14 d

Host species	Newly expanded foliage	Bud scales	Previous year's foliage	Male cones
A. concolor	+++	+	0	NA
J. virginiana	0	0	+	NA
L. kaempferi	+++	+	NA	NA
L. occidentalis	+++	+	NA	NA
P. abies	+++	+	0	+
P. glauca	+++	+	0	NA
P. pungens	+++	+	0	NA
P. nigra	0	+	0	+++
P. ponderosa	+++	+	0	NA
P. strobes	+	+	+	NA
P. sylvestris w/o cones	+	+++	+	NA
P. sylvestris w/cones	0	+	0	+++
P. taeda	+++	+	+	NA
P. menziesii var. glauca	+++	+	0	0
P. menziesii var. menziesii	+++	+	+	+
T. canadensis	+++	0	0	0

NA, not available; 0, no observed signs of feeding on this tissue; +, infrequent and very limited; +++, used through out 14 days and very obvious.

Table 3. ANOVA results by sex for mean pupal weight, adult weight, days to adult and fecundity

Variable	Male						Female					
	Poor	Intermediate	Suitable	*F*	*P*	df	Poor	Intermediate	Suitable	*F*	*P*	df
Pupal weight (mg)	105c	342b	439a	76	<0.0000	2,437	251c	634b	798a	58	0.0000	2,416
Adult Weight (mg)	—	129b	175a	35	0.0000	1,424	154c	370b	490a	53	0.0000	2,413
Days to Adult	—	43b	38a	113	0.0000	1,424	57b	47b	40a	51	0.0000	2,413
Fecundity							—	223b	299a	34	0.0000	1,225

Within each variable means followed by the same letter are not significantly different at $\alpha = 0.05$ (Bonferonni test or z test). One way ANOVA used except for the days to adult where a Kruskal-Wallis one way nonparametric ANOVA was used.

weights followed the same pattern as the pupal weights, but the adults weighed less than the pupae and the weight difference between males and females increased (Table 3).

Mean days to adult for both sexes reared on suitable hosts were shorter than for those reared on intermediate or poor hosts; there were no adult males from poor hosts (Table 3). The sex ratios of surviving adults were ≈1:1 for all host species except *F. grandifolia* (0.5:1, ♀:♂), *Q. alba* (0.7:1, ♀:♂) *A. rubrum* (1:0, ♀:♂), and *L. kaempferi* (1:0, ♀:♂).

For all tree species pooled, 21% of the females were all black, 35% black with white markings, and 44% white with black markings. The females that were white with black markings tended to be more fecund than the all black females. Males tended to be darker with 71% all black, 19% black with white markings, and 10% white with black markings.

Mating and Reproduction. For those species in the intermediate and suitable categories, the highest percentage of successful matings was for adults reared on *Q. alba* and the lowest percentage was for adults reared on *B. populifolia*, which also had the greatest number of attempted matings (Fig. 7). Fecundity was higher for females reared on suitable hosts than for those reared on intermediate hosts and there were no eggs produced by females reared on poor hosts (Table 3 and Fig. 7). There was a significant relationship between adult female weight and fecundity (R^2 = 0.59, b = 5.53 ± 15.74, slope = 0.60 ± 0.03) and between the weight of the eggs a female laid and fecundity (R^2 = 0.87, b = 4.59 ± 7.33, slope = 1.54 ± 0.04). On average, for all tree species pooled, the eggs laid by a female accounted for 29 ± 1% of her body weight. There was no significant difference in the percentage of embryonated eggs that hatched (81 ± 1%) between the suitable hosts and the intermediate hosts ($F = 0.08$, $P < 0.7770$, df = 1, 225).

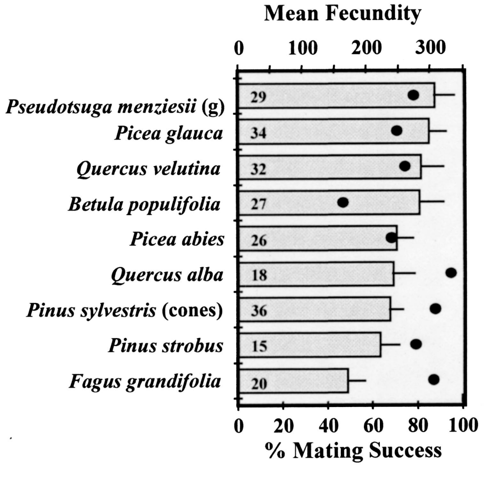

Fig. 7. Mean fecundity (bars with SE lines, number of successful matings inside bars) and percentage successful matings (dots) of *L. monacha* reared on various tree species. g, *P. menziesii* variety *glauca*; cones, males cones present with foliage; one and two refer to the first and second setups on this host.

Discussion

Based on host suitability ratings seven conifer species (*A. concolor, P. abies, P. glauca, P. pungens, P. sylvestris* with male cones, *P. menziesii* variety *glauca*, and *T. canadensis*) and six broadleaf species (*B. populifolia, M. x domestica, P. serotina, Q. lobata, Q. rubra,* and *Q. velutina*) tested were suitable for *L. monacha* survival and development. *L. monacha* should be able to establish and increase in numbers on these species if introduced into North America. *L. monacha* also should be able to establish, but may not increase in numbers (because of higher mortality, slower development and lower fecundity) on the 11 hosts that were rated as intermediate in suitability–five conifer species (*L. occidentalis, P. nigra, P. ponderosa, P. strobus,* and *P. menziesii* variety *menziesii*) and six broadleaf species (*C. caroliniana, C. ovata, F. grandifolia, P. grandidentata, Q. alba,* and *T. cordata*). The other 10 species tested were rated poor (*A. rubrum, A. platanoidies, A. saccharum, F. americana, J. virginiana, L. kaempferi, L. tulipfera, M. alba, P. taeda,* and *P. deltoides*), and *L. monacha* would likely not be able to establish because few if any could complete development on these species.

