

VARIATION IN THE SUITABILITY OF TREE SPECIES FOR THE GYPSY MOTH

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ABSTRACT

Lymantria dispar L. is a polyphagous defoliator that feeds on a variety of trees and shrubs. These hosts vary considerably in their nutritional value for the gypsy moth. Classifications patterned after that of Mosher (1915) are used to group potential hosts into categories that correspond to suitable, marginal, and inadequate. Within species differences in suitability also exist. The role of spatial factors (site effects) and temporal factors (establishment phenology) on the variability of host suitability is examined.

INTRODUCTION

The gypsy moth, *Lymantria dispar* L., has a remarkable range of host species in both its native Eurasia and in North America. Schaefer and others (1988) lists 152 plants on which the gypsy moth has been observed to feed in Japan, with at least 50 being extensively utilized. In Europe, about half of the 185 species of native trees are utilized (Kurir, 1953). Shortly after it was introduced to North America, the gypsy moth was reported to feed on 458 trees, shrubs, and plants in the state of Massachusetts (Fernald and Forbush, 1896). This was 96% of the plants tested! The number of species on which the gypsy moth can sustain itself is far less. Mosher (1915) found that the gypsy moth could complete its entire larval development on 58 woody plants (47% of the species tested). Pest surveys of the federal governments of Canada and the United States reported 79 tree species as sustaining defoliation by the gypsy moth (Nothnagle and Schultz, 1987).

More important than the enumeration of plant species that are hosts of the gypsy moth is the recognition of how well each species fosters the survival and growth of larvae (suitability), and the likelihood that a species will be defoliated in an outbreak (susceptibility). Susceptibility of a species is determined by (1) the probability of populations increasing to outbreak levels in a stand and (2) the probability of larvae feeding on a particular tree in the stand. It is possible for species that are not very suitable for growth to be defoliated because of dispersal of larvae within a stand.

This chapter compares the suitability of several tree species to support gypsy moth growth and examines the effects of spatial and temporal factors on variations in suitability.

FOOD PLANT CLASSIFICATIONS

The Foundation

Mosher's (1915) categorization of the food value of gypsy moth host plants remains the basis of many recent classifications. Mosher placed trees and shrubs in four categories from favored to unfavored. What Mosher meant by favored needs to be clarified and the usage of these four categories needs to be reconsidered.

The four categories used by Mosher were: (I) favored, (II) favored after the earlier larval stages, (III) not particularly favored, and (IV) unfavored. Mosher defined these categories based on experimentation which consisted of confining larvae with the foliage of one species and, for a few species, confining larvae with the foliage of two species. Mosher's classification appears to rely mostly on the tests where larvae were reared with access to a single species; thus, the classification reflects the suitability of species for growth as opposed to preference for a species when given a choice. The term favored, in his context, means that the food is advantageous for development rather than preferred.

Mosher's classification seems to ignore the results of his experiments where larvae were given a choice between two species. For example, when sugar maple was given in combination with beech or paper birch it was fed on as much as the other species, but the beech and paper birch were classified as favored and sugar maple was classified as not particularly favored. Red oak fed in combination with linden was favored by all larval stages over linden, but linden was still listed as a favored species. Larvae grew well when isolated on either red oak or linden.

In the second category, favored after the early larval stages, are pines, spruces, hemlock, chestnut, and beach plum. The pines were all similar in that first instar larvae did not survive on any pine species. The performance of older larvae, however, varied depending on the pine species. Feeding and growth were poor by older larvae on red pine. Little feeding occurred on Scotch pine until the new growth had expanded. On pitch pine, older larvae fed only on the older needles. In some tests, older larvae placed on white pine reached relatively large size, whereas in others the size reached was only moderate. Overall, it seems that growth of older larvae on pine was only moderate. Mosher noted, as I have (Montgomery et al. 1989), that larvae often begin feeding near the base of a pine needle with most of the needle falling to the ground; hence, a pine may be quickly defoliated with little of it actually being eaten.

All larval stages survived on hemlock, though growth was poor for all stages. This is similar to what occurred on black birch and other species placed in class III, not particularly favored.

All first instar larvae died on beach plum while larvae started on plum in the third stage produced small pupae. Larvae were less successful on this species than on about half of the species in the third category.

Larvae on gray birch, a host in Mosher's favorable category, also exhibit the pattern of poor growth in the first instar and good growth thereafter.

To sum, it seems the growth and behavior of larvae on species in category II does not have the uniformity that indicates they should be in a separate class. Mosher's second category should be merged with his third category.

