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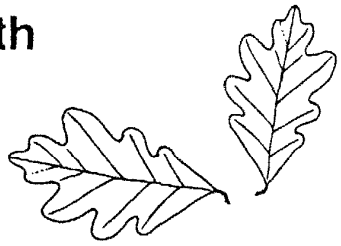

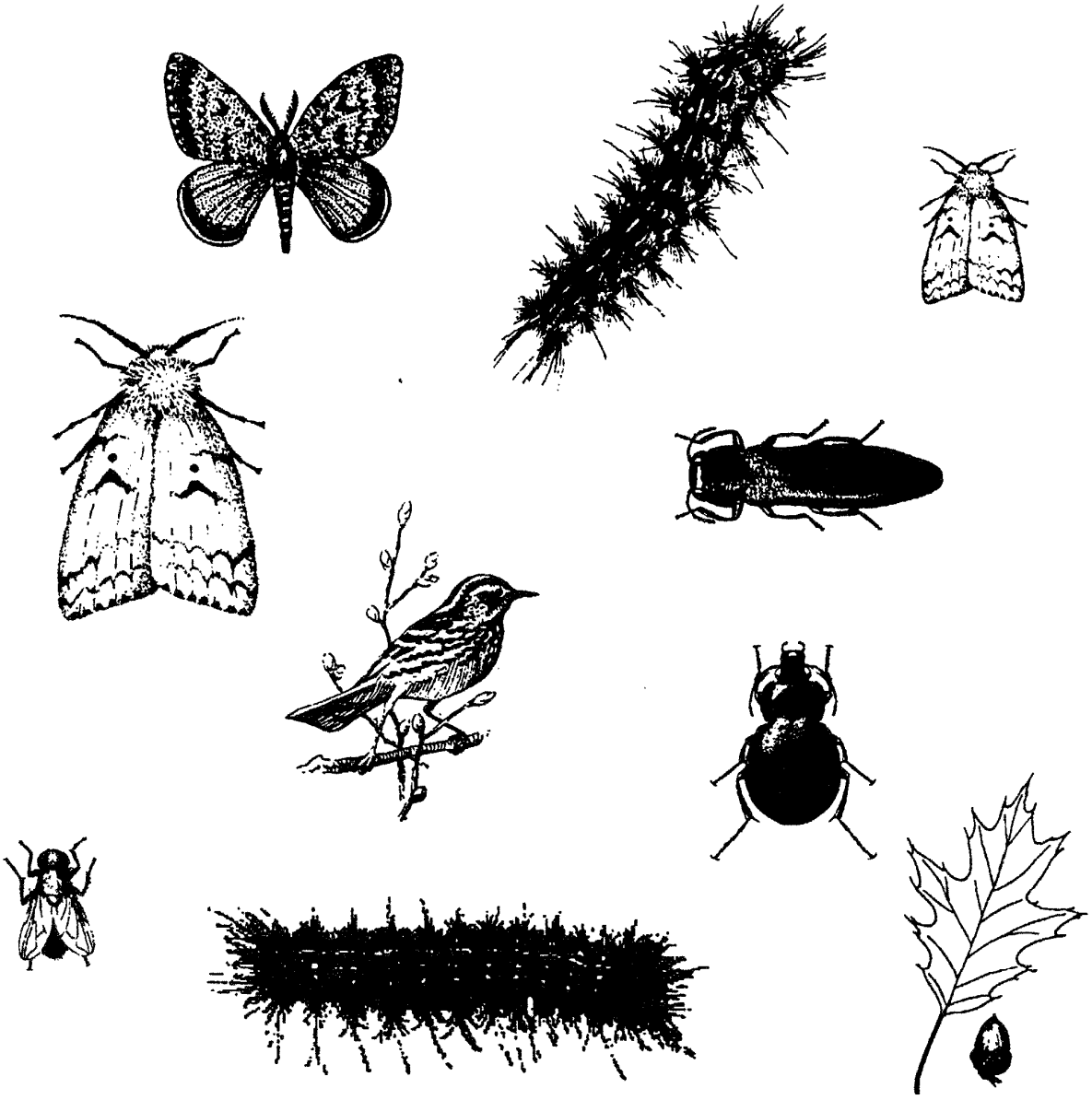

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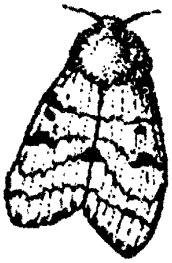

January 22-25, 1990
East Windsor, CT

Edited by
Kurt W. Gottschalk, Mark J. Twery, and Shirley I. Smith

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Cooperative State Research Service

FOREWORD

In July of 1989 representatives of Forest Service-Research (FS-R), Animal and Plant Health Inspection Service (APHIS), and Agricultural Research Service (ARS) began regular meetings to discuss opportunities for improving cooperation among the agencies conducting research on gypsy moth. Representatives from the Cooperative State Research Service (CSRS) and Forest Service-State & Private Forestry (FS-S&PF) were added over the next few months. The group is known as the USDA Gypsy Moth Research and Development Coordinating Group and has the following objectives:

a. To monitor the progress of Service programs and any breakthroughs which may influence USDA policies;

b. To keep the Services and the Gypsy Moth Working Group appraised of progress in research and methods development;

c. To identify research and methods development issues and concerns;

d. To set priorities;

e. To maximize use of current resources as well as to provide appropriate rationale to justify increased resources.

The Coordinating Group resolved at its initial meeting that a combined interagency review of gypsy moth research and development activities would add immeasurably to better communication as well as provide a comprehensive overview of ongoing research. Members of the Coordinating Group also agreed that a proceedings should be published following the meeting.

These proceedings document the efforts of many individuals: those who made the meeting possible, those who made presentations, and those who compiled and edited the proceedings. But more than that, the proceedings illustrate the depth and breadth of studies being supported by the agencies and it is satisfying, indeed, that all of this can be accomplished in a cooperative spirit.

USDA Gypsy Moth Research and Development Coordinating Group
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T. Hofacker, FS-S&PF
M. McFadden, FS-R, Chairperson

USDA Interagency Gypsy Moth Research Review
January 22-25, 1990
Ramada Inn
East Windsor, Connecticut

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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 rational 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	*Quercus alba*
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*
Quercus alba	1.00
Q. ellipsoidalis	1.05[5]
Q. falcata	1.22[4]
Q. nigra	1.50[4]
Q. phellos	0.58[7]
Q. prinus	1.05[3]
Q. rubra	0.99[1], 1.23[2], 0.88[3], 0.66[5]
Q. stellata	1.08[3]
Q. velutina	0.95[5], 0.52[7]
Fagus grandifolia	0.48[1], 0.68[2], 0.56[5], 0.58[6]
Liquidambar styraciflua	1.24[4], 1.12[7]
Salix lucida	1.21[3]
Populus deltoides	1.14[3]
P. grandidentata	0.99[3], 1.47[5]
P. tremuloides	1.51[3], 1.46[5]
Alnus serrulata	0.45[3]
Betula lenta	0.48[3]
B. papyrifera	1.01[5]
B. populifolia	1.64[2], 1.26[3]
Carpinus caroliniana	0.88[3]
Amelanchier arborea	0.79[5]
Carya tomentosa	0.62[6]
Acer rubra	0.51[1], 1.10[4], 0.69[6], 0.30[7]
A. saccharum	0.37[1]
Tsuga canadensis	0.21[1]
Fraxinus americana	-0-[1]
Pinus strobus	-0-[7]
P. taeda	-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.

