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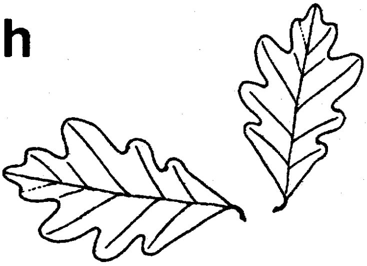

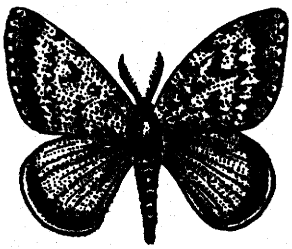

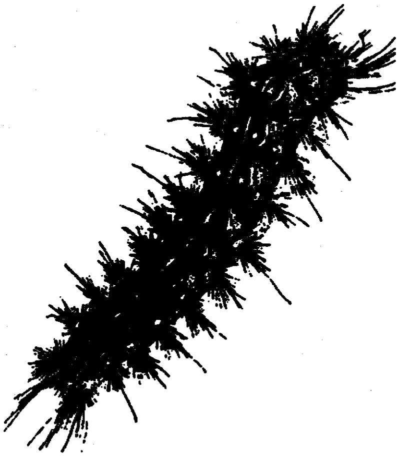

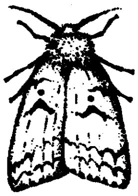

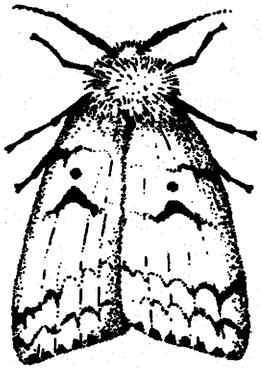

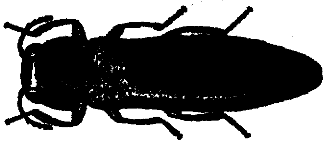

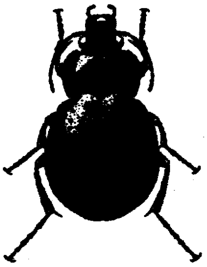

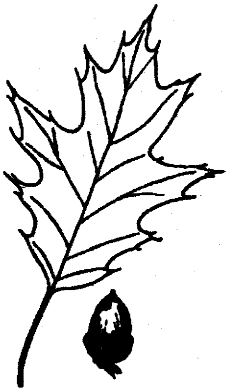

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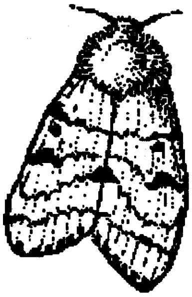

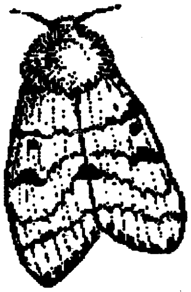

January 22-25, 1990
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Edited by
Kurt W. Gottschalk, Mark J. Twery, and Shirley I. Smith

Sponsored by:

- Forest Service Research
- Forest Service State and Private Forestry
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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
R. Bram, ARS
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R. Riley, CSRS
T. Hofacker, FS-S&PF
M. McFadden, FS-R, Chairperson

USDA Interagency Gypsy Moth Research Review
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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.