Usage

Mosher's classifications have been used by others with modifications. Campbell and Sloan (1977) defined food classes based on Mosher (1915) as A, favored; B, eaten but not favored; and C, not usually eaten. They did not specify what species were placed in each class. They developed a composite of defoliation ratios for several tree species in the Melrose Highlands for the period 1911-1921. Species receiving more defoliation than expected based on Mosher's classification as not particularly favored hosts were *Betula nigra*, *Sassafras albidum*, and *Ostrya virginiana*. Beech, a favored species, received less defoliation than expected. *Pinus sylvestris* was the least defoliated species and *P. strobus* and *P. rigida* were in the lowest third of the defoliation rankings. This is further evidence that Mosher's classification of pines as favored food after the earlier instars is inappropriate.

Houston and Valentine (1977) divided tree species into 3 categories in order to develop principal-component ordinations of stand susceptibility. The three categories were most preferred, intermediate and least preferred. The most preferred category was subdivided into three classes: (1) the white oaks, *Quercus alba* and *Q. prinus*; (2) *Q. coccinea*, *Q. illicifolia*, *Q. rubra*, and *Q. velutina*; and (3) the remaining species in Mosher's most favored class except serviceberry, beech, and witch-hazel which were placed in the intermediate class. The classifications of dogwood, walnut, and butternut were raised to the intermediate class. No rationale for these classifications was given and the literature provides little support for these changes.

White, red, and black oaks were defoliated about the same in the Melrose Highlands (Campbell and Sloan 1977). Herrick and Gansner (1987) reported that average defoliation in central Pennsylvania was 60% for chestnut oak, 56% for black oak, 47% for scarlet oak, 34% for red oak, and 31% for white oak. Thus, there is no evidence that *Q. alba* and *Q. prinus* should be placed in a food class separate from the other oaks. It does seem correct to place beech in an intermediate category; it was in the middle of the defoliation rankings in both the Campbell and Sloan (1977) and Herrick and Gansner (1987) studies.

Valentine and Houston (1984) defined preferred trees as *Quercus* spp., *Alnus* spp., *Malus* spp., *Betula papyrifera*, *B. populifolia*, *Populus grandidentata*, *P. tremuloides*, and *Tilia americana*. They did not classify any other trees since their intention was to identify stand susceptibility to defoliation and this only required measurements of preferred host trees on the stand.

Referring to tree species as preferred or unpreferred by the gypsy moth implies that the insect actively selects among the plants available to it. Although all larval stages can reject and leave hosts, the role of preference in determining defoliation levels is uncertain since active selection of the host plant is rather weak in the gypsy moth compared to other Lepidoptera (Lance 1983).

Suggestions

The terminology for classification of gypsy moth food plants should consider whether or not the focus of classification is on the host plant or the herbivore. For instance, the value of the plant to support growth of the herbivore could be classed as suitable, marginal, and inadequate, while the likelihood of a plant being defoliated could be rated as susceptible, resistant, and immune. Three categories should be sufficient for classification.

For management purposes it may be more economical to consider only those species that are clearly suitable and not worry about whether the remaining species are marginal or inadequate.

SPECIES SUITABILITY

The suitability of host plant is usually measured by the survival, duration of development, and the weight gain or the pupal weight of larvae confined to the host plant. These variables are also influenced by the rearing conditions and how the experiment is conducted. Rearing is labor intensive and therefore no more than 5-10 species are evaluated at one time. Thus, no long lists of suitability derived from rigorous experimentation exist.

Data Problems

I know of seven studies where the gypsy moth was reared from newly hatched larvae until pupation on angiosperms (Table 1). In six of these studies, all except study 5, the larvae were fed

cut foliage at intervals of three days or less. Larvae and cut foliage were held in small containers that presumably were at or close to saturated humidity except in study 4 where foliage and larvae were held in mesh cages at the fluctuating ambient humidity of a quarantine facility. In study 5 larvae were reared in mesh bags on intact foliage in the field.

Table 1. Female pupal weights of larvae reared on excised foliage except for study 5 which confined larvae on living foliage.

Study	Reference	<i>Quercus alba</i>
1	Hough & Pimentel 1978	2.05
2	Barbosa & Greenblatt 1979	1.20
3	Montgomery 1986	1.71
4	Berisford et al. 1989	0.75
5	Witter et al. 1989	0.93
6	Raupp et al. 1988;	0.91 earliest rearing
7	Barbosa et al. 1983	1.69

To save space and to help maintain clarity, only the pupal weights attained by the female larvae are considered here. The development times and male pupal weights more or less show the same relationships as female pupal weights. Altogether, the studies examined 30 species. *Quercus alba* was the only species all seven studies had in common. Female pupal weights on *Q. alba* varied from 0.75 to 2.05 grams. The lowest weight may be due to more rapid dehydration of the foliage in an environment with circulating, unsaturated air. The rather low weight in study 5 may be the result of the foliage being induced to produce toxic chemicals either by the bag used to confine the larvae or the feeding of the larvae. I cannot offer speculation as to why the other weights have such a broad range. It is obvious that absolute comparisons of growth variables obtained from different studies would be of little value.