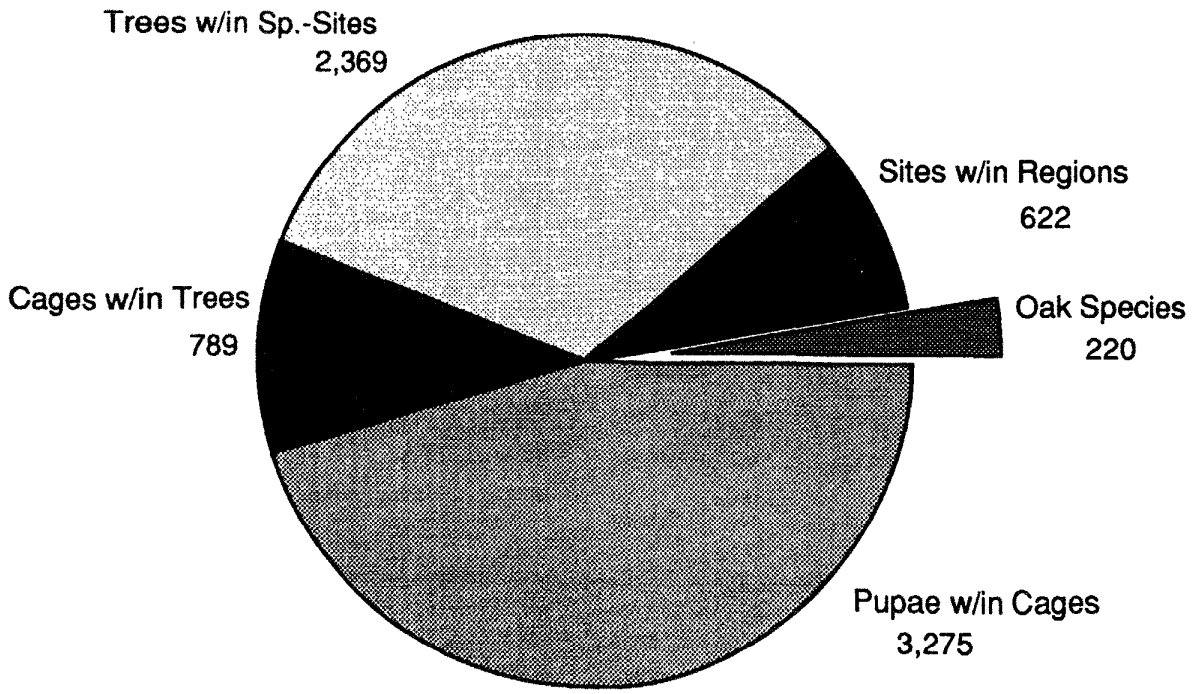

Figure 1. Variance components of random effects on female pupal weights on three oak species.

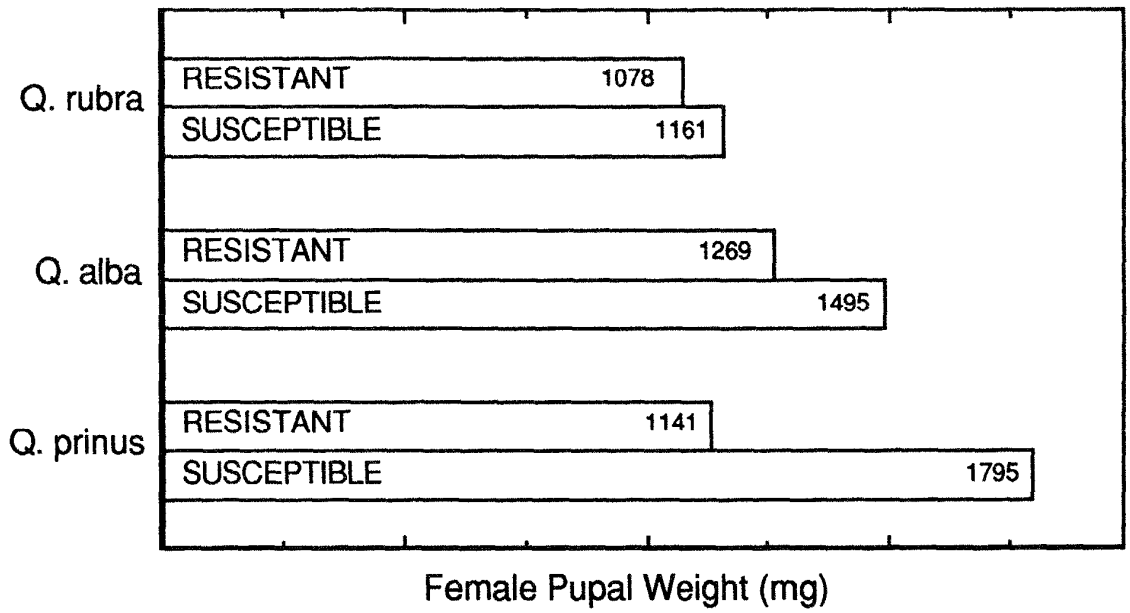

Figure 2. Comparison of female pupal weights of larvae reared on excised oak foliage from resistant and susceptible sites.

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 lead 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).

	Resistant site		Susceptible site	
	Q. prinus	*Q. rubra*	*Q. prinus*	*Q. rubra*
% 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.

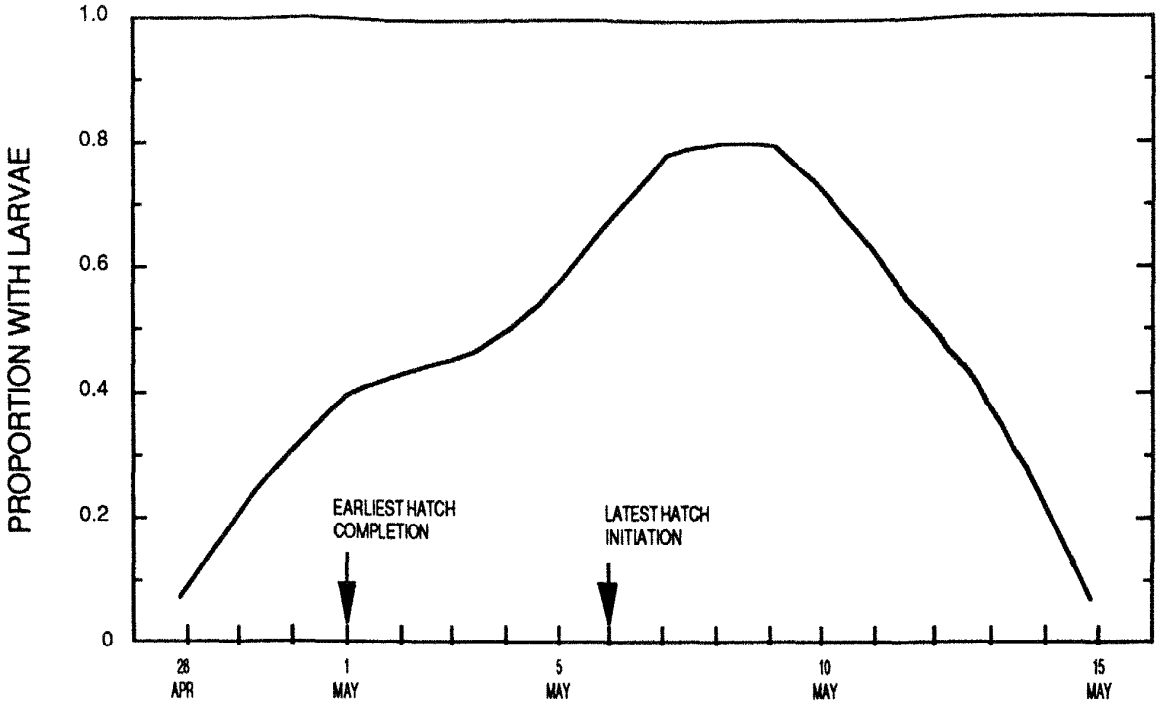

Figure 3. Proportion of 93 gypsy moth egg masses with larvae on them, Ansonia, CT, 1989.

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.

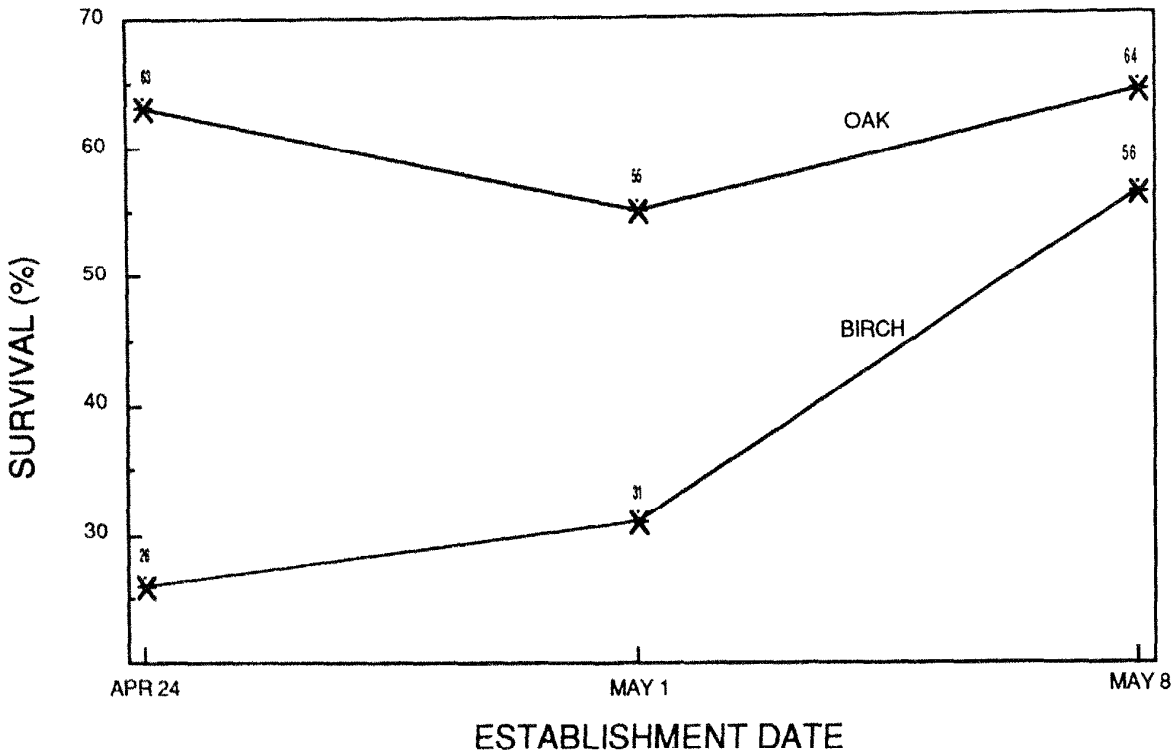

Figure 4. Survival of recently hatched larvae confined on black oak and grey birch foliage in the field on three dates.

