

Host Preferences of the Gypsy Moth in eastern North American versus European Forests

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Abstract

The host preferences reported for gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), are compiled and compared for temperate zone forests in Europe versus eastern North America. Species of *Larix*, *Salix*, *Populus*, *Betula*, *Alnus*, *Ostrya*, *Fagus*, *Quercus*, *Castanea*, *Amelanchier*, *Crataegus*, *Prunus*, *Sorbus*, *Malus*, and *Tilia* are clearly preferred by gypsy moth larvae in both Europe and North America. North American species of *Carya*, *Sassafras*, *Hamamelis*, *Rhus*, and *Nyssa* are acceptable but species of *Maclura*, *Morus*, *Liriodendron*, *Platanus*, *Gleditsia*, *Robinia*, *Gymnocladus*, *Ilex*, *Diospyros*, and *Catalpa* are avoided. Gypsy moth responses to trees in many other genera, including *Pinus*, *Abies*, *Picea*, *Juniperus*, *Acer*, *Juglans*, *Fraxinus*, *Carpinus*, *Celtis*, *Cornus*, *Ulmus*, and *Thuja*, vary from preferred to avoided. The overall pattern of host preferences shows that host selection does not depend on the phylogenetic relationships between tree species. Aspects of foliage quality and the timing of eclosion relative to leaf emergence on different hosts appear more likely to account for observed host preferences.

Résumé

Les préférences alimentaires rapportées pour la spongieuse, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), dans les zones forestières tempérées d'Europe et d'Amérique du Nord ont été compilées et comparées. Les espèces appartenant aux genres *Larix*, *Salix*, *Populus*, *Betula*, *Alnus*, *Ostrya*, *Fagus*, *Quercus*, *Castanea*, *Amelanchier*, *Crataegus*, *Prunus*, *Sorbus*, *Malus* et *Tilia* sont clairement préférées par les larves de spongieuse, aussi bien en Europe qu'en Amérique du Nord. Les espèces nord-américaines de *Carya*, *Sassafras*, *Hamamelis*, *Rhus* et *Nyssa* sont utilisées mais les espèces des genres *Maclura*, *Morus*, *Liriodendron*, *Platanus*, *Gleditsia*, *Robinia*, *Gymnocladus*, *Ilex*, *Diospyros* et *Catalpa* sont évitées. Face aux arbres des genres dont les *Pinus*, *Abies*, *Picea*, *Juniperus*, *Acer*, *Juglans*, *Fraxinus*, *Carpinus*, *Celtis*, *Cornus*, *Ulmus* et *Thuja*, la spongieuse exhibe toute une série de comportements allant de la préférence à l'évitement. Le patron global des préférences alimentaires montre que le choix des plantes hôtes ne dépend pas des relations phylogénétiques entre espèces. Certains aspects de la qualité du feuillage et du synchronisme de l'éclosion relativement à l'émergence des feuilles de différents hôtes constituent des explications plus plausibles des préférences alimentaires.

KEY WORDS: *Lymantria dispar*, Lepidoptera, Lymantriidae, gypsy moth, host preference, feeding preference, North America, Europe

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Introduction

The gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), is native in the temperate deciduous forests of both Europe and Asia (Giese and Schneider 1979). It was introduced to North America near Medford, Massachusetts in 1869 by Leopold Trouvelot, who was raising larvae from French gypsy moth populations for scientific investigations (Forbush and Fernald 1896). Massive outbreaks of gypsy moth were first observed beginning in 1889 around Medford, and then, despite stringent control measures, the gypsy moth spread rapidly throughout central New England during the late 19th Century. The moth has subsequently expanded its primary range north into southern Canada, west to the Ohio valley, and south to Maryland and Virginia (Doane and McManus 1981). Isolated populations are established on the west coast of the United States and at several localities along the periphery of the contiguous range. In 1984, gypsy moth populations were found in Ontario, Quebec, New Brunswick, Nova Scotia, and British Columbia (Kondo and Taylor 1985). All indications are that the North American range of gypsy moth has not yet reached its maximum possible extent.