A Suitability Index

There does seem to be proportionality between the studies; where weights of pupae reared on *Q. alba* were lower than average, pupal weights were lower than average on all species in the study and vice versa. Therefore, I constructed an index to compare the suitability of all species in the studies (Table 2).

All oaks, with the exception of *Q. phellos*, would appear to be suitable host plants. *L. styraciflua* and *P. deltoides* seem to be suitable hosts also. *C. caroliniana* and *A. arborea* are on the border between suitable and marginal. Growth on *F. grandifolia* and *A. serrulata* was marginal. Table 2 indicates that cottonwood is a more suitable host and beech and alder are less suitable hosts than Mosher (1915) indicated. Suitability may vary among species of *Alnus* as it does in *Betula*, since *A. serrulata* is clearly unsuitable and Mosher found *A. incana* suitable.

Table 2. Relative suitability of gypsy moth hosts based on the female pupal weight attained by newly hatched larvae reared on the host.

Species	Relative Index*
<i>Quercus alba</i>	1.00
<i>Q. ellipsoidalis</i>	1.05 ⁵
<i>Q. falcata</i>	1.22 ⁴
<i>Q. nigra</i>	1.50 ⁴
<i>Q. phellos</i>	0.58 ⁷
<i>Q. prinus</i>	1.05 ³
<i>Q. rubra</i>	0.99 ¹ , 1.23 ² , 0.88 ³ , 0.66 ⁵
<i>Q. stellata</i>	1.08 ³
<i>Q. velutina</i>	0.95 ⁵ , 0.52 ⁷
<i>Fagus grandifolia</i>	0.48 ¹ , 0.68 ² , 0.56 ⁵ , 0.58 ⁶
<i>Liquidambar styraciflua</i>	1.24 ⁴ , 1.12 ⁷
<i>Salix lucida</i>	1.21 ³
<i>Populus deltoides</i>	1.14 ³
<i>P. grandidentata</i>	0.99 ³ , 1.47 ⁵
<i>P. tremuloides</i>	1.51 ³ , 1.46 ⁵
<i>Alnus serrulata</i>	0.45 ³
<i>Betula lenta</i>	0.48 ³
<i>B. papyrifera</i>	1.01 ⁵
<i>B. populifolia</i>	1.64 ² , 1.26 ³
<i>Carpinus caroliniana</i>	0.88 ³
<i>Amelanchier arborea</i>	0.79 ⁵
<i>Carya tomentosa</i>	0.62 ⁶
<i>Acer rubra</i>	0.51 ¹ , 1.10 ⁴ , 0.69 ⁶ , 0.30 ⁷
<i>A. saccharum</i>	0.37 ¹
<i>Tsuga canadensis</i>	0.21 ¹
<i>Fraxinus americana</i>	-0.1
<i>Pinus strobus</i>	-0.7
<i>P. taeda</i>	-0.4, -0.7

*Superscripts indicate study as listed in Table 1. The index is the ratio of the pupal weight on the host to the pupal weight on *Q. alba* within the same study.

Mosher tested a different alder species than I did, and I'm not certain what it was. He called *A. incana* speckled alder. *A. incana*, or white alder, is an introduced European species. At the turn of the century, the typical form of *A. rugosa* was incorrectly considered by many to be *A. incana*. Table 2 shows considerable variation in the relative food value of red oak and white oak. The extent that this variation is due to experimental error, methods, geography, and phenology cannot be discerned from these data.

SPATIAL FACTORS

The suitability of host plants for the gypsy moth varies not only among plant species, but also among individuals of the same species. Past studies (Mosher 1915, Barbosa and Capinera 1977, Capinera and Barbosa 1977, Hough and Pimentel 1978, Barbosa and Greenblatt 1979, Barbosa and others 1983, Miller and others 1987, Raupp and others 1988) lacked replication at the level of the tree and hence, not only is it impossible to assess the variability within a species, but the statistical tests of the significance of differences between species in these studies are not valid.

Site by Location Interactions

A test was specifically designed to examine variation among individual trees of a species and whether differences in suitability of tree species vary from location to location (Gross and others 1990). Three oak species, *Q. alba*, *Q. prinus* and *Q. coccinea* located on two sites in each of three distinct physiographic regions were evaluated by placing second instar larvae in mesh bags placed over branches of the trees and rearing them until pupation. The sites were chosen to keep differences in soil moisture class minimal.