In general, these results are in agreement with the reports of feeding intensity for the same or related tree species during the major *L. monacha* outbreak in Poland in 1978–1984. Sliwa (1987) observed common or frequent feeding on species in the genera *Abies, Betula, Fagus, Larix, Picea* (except *P. pungens*), *Malus, Pseudotsuga,* and *Quercus* (except *Q. rubra*), and for *P. sylvestris.* There were four species on which Sliwa (1987) found sporadic or no signs of feeding that are classified as intermediate or suitable; *P. pungens, Q. rubra, P. nigra,* and *P. strobus.* These differences could have been a result of the presence of other more preferred species in outbreak areas, poor phenological synchrony of these tree species with *L. monacha* larvae during the outbreak, or differences in the suitability of the foliage when it is cut, as in the tests reported here.

The classification of the *Larix* species posses a difficulty because heavy feeding on larch was reported in the Polish outbreak, but the two species used in this study tested as intermediate or poor and, in fact, both may have been poor, but the larvae on *L. occidentalis* were not reared for a long enough period to determine if they would experience the same problems as larger larvae did on *L. karmpferi.* This could be explained by the fact that the early instars do use this tree species well and are wasteful feeders. Larvae began feeding near the base of the needle and most of the needle falls to the ground uneaten. The larvae may have fed on the larch trees then moved to other tree species to complete development. This would explain why *L. monacha* does not go into an outbreak on larch (Bejer 1988).

Earlier laboratory testing of tree species reported faster development on suitable deciduous tree species than on Pinaceae species (Maercks 1935, Sattler 1939). *L. monacha* did develop faster on suitable deciduous tree species than on the intermediately suitable *Pinus, Pseudotsuga,* and *Tsuga* species tested, but not faster than the suitable *Abies* or *Picea* species tested. Timing of the testing could explain the differences. *L. monacha* gained less weight and developed slower on *P. glauca* in the second setup than the first, which was 1 wk earlier. When newly hatched larvae were placed on *P. glauca* foliage in mid-June, there was only a 2-mg weight gain in 14 d (Withers and Keena 2001) compared with 100 mg and 60 mg in these tests. When the needles are older they are tougher and the mandibles of *L. monacha* are not strong enough to macerate them until they are in the third instar (Jensen 1996). So, newly hatched *L. monacha* larvae need newly expanded foliage of *Abies, Picea,* and *Pinus* (male cones until newly expanded foliage appears) species to establish and grow well.

The phenological state of the trees had a major impact on establishment, survival, and development of *L. monacha* on many of the tree species tested. Newly hatched larvae refused to feed on unexpanded reddish *Q. alba* leaves but fed and grew rapidly with little mortality once expanded green leaves were available. This resulted in an initial high mortality rate and an overall slower growth rate. When only old needles of *P. sylvestris* with no male cones were available to the *L. monacha* larvae, many died and those that survived grew slowly. Jensen (1996) reported that *L. monacha* larvae will not survive on *P. sylvestris* without male cones because the old needles are tough and low in nutritive value, and new needles appear later in the spring. The presence of male cones also was important for the development of larvae on *P. nigra,* and the absence of cones on *P. strobus, P. ponderosa,* and *P. taeda* may have affected survival and development on these species. Additionally, the larvae on *P. ponderosa* and *P. taeda* may have been affected by secondary compounds present in the new needles on which they fed, which have been shown to reduce growth rate, increase mortality, and extend the larval period in sawflies (Ikeda et al. 1977). Thus, the proper synchrony of *L. monacha* hatch with tree phenology will be critical to its establishment in North America.

Several of the same deciduous tree species suitable for *L. monacha* are suitable for *L. dispar* (L.) (Liebhold et al. 1995) and *L. mathura* Moore (Zlotina et al. 1998). These three species survive and develop well on several species of *Quercus.* Two species, *P. grandidentata* and *T. cordata,* suitable for *L. dispar* (Liebhold et al. 1995) were only intermediately suitable for *L. monacha.* Most Pinaceae species are suitable and even preferred by *L. monacha,* while they are only marginally suitable and often only used during the later instars by *L. dispar* and *L. mathura* (Liebhold et al. 1995, Montgomery 1990, Zlotina et al. 1998). The *Acer, Liriodendron, Morus,* and *Fraxinus* species tested are not suitable for either *L. monacha* or *L. dispar* (Liebhold et al. 1995). These similarities in the suitability of tree species for larvae of the genus *Lymantria* may indicate they have similar abilities to deal with allelochemicals. For example, *L. dispar* will use leaves that contain tannins but tends to avoid leaves that contain alkaloids such as *Acer, Liriodendron,* and *Morus* species (Barbosa and Krischik 1987). However, just because a tree species is suitable in a no-choice test or outbreak situation does not mean it will be a preferred host under normal circumstances.

Should *L. monacha* become established, regions of highest risk in North America, based on host plant availability and climate, include forests west of the Cascade Range, spruce/fir/pines in the upper Midwest, and northeastern North America (Wallner 1996). In addition, many of the suitable species are conifers and affects of *L. monacha* feeding on conifers are more severe because they destroy more needles than they actually consume, feed on buds until new foliage is available, and conifers are less able than deciduous trees to replace lost foliage. Defoliation >70% of *Picea* species by *L. monacha* larvae results in tree death in Europe (Bejer 1988). Therefore *L. monacha* poses a serious threat to several forest ecosystems if introduced because it can survive and develop on many economically important North American and introduced Eurasian tree species.

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