The introduction of gypsy moth to North America began an interesting if unintended experiment on the nature of polyphagy in this serious forest pest. In North America the gypsy moth encountered an entirely different arboreal flora than that which occurs in the Eurasian deciduous forests — no tree species is native in both the old and new world forests of the temperate zone. The forest trees of Europe, Asia, and North America do, however, share many common Tertiary ancestors (Axelrod 1983, Little 1983) thus in North America the gypsy moth has many of the same genera of trees available as hosts, even though the particular species differ from those in Europe and Asia. Because of both extinctions and changes in geographic range associated with the climatic variations and glaciations during the Quaternary (Wright 1977; Davis 1983), the host genera available to gypsy moth also differ somewhat in North America versus Eurasia, (Campbell 1982).

If host selection primarily involves innate recognition of especially favorable genera or families of trees, then the feeding preferences of gypsy moth in eastern North America should closely follow those in Europe. If on the other hand host selection is more a response to some particular aspects of foliage quality and availability that can vary between related species growing under different selection regimes, then we could observe some changes in the feeding biology of old versus new world gypsy moth populations. In particular, some host genera not present in Eurasia should nonetheless be exploited in North America and preferences for host genera occurring in both the old and new world should shift to some degree as a reflection of evolutionary divergence among geographically isolated host species.

The purpose of this paper is to summarize and compare the reported feeding preferences of gypsy moth larvae in Europe and eastern North America to provide some insights into gypsy moth host selection. We have purposely excluded the Asian populations of gypsy moth from the comparison for two reasons. First, we know historically that the North American population stems largely if not entirely from French gypsy moth populations (Forbush and Fernald 1896) which are similar to other European populations (Harrison *et al.* 1983). Second, the Asian populations differ substantially from those in Europe (Goldschmidt 1934; Harrison *et al.* 1983; Schaefer *et al.* 1984), especially in one trait directly influencing host selection: dispersal stage. In both Europe and North America, the female gypsy moth is flightless and thus plays no direct role in dispersal or host selection; early instar larvae disperse by wind to select host trees (Doane and McManus 1981). Conversely in Asia the female moth flies (Schaefer *et al.* 1984), and is reported to show host specific oviposition behaviour (Schaefer 1978). Any changes in the feeding preferences of North American gypsy moth will thus be more interpretable compared to their recent European ancestors than to the more distinct and distantly related Asian populations.

Host preferences reported in Europe and North America

The feeding preferences of European gypsy moth populations have been summarized in two major articles, one by Kurir (1953) and the other by Györfi (1960). Kurir (1953) catalogs all European feeding records for gypsy moth from as early as 1758, and also

reports his own extensive feeding trials under laboratory conditions. He lists hosts in three categories: heavily eaten, sporadically eaten, and generally avoided. Györfi (1960) reports the result of similar laboratory feeding trials on 191 host species, including many shrubs and introduced species of trees which are not considered here. He rates hosts on a five point scale from completely eaten to completely avoided.

Mosher (1915) provided the classic compendium of North American feeding preferences based on series of laboratory feeding trials. He ranked hosts in four classes: favored, favored but only after instar II, acceptable, and avoided. Forbush and Fernald (1896) provide supplemental records of simply acceptability versus avoidance from feeding trials on some species not analyzed by Mosher (1915). More recently North American feeding preferences have also been summarized on the basis of field rather than laboratory data. Campbell and Sloan (1977) used defoliation data gathered between 1911 and 1931 on plots throughout eastern New England to estimate gypsy moth host preferences in natural forest environments. They expressed the defoliation level on each host in proportion to that on white oak, *Quercus alba*; for native trees this defoliation ratio ranged from 1.71 for the highly preferred *Quercus bicolor* to 0.04 for the avoided *Platanus occidentalis*. In southwestern Quebec Lechowicz and Jobin (1983) and Mauffette *et al.* (1983) censused numbers or larvae on individual trees to compare larval numbers on each host to its abundance in the forest. Preferred hosts were defined as those fed on disproportionate to their local abundance; preferences were summarized by an electivity index (Lechowicz 1982) which range from +1 for highly preferred hosts to -1 for completely avoided hosts.