No statistically significant differences in pupal weight were found among the oak species. Tree size was positively correlated with pupal weights among the locations, but tree species by location interaction accounted for little of the overall variability. The largest sources of variation were among larvae on the same tree and among trees of the same species (Fig. 1). These results suggest that in studies of relative, suitability samples of replicate trees within a species is more important than obtaining samples from several sites.

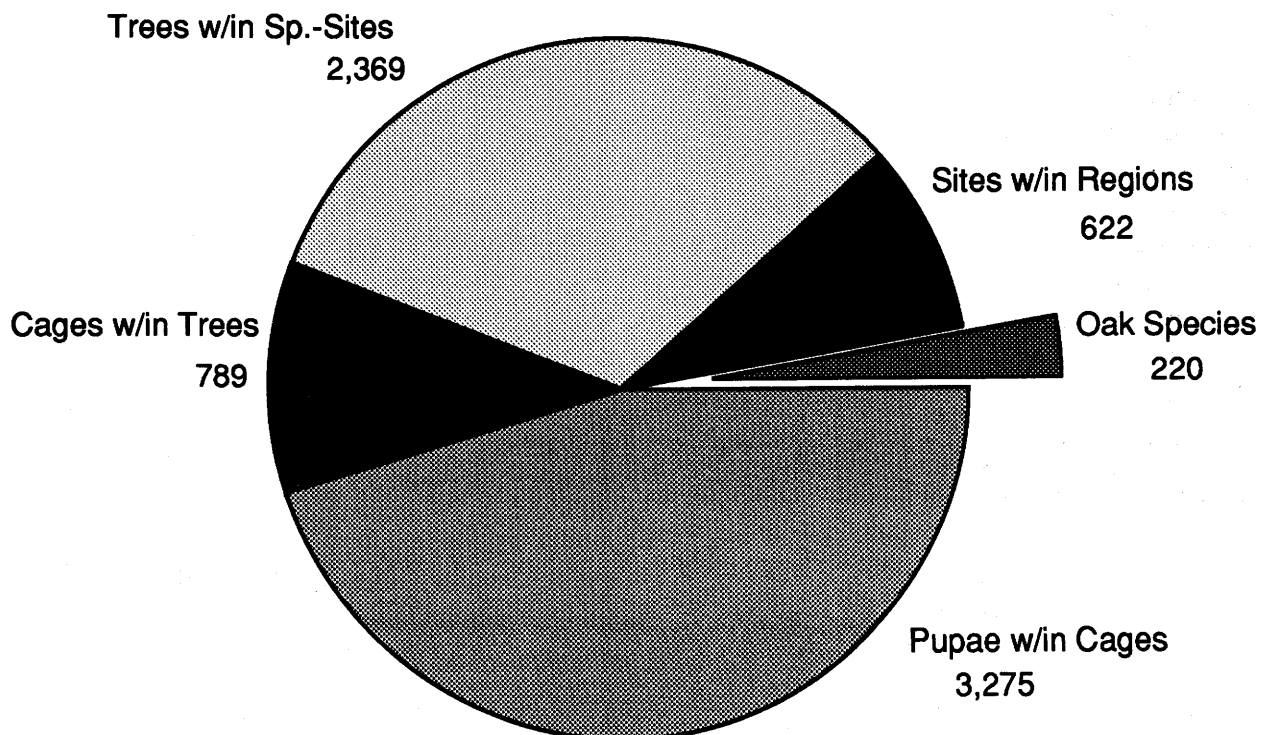


Figure 1. Variance components of random effects on female pupal weights on three oak species.