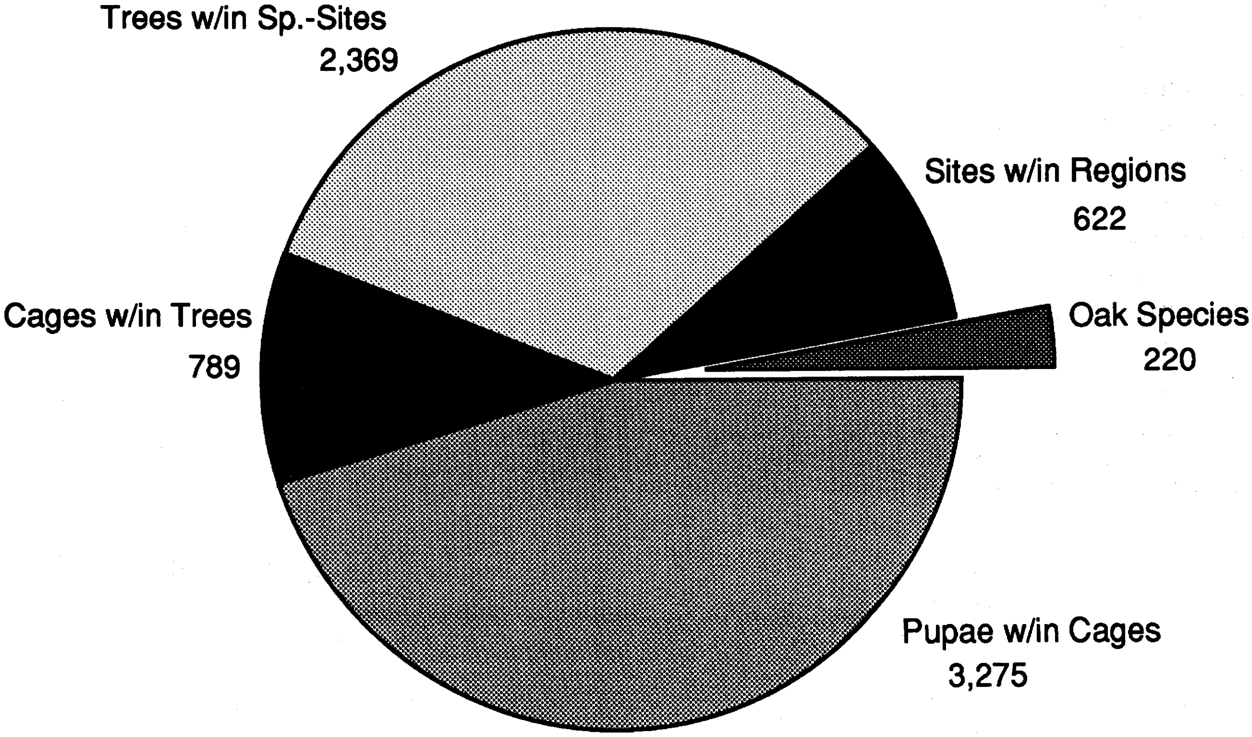

Figure 1. Variance components of random effects on female pupal weights on three oak species.