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.

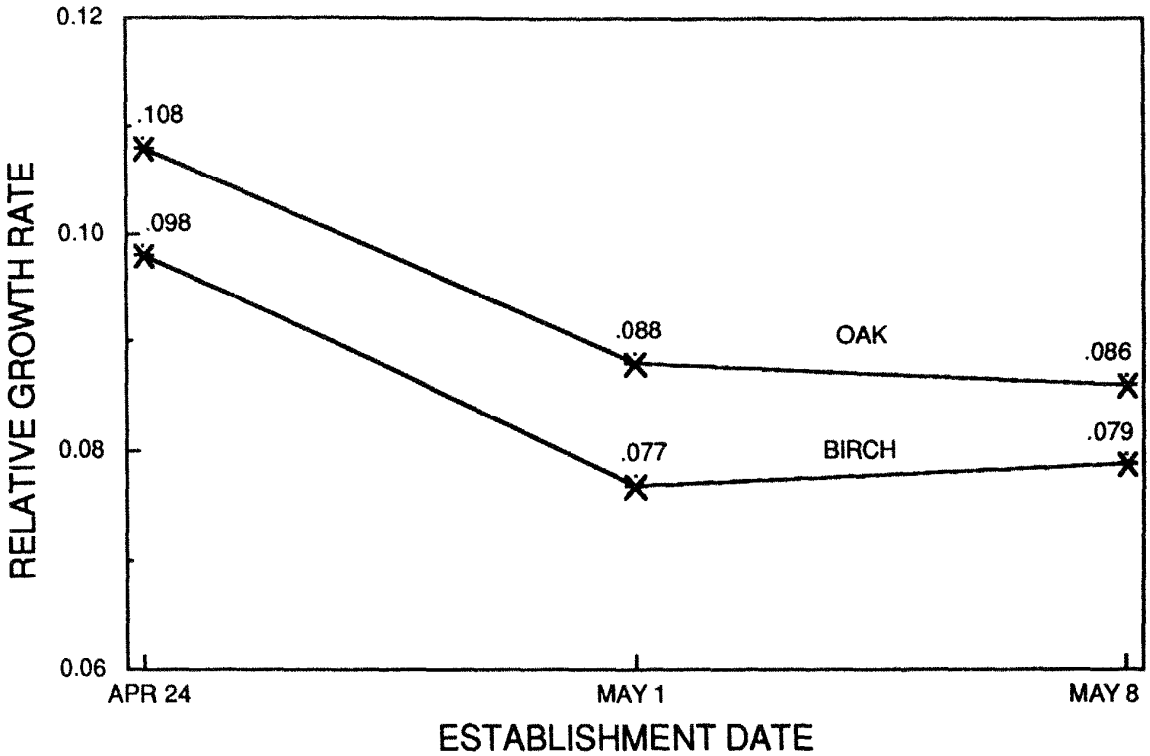

Figure 5. Relative growth rates (mg/mg/degree day) of 3rd - 4th instar larvae established on black oak and grey birch on three dates.

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EPIZOOTIOLOGY OF GYPSY MOTH NUCLEAR POLYHEDROSIS VIRUS

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ABSTRACT

Recent experimental findings demonstrate that two distinct waves of mortality of gypsy moth larvae from nuclear polyhedrosis virus (NPV) occurs during larval development. The evidence suggests that early instars acquire lethal doses of NPV from the surface of the egg mass and the cadavers of these larvae produce inoculum that causes a second wave of mortality among late instars. Transmission of NPV between gypsy moth generations appears to occur primarily by way of contamination of egg masses from environmental sources during oviposition. Other factors influencing NPV epizootiology including Foliage chemistry, weather and genetic effects are discussed.

INTRODUCTION

Epizootics of nuclear polyhedrosis virus (NPV) frequently cause precipitous declines of high density populations of gypsy moth *Lymantria dispar* L. (Bess 1961, Campbell 1963, 1967, Campbell and Podgwaite 1971, Doane 1970). In low density gypsy moth populations, mortality caused by NPV is usually quite low (Campbell and Podgwaite 1971). Epizootics of NPV are typical of high density populations of many species of Lepidoptera (Stairs 1972) including other lymantriids (Murray and others 1989). With gypsy moth, mortality from NPV usually peaks among the late larval stadia (Glaser 1915, Doane 1970, Woods and Elkinton 1987). In this manuscript we review recent findings concerning the causes of gypsy moth NPV epizootics, the mechanisms of transmission between and within host generations and the impact of various factors that influence the level of mortality from NPV.

TRANSMISSION WITHIN A HOST GENERATION

The causes of NPV epizootics in insect populations and why they are associated with high host densities have not been fully elucidated. Possible causes fall into two major categories. The first, which was widely expounded in earlier literature, is that stress factors such as crowding or starvation induce expression of NPV infections that are latent in many, if not most, of the individuals in a population (Bergold 1958, Steinhaus 1958, Aruga 1963, Vago 1963). For gypsy moth, such stresses presumably attain peak values during late instars when defoliation reaches a maximum extent. Consequently, the idea that epizootics are induced by stress appears to explain why highest mortality from NPV occurs among late instars. To date, however, there has been no experimental demonstration that epizootics can be triggered by stress factors associated with high density for gypsy moth, or indeed, for any other Lepidoptera (Evans 1986).

The second major theory holds that NPV epizootics occur when the environment becomes heavily contaminated with polyhedral inclusion bodies (PIBs) that are released in great numbers from cadavers of NPV-killed larvae. For gypsy moth NPV, this idea was championed by Doane (1970, 1975, 1976), who suggested that a certain percentage of early instar larvae become infected with virus in the process of hatching, and that the PIBs released from these larvae when they die provide the inoculum for later instars. Consequently, in situations where both the insect density and the initial virus concentration are high enough, a virus epizootic results. In outbreak or pre-

outbreak populations, we would expect this mortality to be density dependent (i.e. reaches a maximum at high density). However, Doane (1976) predicted that following an epizootic mortality from NPV would be density independent. High levels of mortality from NPV would occur even in populations that have declined to very low levels because the concentration of PIBs in the environment remains very high. (Doane 1970, 1975, 1976; Podgwaite et al 1979).

Research by Woods and Elkinton (1987) has provided strong support for Doane's hypothesis concerning the development of epizootics. Mortality from NPV and other causes was quantified over several years from both high- and low- density populations on Cape Cod, Massachusetts. Larvae were collected from these populations once a week until the onset of pupation. These larvae were reared individually in cups with artificial diet (Bell and others 1981) in an outdoor insectary and inspected at frequent intervals to determine the proportion that died from NPV. Death from NPV was confirmed by examining the cadavers for the presence of PIBs in the body tissues.

The results indicated that in both high and low density gypsy moth populations, mortality from NPV usually follows a bimodal temporal pattern. There is a first wave of mortality among first to third instars followed by a period of reduced mortality and then a second wave when the majority of the larvae are fifth and sixth instars. The highest rates of mortality from NPV always occurred during the second wave (Woods and Elkinton 1987). In addition, the amount of NPV on foliage was measured in samples of oak leaves collected each week from one of the plots. NPV was extracted from the foliage (Podgwaite and others 1979) and the extract was bioassayed by soaking gypsy moth eggs from a laboratory colony in the extract and recording the mortality from NPV among neonates that hatched from the eggs. The bioassay results showed that NPV contamination of foliage also exhibited a bimodal wave that coincided with peak mortality from NPV among the larvae in the natural population. Finally, the bimodal pattern was also produced in laboratory experiments. Gypsy moth egg masses were collected in the field and permitted to hatch. The neonates were divided into two groups. Members of the first group were reared individually in 30 ml cups with artificial diet (Bell and others 1981). The remaining larvae were reared in groups of 10 in 180 ml cups. In both groups there was a first wave of mortality that occurred among instars 1-3. Among the larvae reared individually there was no mortality from NPV among older instars. In contrast, the larvae reared in groups of 10 exhibited a pronounced second wave of mortality among late instars. Both field and laboratory results support Doane's hypothesis that early instar mortality contaminates the foliage with NPV and provides the primary inoculum for late instar infections.