Table 1. Host preferences of the gypsy moth, *Lymantria dispar*, in Europe and in North America; see key * at end of table for preference codes.

	European Tree Species	North American Tree Species
	(n = 85)	(n = 99)
PINACEAE		
Preferred	<i>Larix decidua</i> 1/1	<i>Larix laricina</i> I/O.86/-
Acceptable	<i>Abies cephalonica</i> 1-2/- etc. <i>Picea abies</i> -/4 etc. <i>Pinus sylvestris</i> 2/4 <i>P. nigra</i> 2/4 <i>P. cembra</i> 2/5 <i>P. peuce</i> 1/4	<i>Picea glauca</i> II/-/- <i>P. mariana</i> II/-/- <i>P. rubens</i> II/-/- <i>Pinus banksiana</i> II/-/- <i>P. resinosa</i> II/-/- <i>P. strobus</i> II/0.31/-0.64 <i>P. rigida</i> II/0.22/- <i>Tsuga canadensis</i> II/0.22/-
Avoided	<i>Abies alba</i> -/5 <i>Picea omorika</i> 3/5	<i>Abies balsamea</i> IV/-/- <i>Picea</i> spp. -/0.12/-
TAXACEAE		
Acceptable	<i>Taxus baccata</i> 2/4	
CUPRESSACEAE		
Acceptable	<i>Thuja gigantea</i> 2/- <i>Juniperus communis</i> 2/- <i>J. prostrata</i> 2/-	
Avoided		<i>Chaamaecyparis thyoides</i> IV/0.11/- <i>Juniperus communis</i> IV/-/- <i>J. virginiana</i> IV/0.07/- <i>Thuja occidentalis</i> IV/-/-
SALICACEAE		
Preferred	<i>Salix alba</i> 1/1 <i>S. fragilis</i> 1/1 <i>S. triandra</i> 1/- <i>S. pentandra</i> 1/- <i>S. caprea</i> 1/2 <i>Populus alba</i> 1/3 <i>P. nigra</i> 1/3	<i>Salix</i> spp. -/0.86/0.51 <i>Salix discolor</i> I/-/- <i>Populus</i> spp. -/1.06/- <i>Populus balsamifera</i> I/-/- <i>P. grandidentata</i> I/-/0.34 <i>P. tremuloides</i> I/-/0.05
Acceptable	<i>Populus tremula</i> 2/4	<i>Populus deltoides</i> III/-/0.62
Avoided	<i>Populus canescens</i> -/5	