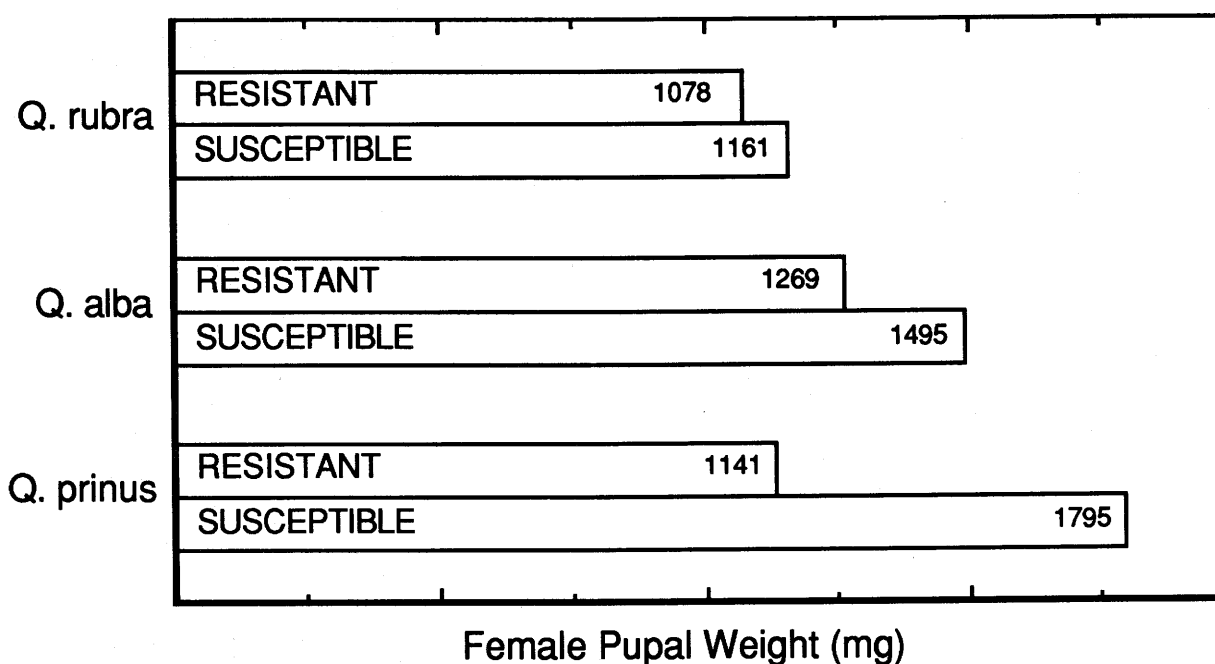


Figure 2. Comparison of female pupal weights of larvae reared on excised oak foliage from resistant and susceptible sites.

Susceptible Stands

Historically, defoliation by the gypsy moth occurs more frequently on xeric sites such as ridge tops, whereas mesic lowlands experience defoliation less frequently. Susceptible stands have been characterized as having an abundance of suitable host species with many structural defects such as bark flaps (Houston and Valentine 1977, Valentine and Houston 1984). Bark flaps and bark fissures allow the gypsy moth larvae to rest off the forest floor which decreases predation by small mammals (Bess and others 1947, Campbell and others 1977).

Differences in the suitability and chemistry of the tree foliage may also explain the resistance and susceptibility of stands.

Larval growth - The growth of gypsy moth larvae on the major oak species in a susceptible ridge top and a more resistant stand in a midslope, deep-soil pocket in Connecticut was examined by Montgomery (1986). The susceptible stand had chestnut oak as the major species, followed by hickory and red oak with white oak and ash comprising the remainder of the stand. The resistant stand had red and black oak as the major species along with a variety of other hardwoods including chestnut and white oak as minor species. Overall, pupae were larger if the larvae were reared on trees on the susceptible site (Fig. 2). The largest pupal weights were obtained on *Q. prinus* growing on the susceptible site. The high nutritional value of the major tree species on the susceptible site would result in high rates of gypsy moth reproduction, which likely would contribute to the site's susceptibility to defoliation.

Foliage chemistry - An inquiry was made into the chemical factors that may influence the nutritional value of foliage from stands in Pennsylvania (Kleiner et al. 1989). Particular attention was paid to tannins which are thought to be a defense of woody plants to reduce the growth of herbivores that may feed on it (Feeny 1970). Contrary to theoretical predictions, tannins were higher in the foliage from susceptible sites (Table 3). The condensed tannin content of foliage was

affected more by site than by species whereas hydrolyzable tannin content was more affected by species. Since *Q. prinus* is the major species, the foliage on susceptible sites has higher levels of both hydrolyzable and condensed tannin.

Tannins have been negatively correlated with growth of gypsy moth larvae feeding on leaves from trees undergoing defoliation (Rossiter and others 1988). However, tannin accounted for only 16 % of the total variation in female pupal weights. This indicates that tannin may not be the primary cause of the reduced nutritional value of leaves from defoliated trees. Bernays (1981) has led the growing criticism of the theory that tannins are generally toxic to herbivores. Tannins have been reported to be feeding stimulants for the gypsy moth (see Montgomery 1989).

Tritrophic interactions - The pathogenicity of the gypsy moth nuclear polyhedrosis virus has been found to be negatively correlated with the hydrolyzable tannin content of leaves of different tree species (Keating and others 1988). Schultz and others (1990) has observed that decreased viral pathogenicity was correlated with increased hydrolyzable tannin content in red oak leaves. These data imply that the persistence of defoliating populations of gypsy moth on susceptible sites may be a consequence of the suppression of viral epizootics by the high tannin content in the foliage from susceptible sites eaten by the larvae.