There have been several other studies that support Doane's hypothesis or show the bimodal pattern of mortality in gypsy moth populations. Higashiura and Kamijo (1978) describe a bimodal or trimodal wave of mortality from NPV in Japanese populations of gypsy moth. Woods and others (1988) showed that *Bacillus thuringiensis* (Bt) applications to gypsy moth populations during the first or second stadium resulted in substantially less mortality from NPV among later instars than was observed among late instars from untreated plots. A similar reduction in mortality from NPV was noted among larvae emerging from egg masses the following year in the treated plots. There are several possible explanations for these results, but an obvious one is that the Bt killed early instars before they died from NPV, thereby reducing the inoculum available to later instars.

Finally, a simulation model of gypsy moth/NPV interaction (Valentine and Podgwaite 1982) has been constructed and reincarnated as the pathogen submodel of the Gypsy Moth Life System Model (Sheehan 1987). The model simulates the deposition and movement of NPV PIBs in the forest canopy and the consumption of foliage by gypsy moth larvae. The model exhibits a clear bimodal pattern of mortality very similar to that observed by Woods and Elkinton (1987) in real populations.

These results should not be interpreted as implying that there is only enough time for two cycles of viral replication and host death in the gypsy moth larval stage. In the laboratory at 28° C, 7-14 days elapse between ingestion of a lethal dose and death of the larvae (Woods and Elkinton 1987), whereas larval development at this temperature takes ca. 28 days for males and 31 days for females (Casagrande and others 1987). Late instar larvae can readily ingest inoculum and die from NPV before pupation. The second wave of mortality in the population consists in part of a third wave (documented by Higashiura and Kamijo 1978) that is rarely distinct from the second. After pupation, however, levels of mortality from NPV are much lower (Murray and others 1990).

All of these studies support, but do not prove, the idea that contamination of foliage with NPV from cadavers of early instars is the primary source of inoculum for the second wave of mortality among late instars. We have initiated studies to examine the alternative hypothesis that late instar gypsy moths acquire NPV from protected daytime resting locations. Beginning with the fourth instar, gypsy moths in low density populations leave the canopy of the forest at dawn and seek resting locations in the litter or under bark flaps (Forbush and Fernald 1896), where they spend the daylight hours. Previous research has shown that such protected locations become highly contaminated with NPV and that infectious NPV persists in such locations for at least a year (Podgwaite and others 1979, Weseloh and Andreadis 1986). In contrast, NPV deposited on foliage is short-lived (Podgwaite and others 1979). It is rapidly denatured by ultra violet light (Jaques 1985) or washed off by rain (Doane 1970). Furthermore, previous studies have shown that gypsy moth neonates can acquire lethal infections of NPV merely by walking over such contaminated substrates (Weseloh and Andreadis 1986, Woods and others 1989). We therefore thought that it was possible that a proportion, perhaps a majority, of larvae that die as late instars acquire NPV from such contaminated resting locations rather than foliage. On the other hand, large larvae require substantially higher doses of NPV to obtain a lethal infection than smaller larvae (Briese and Podgwaite 1985), and it is not clear that any of the NPV contaminant of resting sites would actually be ingested.

In 1989 we ran two experiments designed to investigate this possibility. Both experiments involved application of NPV to burlap bands. In the first experiment Gypchek, a formulated NPV insecticide (Lewis 1981), was applied to burlap bands wrapped around trees in a moderate density gypsy moth population. Burlap bands around other nearby trees remained untreated. The burlaps were visited daily, to prove that the trees were far enough apart that there was negligible movement of larvae between trees. To prove that the trees were far enough apart that there was negligible movement of larvae between trees, the larvae underneath the burlap were marked with a dot of paint that was distinct for each day and treatment. After several days, larvae were collected and reared individually in 30 ml cups on artificial diet. Mortality from NPV was monitored. Results from these experiments will be described elsewhere in detail, but, in summary, there was virtually no mortality from NPV among larvae collected from control trees and a small, but significantly greater, level of mortality among larvae from the treated trees.

The second experiment was similar to the first except that NPV was applied to burlap in the form of larvae that were recently killed by NPV and that experiments were performed on branches of oak foliage inside rearing cages. There were three treatments. In the first treatment dead larvae were smeared on the foliage, in the second treatment the dead larvae were smeared on the burlap bands and the third treatment (controls) received no dead larvae. Most of the larvae recovered from cages that had NPV smeared on the foliage subsequently died from NPV. None of the larvae from the control cages died and a small, but significant, proportion of the larvae from the burlap-treated cages died from NPV.

These experiments prove that it is possible for late instar gypsy moth larvae to acquire lethal infections of NPV from contaminated resting locations. However, it tells us very little about how important this is as a source of inoculum compared to foliage contamination in natural populations.

The only data we have that sheds light on this question are results from experiments in which we created populations of gypsy moths on 1 ha plots by releasing large number of field collected egg masses (Liebhold and Elkinton 1989, Gould and others 1990, Elkinton and others unpublished). The eggs were collected from high density populations and were therefore expected to produce a substantial number of infected neonates (Doane 1969, Woods and others 1988, 1990). However, we surface-disinfected the eggs in a 10% formalin solution before we released them on our plots. Doane (1969) showed that such surface treatments will virtually eliminate the mortality NPV among the emerging neonates. We observed virtually no mortality from NPV among larvae collected from these populations either as early or late instars. In a follow-up study in 1988, we created seven additional populations of gypsy moths of which three received eggs that were not surface-disinfected. One of the surface-disinfected populations was created in a stand that had experienced a high density of gypsy moth and had collapsed the previous year. Presumably this site was heavily contaminated with NPV. Once again the populations created with surface-disinfected eggs experienced little or no mortality from NPV. In contrast, all three populations receiving eggs that were not surface-disinfected experienced a pronounced bimodal wave of mortality from NPV that mirrored that seen in natural populations. We believe that these results strongly imply that late instar mortality larvae originates from larvae that die as early instars as Doane (1970, 1975, 1976) proposed.

Other possible mechanisms of horizontal transmission of NPV in gypsy moth populations include vectoring by predators and parasitoids. Lautenschlager and Podgwaite (1977, 1979) showed that NPV PIBs remain viable after passage through the alimentary tracts of avian and small predators of gypsy moth. Raimo and others (1977) showed that the parasitoid *Cotesia melanoscela* is capable of transmitting NPV infections from diseased to healthy larvae. The importance of these findings to NPV epizootiology has not been investigated.

TRANSGENERATIONAL TRANSMISSION

In the foregoing discussion we presented evidence that acquisition of lethal infections by early instars is the key to epizootic development. How, then do early instars become infected? In other words, how is NPV transmitted between generations of gypsy moth? There are two possible basic mechanisms: either the infection is transmitted from the female to her offspring (vertical transmission) or else larvae or eggs become infected from NPV inoculum in the environment. The latter mechanisms are usually considered horizontal transmission (Andreadis 1987), although some researchers use the term vertical transmission to refer to both forms of transmission across host generations.

Shapiro and Robertson (1987) presented evidence for vertical (maternal) transmission of NPV in gypsy moth. They fed LD_{50} and LD_{80} doses of NPV to gypsy moth larvae and observed PIBs in the host tissues of the adult survivors. They found that 4.7% and 11.5% of the respective progeny of these adults died from NPV. However, other studies have failed to demonstrate vertical transmission. Shields (1984) found no mortality from NPV among the offspring of the survivors of LD_{50} doses of NPV nor any developmental or physiological differences between these and undosed (control) larvae. Murray and Elkinton (1989) found no evidence for maternal transmission among the offspring of larvae that survived low doses (LD_{17}) of NPV. Finally, Murray and others (1990) found no viral DNA in the adult tissues of gypsy moths that survived various doses of NPV. Viral DNA was detected in hemolymph extracted from some of the pupae arising from dosed larvae but all of these individuals died from NPV before adult eclosion. At present we cannot explain the differences between these results and those of Shapiro and Robertson (1987).

Doane's finding (1969) that nearly all of the mortality of larvae reared from field collected egg masses could be eliminated by surface disinfection suggests that maternal transmission, if it exists,

occurs largely by way of surface contamination (transovum transmission) as opposed to within the egg (transovarial transmission). To date there has been no conclusive demonstration of transovarial transmission of NPV in any Lepidoptera (Evans 1986), although there is circumstantial evidence for it (reviewed in Burand and others 1986). For gypsy moths this evidence includes experiments which showed that NPV mortality can be induced with chemical stressors (Yadava 1971) or by foreign viruses (Longworth and Cunningham 1968). However, various treatments or stressors that seem to induce infections may merely increase the susceptibility of larvae to normally sublethal laboratory contaminants of NPV. We believe that polymerase chain reaction (PCR) technology will soon enable us to determine if minute quantities of viral DNA exist in gypsy moth embryos and help determine if transovarial transmission occurs.