	European Tree Species	North American Tree Species
JUGLANDACEAE		
Preferred	<i>Juglans regia</i> 1/1	
Acceptable		<i>Carya</i> spp. -/0.30/- <i>Carya cordiformis</i> III/-/0.34 <i>C. glabra</i> III/-/- <i>C. ovata</i> III/-/0.85 <i>C. tomentosa</i> III/-/-
Avoided		<i>Juglans nigra</i> IV/ <i>Juglans cinerea</i> IV/-/0.78
BETULACEAE		
Preferred	<i>Betula pendula</i> 1/1 <i>B. pubescens</i> 1/1 <i>Alnus glutinosa</i> 1/1 <i>A. incana</i> 1/- <i>A. viridis</i> 1/- <i>Carpinus betulus</i> 1/1 <i>Ostrya carpinifolia</i> 1/- <i>Corylus avellana</i> 1/1	<i>Betula nigra</i> I/0.87/- <i>B. papyrifera</i> I/0.68/0.06 <i>B. populifolia</i> I/0.87/-0.22 <i>Alnus rugosa</i> I/-/-
Acceptable		<i>Alnus serrulata</i> : FF <i>Betula lenta</i> III/0.21/- <i>B. alleghaniensis</i> III/0.24/-0.43 <i>Carpinus caroliniana</i> III/-/- <i>Ostrya virginiana</i> III/0.64/0.62
FAGACEAE		
Preferred	<i>Fagus sylvatica</i> 1/1 <i>F. orientalis</i> 1/- <i>Castanea sativa</i> 1/1 <i>Quercus suber</i> 1/- <i>Q. trojana</i> 1/- <i>Q. cerris</i> 1/1 <i>Q. robur</i> 1/1 <i>Q. petraea</i> 1/1 <i>Q. pubescens</i> 1/1 <i>Q. frainetto</i> 1/-	<i>Fagus grandifolia</i> I/0.45/-0.01 <i>Quercus alba</i> I/1.00/- <i>Q. bicolor</i> I/1.71/- <i>Q. coccinea</i> I/0.98 <i>Q. illicifolia</i> I/-/- <i>Q. imbricaria</i> I/-/- <i>Q. macrocarpa</i> I/-/- <i>Q. muehlenbergii</i> I/-/- <i>Q. palustris</i> I/-/- <i>Q. prinus</i> I/1.00/- <i>Q. rubra</i> I/0.90/0.65 <i>Q. stellata</i> I/-/- <i>Q. velutina</i> I/1.02/-
Acceptable		<i>Castanea dentata</i> II/0.46/- <i>C. pumila</i> : FF <i>Quercus nigra</i> : FF
ULMACEAE		
Preferred species	<i>Ulmus glabra</i> 1/- <i>U. minor</i> 1/- <i>U. laevis</i> 1/- <i>Celtis australis</i> 1/1	
ULMACEAE		
Acceptable		<i>Ulmus</i> spp. -/0.48/- <i>Ulmus americana</i> III/-/0.01 <i>U. rubra</i> III/-/0.82 <i>U. thomasi</i> : FF <i>Celtis occidentalis</i> IV/-/-
Avoided		
MORACEAE		
Acceptable	<i>Ficus carica</i> 2/-	
Avoided		<i>Morus rubra</i> IV/-/- <i>Maclura pomifera</i> IV/-/-
MAGNOLIACEAE		
Avoided		<i>Liriodendron tulipifera</i> IV/-/-
LAURACEAE		
Acceptable		<i>Sassafras albidum</i> III/0.83/-