Table 3. Characteristics of chestnut and red oak from a resistant and susceptible stand in Pennsylvania. (from Kleiner et al. 1989).

	<u>Resistant site</u>		<u>Susceptible site</u>	
	<i>Q. prinus</i>	<i>Q. rubra</i>	<i>Q. prinus</i>	<i>Q. rubra</i>
% of Basal area	16	53	62	29
Hydrolyzable tannin	21	11	21	9
Condensed tannin	13	9	20	19

TEMPORAL FACTORS

Egg Hatch

The period of time over which gypsy moth eggs hatch is longer than is generally thought. Usually 2 to 3 weeks elapse from when larvae begin to emerge from the egg masses in a stand until they have dispersed from all of the egg masses. An example (Fig. 3) shows that a few egg masses had begun and had completed their hatch before other egg masses even began to hatch. Most egg masses had emergence before May 4, but peak dispersal from the egg mass did not occur until May 10. Average temperatures were close to 10° C. throughout the period except for April 28-30 = 12.5-13.3° C, and May 6-7 = 16.7 and 15.83° C.

Since development on the host cannot begin until the larvae leave the egg mass, phenological models should initiate larval growth at peak dispersal rather than at peak hatch. The two-week interval between when dispersal begins and ends means that some larvae will begin development on much younger foliage than other larvae.

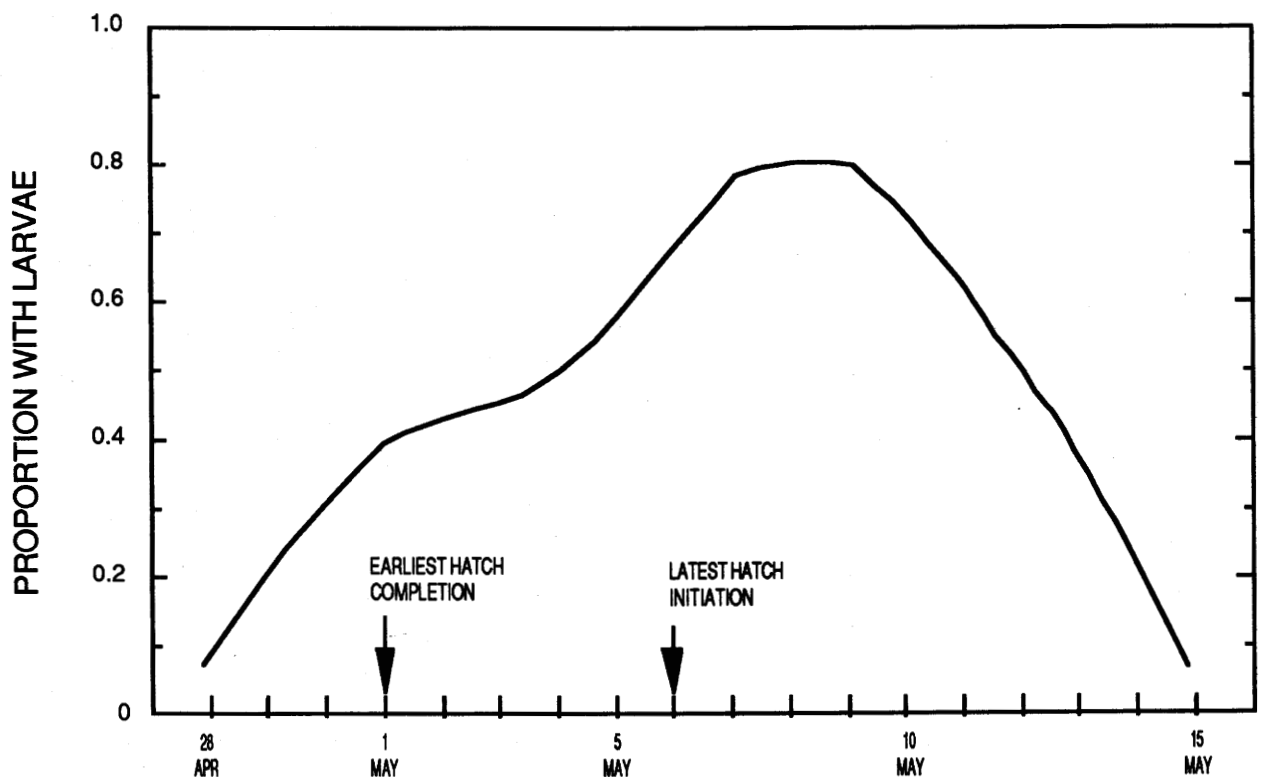


Figure 3. Proportion of 93 gypsy moth egg masses with larvae on them, Ansonia, CT, 1989.