Murray and Elkinton (1989) reported experiments indicating that gypsy moth egg masses acquire NPV contaminant primarily from the surface on which they are deposited. In the first experiment the mated adult females that had survived a dose of NPV as larvae as well as mated undosed females were allowed to oviposit on tree stems in a site with a low density natural population of gypsy moths. Other dosed and undosed females were allowed to oviposit into plastic cups that were held over the winter in an outdoor insectary. The following spring the egg masses from the four groups were collected and the neonates were reared on diet to determine the proportion that acquired a lethal dose. There was no difference in NPV-caused mortality among neonates from dosed and undosed parents but more of the neonates from egg masses that were laid on trees in the field died from NPV than neonates from egg masses deposited into cups. In another study, that we called the site switching experiment, females were collected as pupae from a high density site that had experienced high levels of mortality from NPV and from a low density site that experienced little mortality from NPV. The adult females from the high density site were caged on trees, mated and allowed to oviposit in the low density site and the low density females oviposited in the high density site. Other females were caged and oviposited in the same site from which they were collected and another group of females from the high density site were mated and allowed to oviposit into cups in the laboratory. The following spring the eggs were collected and the neonates reared on diet to determine NPV-caused mortality as before. Higher levels of mortality occurred among larvae reared from egg masses oviposited in the high density site regardless of the source of the mother. Mortality among neonates that hatched from eggs deposited in the low density site was not different from the mortality among those hatched from eggs deposited into cups.

A third experiment examined the role of rainfall in the contamination of egg masses with NPV. Mated laboratory-reared females were allowed to oviposit on tree stems in the high and low density sites underneath waxed cardboard shelters that kept off the rain but left the egg mass otherwise exposed to the open air. Other females oviposited on tree stems without shelters. Again these egg masses were collected just before hatch the following spring and mortality of neonates from NPV was recorded. There was no difference in mortality among neonates from sheltered versus unsheltered egg masses, but again there was much higher levels of mortality among larvae hatched from egg masses that were oviposited in the high density site compared with larvae from egg masses deposited in the low density site. The level of mortality among neonates from the egg masses laid in the high density site ranged from 20 - 46% and was comparable to that observed among neonates from naturally occurring egg masses at this site. These values are far higher than the 11% mortality reported by Shapiro and Robertson (1987) arising from maternal transmission. Our conclusion is that if maternal transmission does occur, it probably is less important than environmental contamination of eggs as a mechanism of transgenerational transmission, at least in high density sites.

Circumstantial evidence in support of this view has been obtained by Woods and others (1990) who found that egg masses collected from tree stems are more highly contaminated with NPV than egg masses collected from the ground or from understory vegetation. During an epizootic, late

instar larvae die in great numbers in resting locations on tree stems and contaminate the bark with PIBs.

The exact mechanism by which egg masses become contaminated by NPV remains to be determined. Murray and Elkinton (1989) found that egg masses recovered in August a few days after oviposition and held over the winter in an insectary did not have a significantly different NPV load than egg masses that overwintered on the stems of trees. This result suggested that the contamination occurs during the process of oviposition. The adult females may become externally contaminated as they drag their abdomen over the bark surface or the egg masses may be deposited directly onto contaminated substrates. In follow-up studies, Murray and Elkinton (1990) sprayed NPV (Gypchek) onto the bark surface of bolts cut from living oak trees. Uninfected laboratory-reared females were mated and allowed to oviposit on the contaminated bark surface and on bolts that had received no NPV. The egg masses were held over the winter, removed from the bark prior to hatch and the neonates were assayed as above. Neonates emerging from egg masses on the contaminated bark had much higher levels of mortality from NPV than neonates from uncontaminated bark. Furthermore, neonates from the innermost part of the egg masses near the bark surface, had higher levels of mortality than from the outer layer of the egg masses. These results support the conclusion that NPV is transferred from the contaminated substrate to the egg mass during oviposition. The egg mass may provide a protective cover for the PIBs that otherwise might not survive exposure to UV radiation or other factors over the 9 month interval between oviposition and hatch.

Other possible sources of egg mass contamination may be from the adult male during the process of mating or from egg parasitoids such as *Ooencyrtus kuvanae*. None of these mechanisms have been investigated experimentally. However, in the experiments of Murray and Elkinton (1989), cited above, females in the site switching experiment were mated with naturally occurring males at the site of oviposition whereas in the other two experiments (dosed versus undosed parental females and sheltered versus unsheltered egg masses) the females were mated with laboratory reared, uninfected males. High levels of NPV mortality were observed among neonates from egg masses deposited in the high density site regardless of parental source, suggesting that the male parent contributed little to egg mass contamination.

Other studies suggest that infection of neonates after they leave the egg mass may be another important route of transgenerational transmission. In laboratory experiments Weseloh and Andreadis (1986) showed that neonates can acquire lethal infections of NPV by walking over naturally occurring contaminated surfaces including soil and pupal-debris mats from high density populations. These findings were corroborated in field experiments by Woods and others (1989) who showed that neonates acquired lethal infections by crawling over contaminated bark. A limitation of both of these studies was that larvae were transferred onto artificial diet. As far as we know, larvae can acquire NPV infections only by ingestion. This either occurred while the larvae were crawling over the contaminated surfaces or they may have transferred the PIBS onto the diet from which they were later consumed. Such transfer may occur more readily on diet than on foliage in the field. However, we investigated this in the experiments described above with older larvae. We found that older larvae exposed to contaminated burlap bands and reared subsequently on foliage acquired NPV infections to the same extent as larvae reared on diet. The importance of such mechanisms of between generation transmission remains to be determined. Based on the limited results with artificial populations of gypsy moth described above, we suspect that egg mass contamination is more important. We anticipate future experiments to settle this issue.

FACTORS INFLUENCING MORTALITY FROM NPV

Rainfall and Relative Humidity

Many researchers believe that rainy conditions induce NPV epizootics. Analyses of the Melrose Highlands data by Campbell (1967) indicate that population declines were associated with heavy rainfall occurring in June, most notably during the region-wide collapse of gypsy moth populations that occurred in 1922. Of course, in most of these studies, the actual cause of population decline were unknown. In 1989 a dramatic epizootic of *Entomophaga maimaiga* decimated populations of gypsy moth in New England, a year with near record rainfall in May and June. The evidence suggests that this agent was introduced in 1910 or 1911 (Hajek and others unpublished) from Japan. The known association of *E. maimaiga* epizootics with rainy conditions in Japan (Shimazu and Soper 1987) and its ubiquitous occurrence throughout the northeast in 1989 suggests that it may have caused many of the previous population declines in rainy years.

Experiments by Wallis (1957) suggested that high relative humidity was associated with NPV infection. However, the laboratory data cited were never actually presented and the observations of NPV mortality in field populations show no more than onset of high mortality among late instars which happened to coincide with a period of heavy rainfall in that particular place and year. No such correlations were observed in the populations studied by Woods and Elkinton (1987). Furthermore, the mechanisms by which rainfall would promote NPV infection have not been established. Rainfall might serve to distribute PIBs more evenly across the foliage surface thereby increasing the chance of larval encounter. This has been demonstrated with NPV of Douglas fir tussock moth (Thompson 1978). However, rainfall also washes larval cadavers off the foliage entirely (Doane 1970), thereby removing the inoculum from potential consumption. We conclude, therefore, that there is little evidence for rainfall or relative humidity enhancing gypsy moth infection from NPV.

Host tree species and foliage chemistry

Keating and Yendol (1987) demonstrated that larvae fed NPV on aspen leaves were much more likely to become infected larvae fed NPV than on oak leaves. These findings are supported by observations of Bess (1961) that epizootics of NPV occur more frequently and at lower population density in aspen than in oak stands. Follow-up studies (Keating and others 1988) indicated that foliage containing large quantities of tannins in foliage have reduced susceptibility to NPV. Tannins apparently bind to virus particles in the midgut and perhaps inhibit passage across the peritrophic membrane. Tannins also affect midgut pH (Schultz and Lechowicz 1986) which in turn affects the dissolution rates of PIBs and the consequent release of virus particles. Other research demonstrates that tannin concentrations increase in the foliage of trees experiencing defoliation. (Schultz and Baldwin 1982, Rossiter and others 1988). These findings have lead to speculation that larvae feeding on trees undergoing defoliation may become more resistant to NPV epizootics.