	European Tree Species	North American Tree Species
HAMAMELIDACEAE		
Preferred		<i>Liquidambar styraciflua</i> I/-/ <i>Hamamelis virginiana</i> I/-/-
PLATANACEAE		
Avoided		<i>Platanus occidentalis</i> IV/0.04/-
ROSACEAE		
Preferred	<i>Pyrus communis</i> 1/- <i>P. amygdaliformis</i> 1/- <i>Malus sylvestris</i> 1/- <i>M. trilobata</i> 1/ <i>Sorbus domestica</i> 1/- <i>S. aucuparia</i> 1/- <i>S. torminalis</i> 1/- <i>S. aria</i> 1/- <i>S. mougeotti</i> 1/- <i>S. latifolia</i> 1/- <i>Amelanchier ovalis</i> 1/- <i>Crataegus monogyna</i> 1/- <i>C. laevigata</i> 1/- <i>Prunus spinosa</i> 1/- <i>P. cerasifera</i> 1/- <i>P. domestica</i> 1/- <i>P. avium</i> 1/- <i>P. cerasus</i> 1/- <i>P. malaheba</i> 1/- <i>P. padus</i> 1/- <i>P. laurocerasus</i> 1/-	<i>Sorbus americana</i> I/-/- <i>Amelanchier</i> spp. -/-/0.58 <i>Amelanchier canadensis</i> I/-/- <i>Crataegus coccinea</i> : FF <i>C. crus-galli</i> : FF
Acceptables		ROSACEAE <i>Malus</i> spp. -/2.20/-0.70 <i>Prunus</i> spp. -/0.17/- <i>Prunus pensylvanica</i> III/-/0.53 <i>P. serotina</i> -/0.40/0.09 <i>P. virginiana</i> III/-/-
LEGUMINOSAE		
Acceptable	<i>Cercis siliquastrum</i> -/4	
Avoided	<i>Laburnum anagyroides</i> -/5	<i>Gleditsia tricanthos</i> IV/-/- <i>Robinia pseudoacacia</i> IV/0.18/- <i>Gymnocladus dioicus</i> IV/-/-
ANACARDIACEAE		
Preferred	<i>Cotynus coggygria</i> -/2	<i>Rhus typhina</i> I/-/- <i>R. copallina</i> I/-/-
AQUIFOLIACEAE		
Avoided		<i>Ilex opaca</i> IV/-/- <i>I. laevigata</i> IV/-/-
ACERACEAE		
Preferred	<i>Acer platanoides</i> 1/1 <i>A. campestre</i> 1/1 <i>A. pseudoplatanus</i> 1/1 <i>A. tataricum</i> 1/1 <i>A. heldreichii</i> 1/- <i>A. monspessulanum</i> 1/-	
Acceptable		<i>Acer negundo</i> I/-/-0.47 <i>Acer rubrum</i> III/0.38/-0.57 <i>A. saccharinum</i> III/-/-0.69 <i>A. saccharum</i> III/0.18/-0.18
Avoided		<i>Acer pensylvanicum</i> IV/-/-0.98 <i>A. spicatum</i> IV/-/-
HIPPOCASTANACEAE		
Acceptable	<i>Aesculus hippocastanum</i> 2/4	

	European Tree Species	North American Tree Species
TILIACEAE		
Preferred		<i>Tilia americana</i> I/1.12/0.10
Acceptable	<i>Tilia tomentosa</i> -/4 <i>T. cordata</i> 1/3 <i>T. platyphyllos</i> 1/3-4	
NYSSACEAE		
Acceptable		<i>Nyssa sylvatica</i> III/0.27/-
EBENACEAE		
Avoided		<i>Diospyros virginiana</i> IV/-/-
CORNACEAE		
Acceptable	<i>Cornus mas</i> 1/2	
Avoided		<i>Cornus florida</i> IV/-/-
BIGNONIACEAE		
Avoided		<i>Catalpa speciosa</i> IV/-/-
OLEACEAE		
Acceptable	<i>Fraxinus excelsior</i> 2/3 <i>F. angustifolia</i> ssp. <i>oxycarpa</i> 2/-	
Avoided	<i>Fraxinus ornus</i> 3/5	<i>Fraxinus</i> spp. -/0.06/- <i>Fraxinus americana</i> IV/-/-0.80 <i>F. pennsylvanica</i> IV/-/-0.99 <i>F. nigra</i> IV/-/-0.99 <i>F. quadrangulata</i> IV/-/-

* European host preferences *a/b*: — after Kurir (1953) *a* takes values 1 = heavily eaten; 2 = sporadically eaten; 3 = completely avoided.

— after Györfi (1960) *b* takes values 1 = completely eaten; 2 = heavily eaten; 3 = eaten; 4 = slightly eaten; 5 = completely avoided.

North American host preferences *c/d/e*: — after Mosher (1915) *c* takes values I = favored food; II = favored food in later instars; III = acceptable food; IV = unfavored food.

— after Campbell and Sloan (1979) *d* takes values from 2.20 to 0.04 where 1.00 is defoliation on *Quercus alba*; values less than 1.00 are for species less defoliated (less preferred) than *Quercus alba*.