Establishment Phenology

Phenological relationships between time of establishment on the host plant and larval survival and growth were examined on black oak and grey birch. In 1987 hatched larvae were placed on hosts in the field one week prior to, at the time of, and one week after peak hatch of eggs in nature. Survival on birch was best on the latest establishment date, but date had little effect on survival on oak (Fig. 4). Towards the end of larval development, larvae that were established the earliest had the highest growth rates (Fig. 5).

The phenological window for optimal survival was much narrower for birch than for oak, but late in the season larvae that had survived had better growth rates on birch than on oak. The more restricted period to establish on birch helps to explain why birch receives relatively less defoliation than oak even though larvae attain larger size on birch than on oak. The data also illustrate how the optimal time of hatch must be a balance between the risk of not surviving and the risk of not growing well. A long period of hatch would spread these risks.

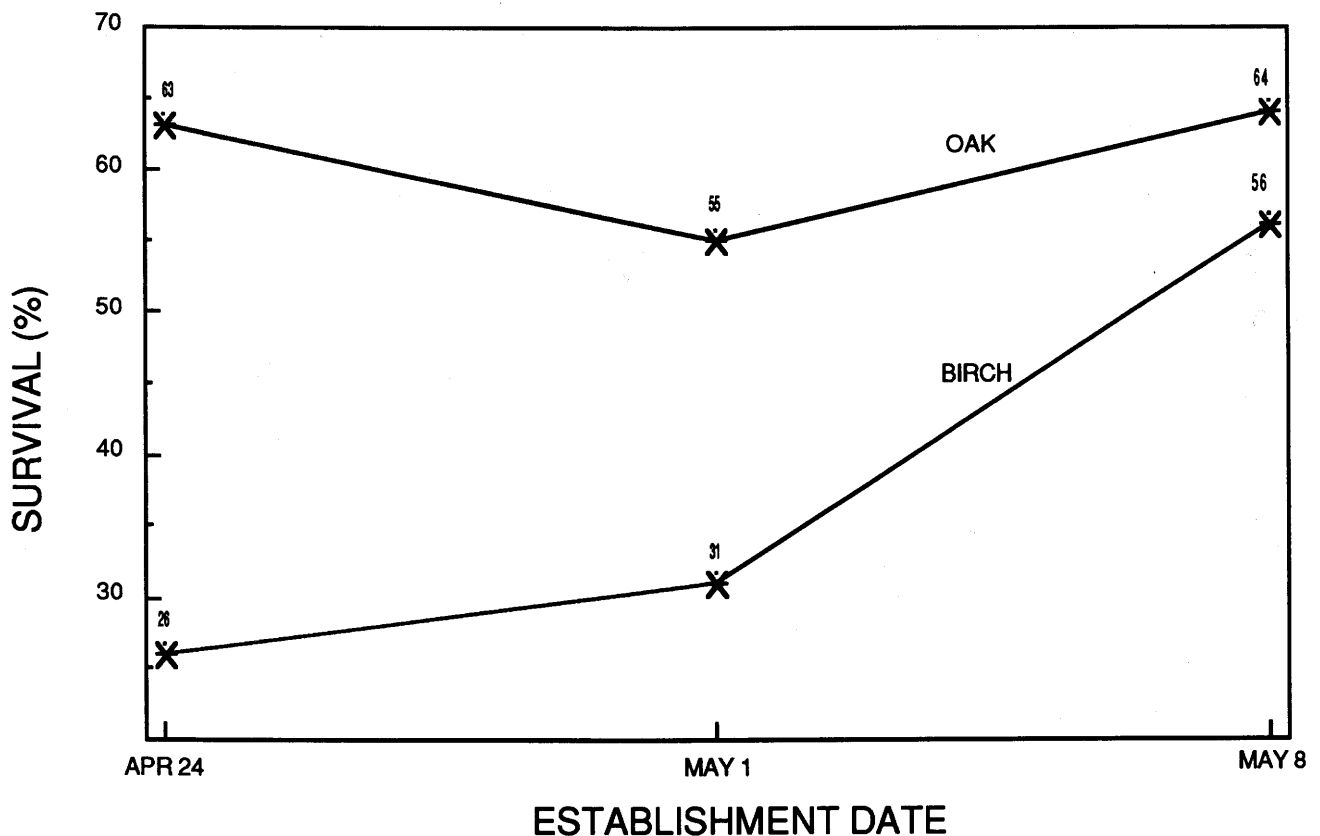


Figure 4. Survival of recently hatched larvae confined on black oak and grey birch foliage in the field on three dates.