Genetics and evolutionary considerations

Theoretical studies of host/pathogen interactions (Levin and others 1982, May and Anderson 1983) indicates that the virulence of the pathogen is related to the mechanisms of transmission. In systems where vertical transmission predominates, pathogens frequently evolve to produce benign avirulent infections. There are many examples of such trends towards benign mutual coexistence of host and pathogen including myxomatosis in rabbits in England and Australia (Fenner and Ratcliffe 1965), trypanosomiasis in native versus introduced ruminants in Africa, (Allison, 1982) and plague bacillus in rats (Levin and others 1982). However, if transmission depends primarily upon infective particles which are released from host cadavers, as is the case for insect NPVs, then, in general, selection should favor more virulent strains. On the one hand, selection should favor viruses which replicate quickly and are released into the environment in the shortest period of time.

On the other hand, if the virus kills its host too quickly, then the larva may not have grown to a size that permits maximum production of virus particles. Intermediate levels of virulence and replication rates seem to be the rule among insect NPVs (Anderson and May 1980, 1981, May and Anderson 1983). Even when selection favors the most virulent strain of the virus, selection acting on the host favors resistance so the resulting populations may reflect a balance between these opposing forces.

The experiments cited above suggest that there are a variety of mechanisms of transmission of NPV and we do not yet know their relative importance. We believe that the importance of these individual mechanisms may vary between high and low density populations. When population densities are high there is a sufficient density of cadavers that died of virus during early instars so that older instars have a high probability of consuming a lethal dose. Similarly, high concentrations of NPV on tree stems may heavily contaminate egg masses (Murray and Elkinton 1989). In low population densities, which are often less than 10 larvae per tree, the probability of encountering a lethal dose of virus is obviously quite small. Indeed, theoretical studies by Anderson and May (1981) suggest that without some mechanism of survival or reservoir, NPVs are likely to go extinct when their hosts are at low density. If maternal transmission occurs, as Shapiro and Robertson's (1987) results indicate, it seems likely that it would be a far more reliable mechanism of transmission relative to environmental transmission at low population density, even if the probability that an offspring would become infected by maternal transmission is quite low. Consequently, we believe that viral reproductive strategies may vary with host population density and that more virulent genotypes may be selected for at higher population densities. In many systems stable polymorphisms of mixed genotypes or intermediate levels of virulence may be maintained.

There already exists a considerable body of evidence that different strains of NPV vary in virulence. A ten fold difference in LD_{50} was reported by Vasiljevic and Injac (1973) for Yugoslavian isolates of the virus, while Shapiro and others (1984), found as much as a sixteen fold difference in the activity of North American virus isolates. A large number of NPV wild isolates have been shown to be genotypically heterogeneous (Falkner and Carstens 1986). We do not know whether any of these differences are related to the density of the population from which they were collected.

Selection for resistance of gypsy moth to NPV infections may also occur, particularly during an epizootic. Gypsy moths from different locations vary in susceptibility to a given viral isolate (Rollinson and Lewis 1973, Skatulla 1987). Myers (1988) has speculated that short term genetic changes in susceptibility to pathogens may account for the cyclic pattern of population densities of many forest insects, although there is no direct evidence for this. We anticipate future studies to determine if there are systematic changes in NPV virulence and host susceptibility before during and after an NPV epizootic.

SUMMARY

Two distinct waves of mortality from NPV occur during larval development of gypsy moth. The evidence suggests that early instars acquire lethal doses of NPV from the surface of the egg mass and the cadavers of these larvae provide inoculum that causes a second wave of mortality among late instars. Transmission of NPV between gypsy moth generations appears to occur primarily by way of contamination of egg masses from environmental sources during oviposition. Other factors including foliage chemistry, and genetic effects influence the level of mortality caused by NPV. Future studies involving experimental manipulation of field populations coupled with simulations with the gypsy moth life system model will serve to validate and extend these findings.

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EFFECTS OF DEFOLIATION BY GYPSY MOTH

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ABSTRACT

Defoliation of trees by the gypsy moth (*Lymantria dispar* L.) has many and varied effects. It causes economic losses through lost forest production and reduced aesthetic qualities of the forest. However, defoliation may improve habitat for many species of wildlife and contribute to increased diversity of eastern forests. Effects on water resources, recreation, and other values differ with different levels of defoliation and different forest types. Primary and secondary effects of defoliation on forested ecosystems are reviewed.

INTRODUCTION

Defoliation of forests by insects is a ubiquitous problem which has been studied in many systems (Kulman, 1971). Assessments of damage caused by forest defoliators must include the many ways in which forests are changed by defoliation (Alfaro 1988, Stark 1987, Schowalter and others 1986). Defoliation of trees by the gypsy moth (*Lymantria dispar* L.) in particular has profound effects on many levels. There are direct effects on the trees themselves, effects on the other components of the forest ecosystem such as animals and other plants, and effects on people, both direct and indirect. Since the gypsy moth was introduced in 1869, its range has been limited to northeastern North America. However, the insect's range has been expanding steadily and nearly all forested areas in North America may eventually be affected to some degree.

The problem is most important on oaks (*Quercus* spp.) in the Northeast, though many other species are affected. In the forests of the region oaks are both the most favored hosts of the gypsy moth and the most valuable hardwood timber species . Mosher's (1915) early work defining feeding preferences of the gypsy moth in North America (Table 1) has been confirmed by more recent studies (Gansner and Herrick 1985, Fosbroke and Hicks 1989). Additional work on host species with a more southerly range indicates that sweetgum and loblolly pine (Barbosa and others 1983, 1986) may be important hosts as the insect invades the South. Oaks in the South certainly remain an important factor in the vulnerability of the forest because there are so many overtopped trees (McGee and Bivens 1984), which are the most likely to die after defoliation (Herrick and Gansner 1987).

EFFECTS ON TREES

The effects of defoliation on trees is due primarily to the reduction of carbohydrate production (Kozlowski 1969, Heichel and Turner 1976), which results in increased vulnerability to pests that kill stressed trees, growth loss, and subsequent indirect changes in the forest. In a multi-layered, mixed-species forest stand, defoliation occurs first on understory trees and later on overstory trees. Similarly, trees in poor condition often are defoliated before their counterparts in good condition. Mortality is most prevalent during and after the initial outbreak of gypsy moth; some stands may experience 80-100% mortality of overstory trees (Campbell and Sloan 1977, Gansner and Herrick 1984). This initial outbreak may last from 3 to 10 years in a region, and individual stands may suffer moderate to heavy defoliation in more than half of those years (Herrick and Gansner 1987). Such extensive damage has not been found in most defoliated stands, however. Even in areas with highly susceptible forest types, many stands experience few defoliations. This phenomenon

results in a majority of the forest suffering minor or moderate levels of mortality (Gansner and Herrick 1984).

Mortality

Losses to mortality necessarily are correlated with frequency and intensity of defoliation, which in turn are correlated with tree species according to gypsy moth feeding preferences (Brown and others 1988, Stephens 1971, 1981b, Hicks and Fosbroke 1987, Campbell and Sloan 1977, Stalter and Serrao 1983, Quimby 1987). However, there are distinct differences among species in their ability to survive defoliation. Hemlock (*Tsuga canadensis*) is among the most vulnerable species despite its status as only a moderately preferred host (Gottschalk and Twery 1989). Hemlock seldom survives even one complete defoliation (Stephens 1988), whereas some oaks on dry sites may survive repeated defoliations indefinitely (Houston and Valentine 1977, Bess and others 1947). The differences are due to many factors, including where the tree's reserve energy is stored, how much energy is required to refoliate, and how much energy is needed to maintain respiration during the refoliation process (Wargo 1981a, 1981b). For example, hemlock's reserves are stored in its needles, so after defoliation there is no available reserve energy, no refoliation occurs, and the tree dies. Which agent causes tree mortality is dependent on locality and other contributing factors (Staley 1965, Starkey and Oak 1989).

Diameter Growth

The standard approach to measuring growth loss for an individual tree has been to record changes in diameter growth at breast height (dbh). Baker (1941) found growth losses directly proportional to the extent of defoliation. Such losses are over and above losses to mortality, and are likely to be the more important component of forest productivity impact after the initial wave of mortality following gypsy moth's first outbreak in an area. Diameter growth loss may, however, overestimate total volume losses by up to 20% because of changes in distribution of wood production. During and shortly after a defoliation episode growth at dbh is reduced by a greater proportion than growth at points higher in the bole (Twery 1987). An additional problem with analysis of growth only at dbh is the difficulty of separating defoliation from other factors such as drought or extreme temperatures (Mott and others 1957).