— after Mauffette et al. (1983) *e* takes values from -1 to +1 where 0 equals neutral feeding, +1 complete preference, and -1 complete avoidance.

An FF following a North American species indicates the food was either acceptable or avoided as indicated according to Forbush and Fernald (1896) but was not assayed by later investigators.

These European and North American records of gypsy moth feeding preferences are summarized in Table 1 and form the basis for the following discussion. Hosts have been grouped by family and categorized into three preference classes on the basis of the foregoing reports. The nomenclature for the European trees follows Moore (1982) and Polunin and Everard (1976), and, for the North American trees Little (1979).

Comparison of European and North American host preferences

The following genera are consistently acceptable as host trees for gypsy moth in Europe and North America: *Larix* in the Pinaceae, *Salix* and *Populus* in the Salicaceae, *Betula*, *Ainus*, and *Ostrya* in the Betulaceae, *Fagus*, *Quercus*, and *Castanea* in the Fagaceae, *Amelanchier*, *Crataegus*, *Prunus*, *Sorbus*, and *Malus* in the Rosaceae, and *Tilia* in the Tiliaceae. There are no native genera represented on both continents which are consistently reported to be avoided by gypsy moth. There are, however, a number of genera which on both continents include some species acceptable as hosts and others that are avoided. These include *Pinus*, *Abies*, and *Picea* in the Pinaceae, *Juniperus* in the Cupressaceae, *Acer* in the Aceraceae, and *Fraxinus* in the Oleaceae.

Interestingly there are genera to which the gypsy moth shows opposite responses in Europe versus North America. For example, *Juglans regia* is a favored food in Europe, but both *Juglans nigra* and *J. cinerea* are avoided in North America. *Cornus mas* is preferred in Europe but *Cornus florida* avoided in North America. *Carpinus* in the Betulaceae and *Celtis* in the Ulmaceae show the same contrasting host preferences on the two continents, and to a lesser degree *Ulmus* in the Ulmaceae and *Thuja* in the Cupressaceae.

It is the genera found in North America but not native in the gypsy moth European range which provide the most direct test of the adaptability of the gypsy moth host selection process. There is a large set of possible but novel hosts which gypsy moth encounter in North America that are avoided. These include *Maclura* in the Moraceae, *Liriodendron* in the Magnoliaceae, *Gleditsia*, *Robinia*, and *Gymnocladus* in the Leguminosae, *Diospyros* in the Ebenaceae, and *Catalpa* in the Biognoniaceae. Conversely, there are also a significant number of novel genera which are accepted and even very preferred by North American gypsy moth including *Liquidambar* and *Hamamelis* in the Hamamelidaceae, *Sassafras* in the Lauraceae, *Carya* in the Juglandaceae and *Nyssa* in the Nyssaceae. It is noteworthy that larvae not only prefer a novel species like *Liquidambar styraciflua* but actually grow faster and are more fecund on *Liquidambar* than on either *Quercus velutina* or *Q. nigra* (Barbosa *et al.* 1983).

Discussion

We might anticipate *a priori* that host phylogeny would account for the overall pattern of trees avoided and preferred by gypsy moth in Europe versus North America. Under this phylogenetic hypothesis, the gypsy moth populations introduced from Europe to North America should prefer host trees most closely related to those preferred in Europe. Following Cronquist's (1981) evaluation of the phylogenetic relations among genera, this expectation is borne out for most genera in the Fagaceae, Salicaceae, Betulaceae, Rosaceae, and Tiliaceae, but certainly not for all host genera (Table 1). Tree species within a single genus can differ in acceptability even on the same continent as illustrated by the preference for *Abies cephalonica* in Europe but complete rejection of *Abies alba*. Similarly, congeners frequently differ in acceptability between continents as illustrated by *Celtis australis* which is strongly preferred in Europe while *Celtis occidentalis* is avoided in North America. Finally we cannot predict preference for novel hosts encountered in North America on the basis of European preferences for closely related genera. *Juglans regia* is very highly preferred in Europe, but species of *Juglans* in North America are avoided while the closely related genus *Carya* (Manning 1978) is only marginally acceptable. Shared ancestry, either within or between host families, does not account for the overall pattern of gypsy moth host preference.