SUMMARY

Classifications of the suitability of gypsy moth host plants tend to be overzealous. It is important for management to distinguish the tree species that are suitable; i.e., that foster rates of growth that result in maintenance or increases in population densities. Efforts to make fine distinctions between the suitability of marginal species, in particular, may not be worthwhile.

More attention should be given to the variation of individuals within a species. Variation in suitability has been traced to site effects, phenological relationships, dbh (reviewed herein), solar radiation (Montgomery 1989), and defoliation (Rossiter and others 1988). Tree genetics is undoubtedly also important.

It is now recognized that the host plant may provide the herbivore more than nutrition and shelter. The secondary non-nutritive chemicals in host plants may ward off disease infection. Indeed, the gypsy moth may select hosts that have weak toxicity because the toxin is stronger to its enemies (Schultz and others 1990). It is important to confirm this concept on a population level.

The host plant likely has an important role in triggering changes in gypsy moth abundance. Variation in host plants that lead to gypsy moth outbreaks would occur at the individual and temporal levels.

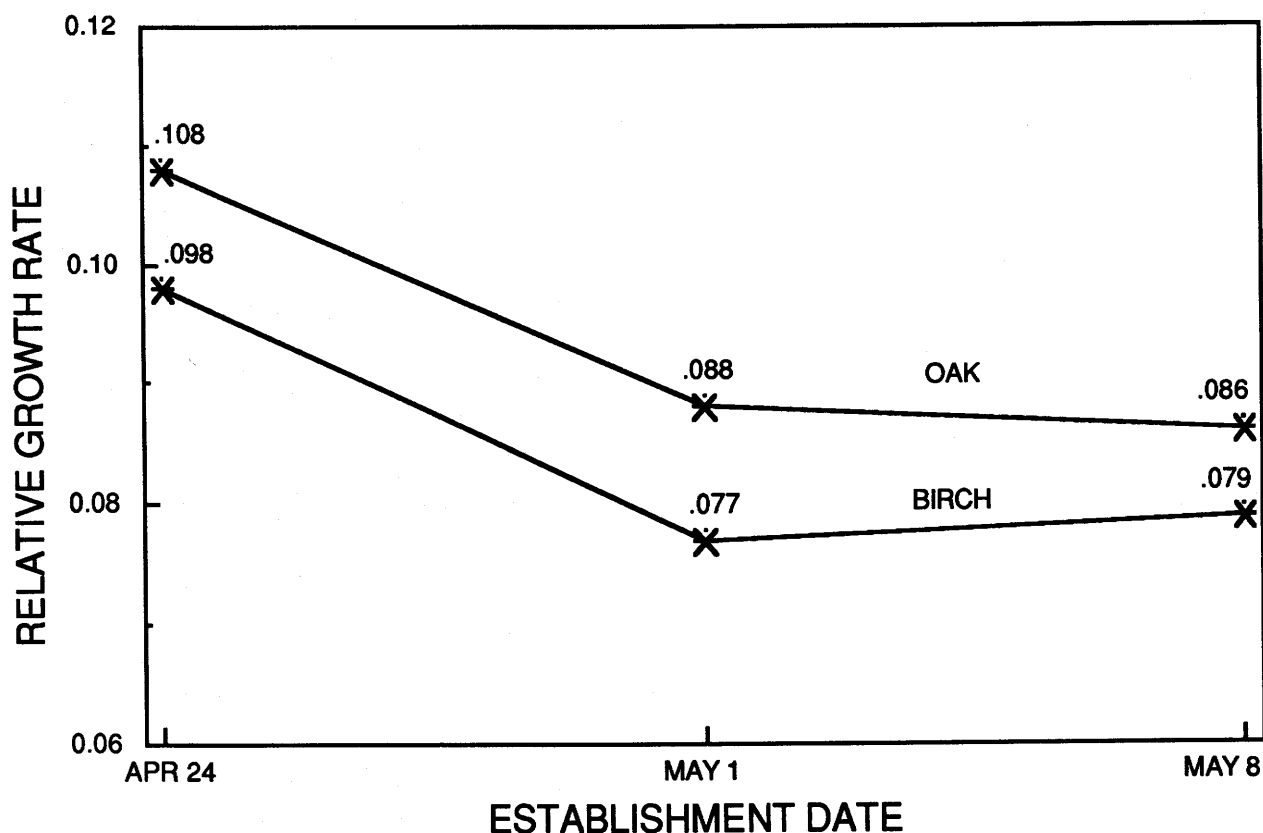


Figure 5. Relative growth rates (mg/mg/degree day) of 3rd - 4th instar larvae established on black oak and grey birch on three dates.

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