Volume Growth

Volume growth decreases when a tree is defoliated. In southern New England, Twery (1987) found an average decrease of 20% in stem volume growth of oaks in any year a tree was defoliated compared to the previous, undefoliated year. On average, chestnut oak is affected the most, showing an average growth loss of 33% in such years. Some individual trees, however, showed annual decreases of 50–65% in volume growth when completely defoliated. European studies reported by Gradwell (1974) show similar effects, averaging 59% for heavily defoliated trees.

Growth loss in an individual tree is not confined to the years of defoliation but is evident up to 3 years after a defoliation episode (Twery 1987, Wargo 1981a). Defoliation in a stand of oaks reduces the overall growth of survivors considerably, the effect is carried beyond the year of defoliation, and the growth of the stand recovers after about 3 years. Certainly, some of this effect is a result of reduced leaf area in recovering trees (Heichel and Turner 1976, Wargo 1981a, Picolo and Terradas 1989). For a 2-year defoliation episode that affects forests once each decade, Twery (1987) estimated the average overall reduction in volume increment at 9.7% per year for the stand over the decade, excluding mortality.

Table 1: Categorization of gypsy moth host preferences (adapted from Mosher 1915, Mauffette *et al.* 1983, and Montgomery, this proceedings).

Susceptibile: species readily eaten by gypsy moth larvae during all larval stages.

Overstory: apple, basswood (American linden), bigtooth and quaking aspen, gray, paper (white), and river birch, larch (tamarack), mountain-ash, all oak species, sweetgum, willow.

Understory: hawthorn, hazelnut, hophornbeam, hornbeam, serviceberry, witch-hazel

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Resistant: species fed upon when preferred foliage is not available and/or only by some larval stages.

Overstory: beech, black (sweet) and yellow birch, blackgum (tupelo), Ohio and yellow buckeye, butternut, sweet and black cherry, eastern cottonwood, cucumbertree, American and slippery elm, hackberry, all hickory species, boxelder, Norway, red, and sugar maple, pear, sassafras, black walnut, chestnut, eastern hemlock, all pine species, all spruce species.

Understory: blueberries, pin and choke cherry, paw paw, persimmon, redbud, sourwood, sweetfern.

Immune: species that are rarely fed upon.

Overstory: all ash species, baldcypress, northern catalpa, eastern redcedar, balsam and fraser fir, American holly, horsechestnut, Kentucky coffee-tree, black and honey locust, mulberry, sycamore, tuliptree (yellow-poplar).

Understory: all azalea species, dogwood, elderberry, grape, greenbrier, juniper, mountain, silver and striped maple, rhododendron, all rubus species, sheep and mountain laurel, spicebush, sarsaparilla, all viburnum species

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Measurements of overall mortality and percentage volume loss per unit land area may not be meaningful, however. The mortality of subcommercial individuals may actually improve the growth of the remaining stand through a thinning effect, or a decrease in growth in an immature stand may be partially recovered by the delay it induces before competitive crowding occurs (Twery and Gottschalk 1988). Twery (1987) found that oaks that remained undefoliated while their neighbors were defoliated actually grew much better than average during the year of defoliation. Similarly, Campbell and Garlo (1982) reported increased growth of pitch pine (*Pinus rigida*) in New Jersey after gypsy moth defoliation of black oaks (*Q. velutina)* in mixed pine-oak stands.

To avoid damage from gypsy moths, Hall (1935) recommended growing pitch pine on Cape Cod, and Behre and others (1936) recommended cutting practices to remove oaks and suggested the planting of conifers. Even earlier, Fiske (1913) and Clement and Munro (1917) were suggesting similar ways to reduce the damage from gypsy moth by stand conversion or maintenance of vigorous stands. This approach is currently impractical in many areas because of the high value of oaks, a lack of alternative commercial timber species, and the large area involved. In areas such as

Cape Cod or the Pinelands of New Jersey, though, stand conversion may be worthwhile for timber production.

Quality Changes

Defoliation and resultant slow growth in oaks have negative implications for wood quality. Growth during years when an oak is defoliated consists almost exclusively of large, earlywood vessels. This wood has a much lower specific gravity than latewood. Because strength is directly related to density, several adjacent rings excessive earlywood may induce manufacturing problems or structural failures in use (Hill 1954, Panshin and de Zeeuw 1970). It is not the low density of the wood, per se, that causes the problems. In fact, very slowly grown oak brings the highest value in parts of Europe. Rather, it is the alternation of layers of unequal density which may cause problems with drying, veneer slicing, or other machining processes. Reduction in wood quality may also result from defoliation via the formation of epicormic branches from latent or adventitious buds. These branches produce knots in previously clear areas of the bole, lowering the production of high-value products like veneer.

Qualitative changes in foliage also result from defoliation. Schultz and Baldwin (1982) found significantly higher quantities of tannins and other phenolics in leaves of red oak trees which had been defoliated previously by the gypsy moth. The regrowth foliage of defoliated trees also has been shown to fix carbon at higher rates per unit area than does primary foliage (Heichel and Turner 1983). However, because the leaf area was smaller and the duration of net production was shorter, no defoliated trees approached the net production of undefoliated trees.

TIMBER VALUES

Mortality, growth losses, and changes in wood quality, all have direct secondary effects on timber values. The standing crop of timber degrades quickly after mortality, causing losses of up to 25% within 5 years (Garges and others 1984, Karasevicz and Merrill 1989, Gottschalk and others 1989). Because in some areas as much as 50-90% of the forest is killed, (Herrick and Gansner 1987) these losses can be extremely disruptive to timber markets. The quality of the wood for pulp and papermaking is not degraded substantially in the first 5 years after death of the tree (Kessler and Labosky 1988). The most dramatic effect is the immediate downgrading of potential veneer logs to sawtimber as the tree dies, resulting in value losses of 50% or more. Also affected is the potential growth in value of future crops. Stands that are understocked due to mortality following defoliation cannot utilize the site's growing potential fully, and fully stocked stands with trees that grow more slowly because of defoliation both contribute to the decreased value growth (Gansner and Herrick 1982; Herrick and Gansner 1988). Additionally, the threat of gypsy moth may cause managers to change their land management strategies from faster growing species toward those that are less susceptible to defoliation. For example, although sweetgum (*Liquidambar styraciflua*) grows faster than sycamore (*Platanus occidentalis*) on the coastal plain of Virginia, its higher susceptibility to gypsy moth may result in the management of more sycamore plantations.

LONG-TERM ECOLOGICAL EFFECTS

Further secondary effects on the forest can be found by examining shifts in the ecological balance of affected stands. By removing leaves from some trees and not others, the gypsy moth can change the competitive balance between species and individuals. Decreased leaf area results in decreased carbohydrate production and increased demand for carbohydrate reserves to refoliate. Trees stressed this way lose advantages they may have had in direct competition for growing space, but the effects are also more far reaching. The stresses play a role in allowing secondary organisms such as the two-lined chestnut borer (*Agrilus bilineatus* Weber) and shoestring root rot

(*Armillaria* spp.) to invade and kill a tree (Wargo 1977). Defoliated trees lose seed production capabilities both in the year of defoliation and in at least one subsequent year (Gottschalk 1990). Mortality of trees in a stand also opens more light, space, and other resources to the remaining trees, which are likely to be a different balance of species than those trees which died. In a study of red oak growth in southern New England, Kittredge (1988) found greater growth among oaks that competed with other species compared to those in purer stands. Mixed stands, which are less susceptible to the gypsy moth, thus also may provide faster growing oaks than predominantly oak stands.

Replacement of stands that suffer extensive mortality also is affected by defoliation. Because oak seedlings are also defoliated in extended outbreaks (Shaw 1974), advance regeneration of species that are less susceptible to the gypsy moth is favored. Oaks, which often gain their place in a new stand through stump sprouts, may lose dominance because trees that die from secondary agents after defoliation cannot generate vigorous sprouts. Work by Allen and Bowersox (1989) indicates the extent of this replacement of oak. Stands in Pennsylvania that were dominated by oak before defoliation had only minor proportions of oak in the understory 6-7 years after mortality, especially on the Allegheny Plateau. Although low proportions of oak suggest that it will not be an important component in the next generation of forests, work by Oliver (1978) indicates that a small number of oaks in young stands may gain dominance after the stands reach 50 years of age. In susceptible stands other than oak, such as southern pine–sweetgum stands on the coastal plain of the Southeast, similar selective pressures may shift the species composition toward those species which are less vulnerable to defoliation.

Effects on other forest vegetation may also be great. Shrub and herb density and cover increase dramatically after overstory mortality due to increases in available light, moisture, and nutrients. The increased light also warms the soil sufficiently to induce germination of seeds buried in the forest floor. Short-term changes from defoliation, additional light for the months of June and July, and an extra flush of nutrients from the frass and partially eaten leaf fragments, cause little detectable change in the understory in the absence of tree mortality. Apparently, any response induced in the understory in one growing season is suppressed by the regrowth of the overstory the following season. Collins (1961) found that understory trees that were not defoliated in the same season as their overtopping neighbors had increased growth, but no such effects were found by Twery (1987) or by Hicks and Hustin (1989).