A likely alternative hypothesis to explain host preference in gypsy moth is that host selection depends on one or more critical plant traits that can vary among trees evolving in diverse selection regimes. Decisive support for this host quality hypothesis has, however, proven difficult to acquire. Lechowicz (1983, unpublished) has shown that host acceptability to gypsy moth increases with leaf nitrogen and water content and decreases with condensed tannin content. No one of these traits alone predicted host acceptability, nor did either leaf toughness or buffer capacity influence acceptability. Similarly, no simple correlations exist between gypsy moth growth rate and any of 25 amino acids or 12 mineral nutrient concentrations in host foliage (Barbosa and Green Blatt 1979; Valentine *et al.* 1983). There are innumerable tannins, simple phenolics, terpenes, alkaloids, saponins, glycosides, coumarins, and other secondary chemicals that differ among host trees (Hegnauer 1962, 1964, 1966, 1969, 1973; Gibbs 1974) and which have not been tested for their effects on gypsy moth feeding activity, but the likelihood that any single class of allelochemicals accounts for the overall pattern of gypsy moth host preferences remains to be demonstrated. It seems most likely that this generalist herbivore simply responds not to one but to many interacting behavioural cues and aspects of resource quality in selecting its host.

The host selection process in gypsy moth is also very dependent on the dynamics and climatic dependence of eclosion versus leaf development. Eclosion is predictable from only thermal sums (Johnson *et al.* 1983) while leaf emergence depends on both thermal sums and photoperiodic cues (Valentine 1983). Moreover, all tree species do

not leaf out at the same time in the spring (Lechowicz 1984). Since photoperiodic cues are fixed astronomical events but thermal sums depend on essentially random year to year climatic variation, dispersing first instar gypsy moth larvae do not always encounter foliage on the same host species. The quality of the foliage they do encounter also depends strongly on its age, since leaf nutritional quality declines rapidly in the first few weeks of leaf ontogeny (Hough and Pimentel 1978, St. Jacques 1984). This problem of match or mismatch between dispersal and the availability of very favorable hosts may favor the broad host tolerance observed in gypsy moth and account for the observed lack of host races in this polyphage (Roby 1982). Given the differential regulation of eclosion and leaf emergence, and the highly stochastic nature of wind dispersal, gypsy moth larvae that do not tolerate a broad range of hosts are unlikely to survive.

The multifactorial and dynamic basis of host selection in gypsy moth does not preclude recognition of some consistent host preferences for gypsy moth in north temperate forests. Species of *Larix*, *Salix*, *Populus*, *Betula*, *Alnus*, *Ostrya*, *Fagus*, *Quercus*, *Castanea*, *Amelanchier*, *Crataegus*, *Prunus*, *Sorbus*, *Malus*, and *Tilia* are clearly preferred by gypsy moth larvae in both Europe and North America. North American species of *Carya*, *Sassafras*, *Hamamelis*, *Rhus*, and *Nyssa* are acceptable, but species of *Maclura*, *Morus*, *Liriodendron*, *Platanus*, *Gleditsia*, *Robinia*, *Gymnocladus*, *Ilex*, *Diospyros*, and *Catalpa* are avoided. Gypsy moth responses to species of *Pinus*, *Abies*, *Picea*, *Juniperus*, *Acer*, *Juglans*, *Fraxinus*, *Carpinus*, *Celtis*, *Cornus*, *Ulmus*, and *Thuja*, can vary from preferred to avoided within genera. Our ability to predict preferences for particular species in these variable genera and for novel genera will have to await a more complete understanding of the host selection process.

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