WILDLIFE

Wildlife species are affected by gypsy moths in many ways, primarily through changes in habitat. Many of the forest vegetation changes described above are favorable to many species of wildlife, so the consequences of defoliation by gypsy moth are not uniformly negative. For example, unsalvaged dead trees create more snags for cavity-nesting animals, and limbs and boles that fall to the forest floor provide additional cover or shelter for small mammals and other ground-dwelling animals. The extensive growth of understory herbs, shrubs, and grasses produces a bounty of food and cover for many more wildlife species. The food may be in the leaves of the new vegetation or in the fruits of such shrubs as blueberry (*Vaccinium* spp.) or hazelnut (*Corylus* spp.). The increased vertical stratification of the foliage in the forest benefits many species of birds.

Potentially detrimental effects on wildlife include both the short- and long-term loss of hard mast production, especially acorns. Many wildlife species supplement their diet with acorns, so a loss of this resource reduces the capacity of an area to support some species, especially the gray squirrel (*Sciurus carolinensis*). Increased light reaching the forest floor after tree mortality causes higher stream temperatures and thereby affects a stream's ability to support fish or other aquatic life. Increased woody debris in streams also affects the quality of the aquatic habitat. Increased

patchiness and stratification of the forest resulting from selective tree mortality may improve the habitat for some species of wildlife, but it also may eventually decrease the capacity of a forest to support those species which prefer extensive undisturbed areas. Pileated woodpeckers (*Drycopus pileatus*) are likely to benefit from gypsy moth because they prefer areas with large trees and large quantities of dead woody material, and adjust their territory size in response to changes in such structural variables (Renken and Wiggers 1989).

According to one recent study[1], numbers of species and total abundance of non-game birds increase with the disturbance created by gypsy moth, while other studies have reported inconclusive results (DeGraaf 1987, Cooper and others 1987). As mentioned previously, gray squirrels are adversely affected by gypsy moth through loss of their primary food supply (Gorman and Roth 1989). Other small mammals experience different effects depending on the specific result of a disturbance (Smith 1985). White-footed mice (*Peromyscus leucopus*) seem adaptable in their choice of species of acorns depending on availability (Briggs and Smith 1989), and if other food sources are available they may not be affected by lack of mast in any given year. Gypsy moth pupae and larvae are commonly part of the spring and summer diet of the opportunistic small mammals of the forest floor (Smith 1985). Invertebrates on the forest floor have not been studied in areas disturbed by gypsy moth, but Jennings and others (1988) found increases in abundance and diversity of forest invertebrates after strip cuttings and similar disturbances caused by spruce budworm (*Choristoneura fumiferana* Clem.).

Endangered species of animals also may be affected by the gypsy moth. For example, an endangered salamander in northern West Virginia lives on the floor of oak stands. Destruction of its habitat by defoliation and mortality of the overstory trees and subsequent changes in the temperature regime of the forest floor must be considered among the potential effects of gypsy moth. The Virginia big-eared bat (*Plecotus townsendii virginianum*) also may be affected by gypsy moth and human attempts to control the defoliation. This bat feeds on insects within the forest, often foraging on the tree trunks. Defoliation that results in mortality of trees may perhaps be more likely to deplete the bat's food source than a chemical spray to control gypsy moth, although Doane and Schaefer (1971) did find effects on some non-target species of insects and birds from aerial application of insecticides.

WATER RESOURCES

Another indirect effect of defoliation by gypsy moth extends to water resources. Gypsy moths can influence both the the quantity and quality of water in watersheds managed for their yield of supplies of drinking water. The quantity of water yielded from a watershed increases when it is defoliated (Corbett and Lynch 1987) because fewer leaves are available to transpire moisture from the soil. Quality, however, may suffer greatly, as the increased detritus falling to the forest floor decomposes in the warmest part of the year, exporting large amounts of nitrogen and other nutrients in the streams (Swank and others 1981) and increasing amounts of fecal coliform (Corbett and Lynch 1987).

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[1]Greer, R.D.; Whitmore, R.C.; Smith, H.R.; Twery, M.J. (In Review). Effects of gypsy moth defoliation on wildlife populations: a modelling study.

PEOPLE

Gypsy moths affect people directly through the reduction of aesthetic and recreational benefits from the forest, economic losses, and public health problems. Some of these effects are more easily quantifiable than others, but all can be important factors in assessing the overall impact of defoliation by the insect.

Aesthetic effects can be divided into effects on distant, panoramic vistas and those on interior views of the forest. Scenic overlooks from highways such as Skyline Drive in Shenandoah National Park lose a great deal of their attractiveness when the hillsides are brown in June and July from a current defoliation. However, if mortality occurs the understory will fill in, and the fact that the hillsides are green in the appropriate season prevents many people from noticing any major change in distant views of the forest. If dead trees are salvaged, however, views of mountains with large cutting operations show evidence of the disturbance for a number of years. Interior views, such as those from hiking trails, produce a more complicated reaction in viewers. The unpleasant effect of being pelted with caterpillar droppings during an outbreak is undisputed, as is the negative reaction to walking through a forest of defoliated trees. In the longer term, though, there is not a linear correlation between the amount of gypsy moth-induced mortality and the evaluation of scenic beauty by viewers of the forest.

Freimund (1990) found an increase in scenic beauty in stands with light to moderate amounts of tree mortality after defoliation by gypsy moth, while heavy mortality caused large decreases in the public's estimation of scenic beauty. On the other hand, if an increase in sunlight passing through the open canopy induces significant amounts of flowering of understory plants, some of the negative reaction to overstory mortality may be offset. Within-stand visual preferences generally favor large trees and extended visual penetration (Rudis and others, 1988). If mortality after defoliation is concentrated in the smaller, overtopped trees (Gansner and Herrick, 1984), the net result may be that some forests become more attractive.

Effects on recreation differ from aesthetic effects primarily in high-use areas. In heavily used areas like picnic grounds and camping sites, gypsy moth's primary role is that of a severe nuisance. During its peak, a gypsy moth outbreak can create the effect of rain from frass and leaf fragments. Severe defoliation on the Allegheny National Forest resulted in a 20% reduction in recreational use of affected areas during the outbreak (Goebl, 1987). Longer term effects include the creation of hazard trees in recreation areas when large, defoliated trees die. While snags are a necessary and beneficial part of the forest in general, large dead trees are unwelcome in areas where they might be likely to harm people when they fall.

The public health problems created by gypsy moth are less obvious but nonetheless important secondary effects of gypsy moth infestations. Contact with larval hairs has been documented to cause skin rashes and other allergic reactions (Tuthill and others, 1984, Shama and others, 1982). Although most individuals suffer no serious, long-term health problems, a community-wide outbreak of rashes during heavy infestations can have a significant economic effect.

Residential property also can be affected greatly by defoliation. The same effects related to recreation are applicable to people's back yards. In addition, the loss of yard trees can cause large reductions in home values (Payne and others 1973). Trees help cool a home site in summer and protect a home from winter winds. Loss of yard trees is certain to increase residential energy use. The economic impact on real estate values may well be one of the larger indirect costs of defoliation. The amount spent by homeowners to prevent defoliation of their trees in areas such as southern New England far surpasses the money spent to protect forests.

SUMMARY

The gypsy moth has affected life in the eastern United States for over a century. It has many adverse effects on the ecosystem, but on some sites some components benefit from either the defoliation itself or the ensuing mortality. The loss of leaves causes stress to the trees that becomes evident through decreased growth and increased vulnerability to secondary, mortality-causing organisms. Because the gypsy moth is a selective feeder, the balance of competition between trees and other vegetation changes, inducing long-term ecological changes. Many kinds of wildlife benefit from the kind of forest disturbance the gypsy moth causes, but some are detrimentally affected. Effects directly on people are through changes in recreational and aesthetic values of forested areas and in the form of public health problems. Despite the severe effects of repeated defoliation over many years, there is considerable evidence that the hardwood forests, and oaks in particular, will continue to be an important part of the landscape of the eastern United States (Stephens 1971, 1981a, Stephens and Waggoner 1980, Gottschalk and others 1989).

Much is known about the connections among the effects of defoliation, but much remains to be discovered. Quantification of the effects is easiest where monetary values can be applied directly, such as timber values. Prediction of the reactions of forest ecosystems where the gypsy moth has not yet invaded will require considerable effort, but advance warning can help minimize damage from defoliation. Among the most difficult questions yet to answer are the causal mechanisms involved in many of the aforementioned interactions. Only when we know how changes in the forest ecosystem interact will efficient and effective integrated methods to manage gypsy moth be possible.

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