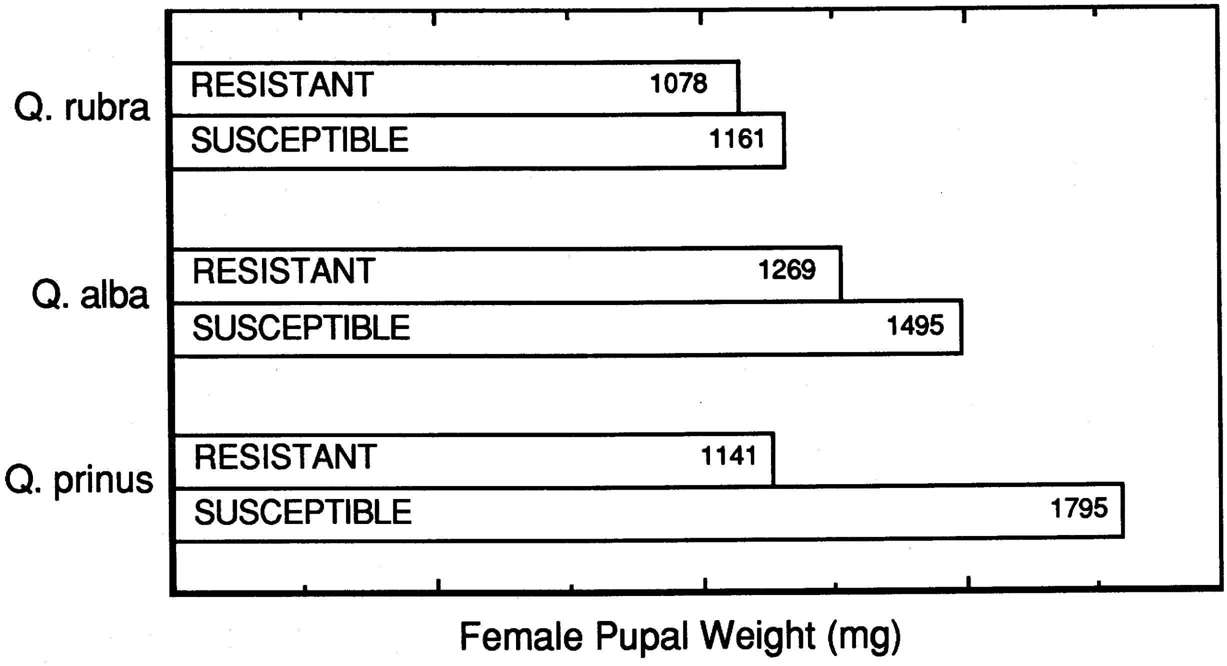

Figure 2. Comparison of female pupal weights of larvae reared on excised oak foliage from resistant and susceptible sites.

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.

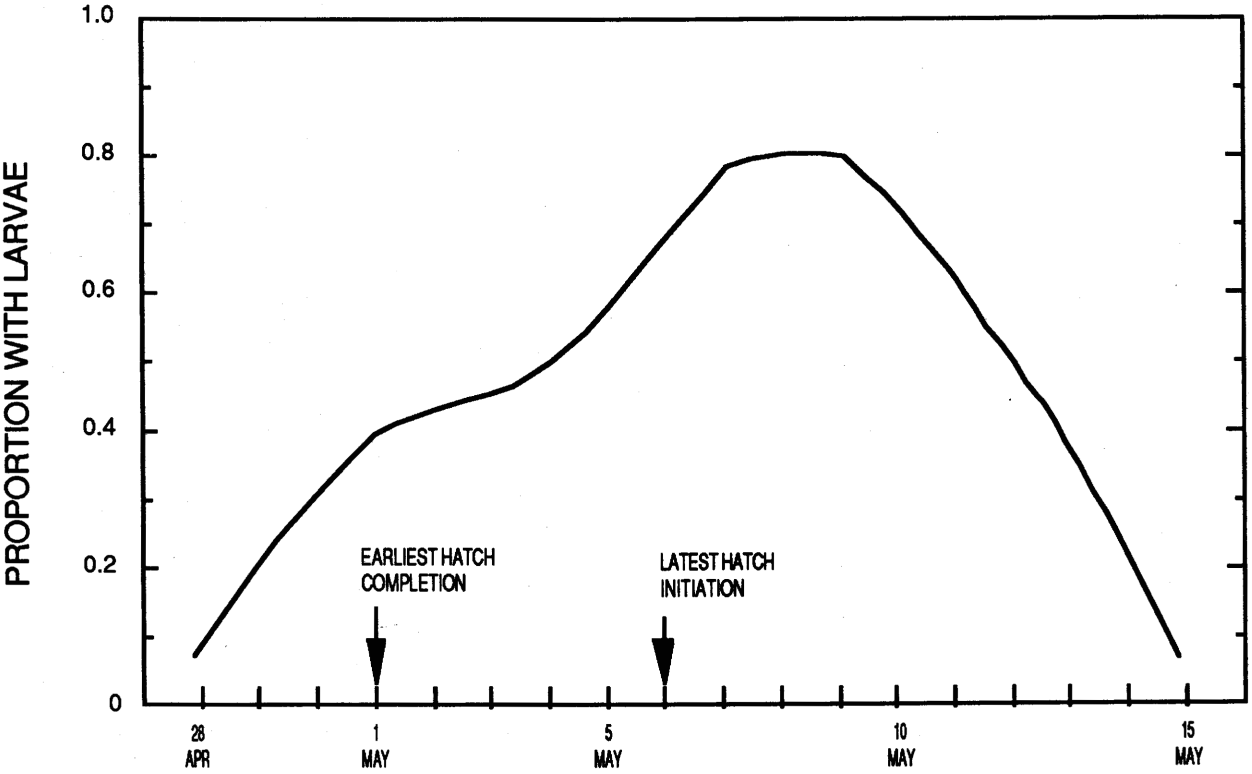

Figure 3. Proportion of 93 gypsy moth egg masses with larvae on them, Ansonia, CT, 1989.

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.

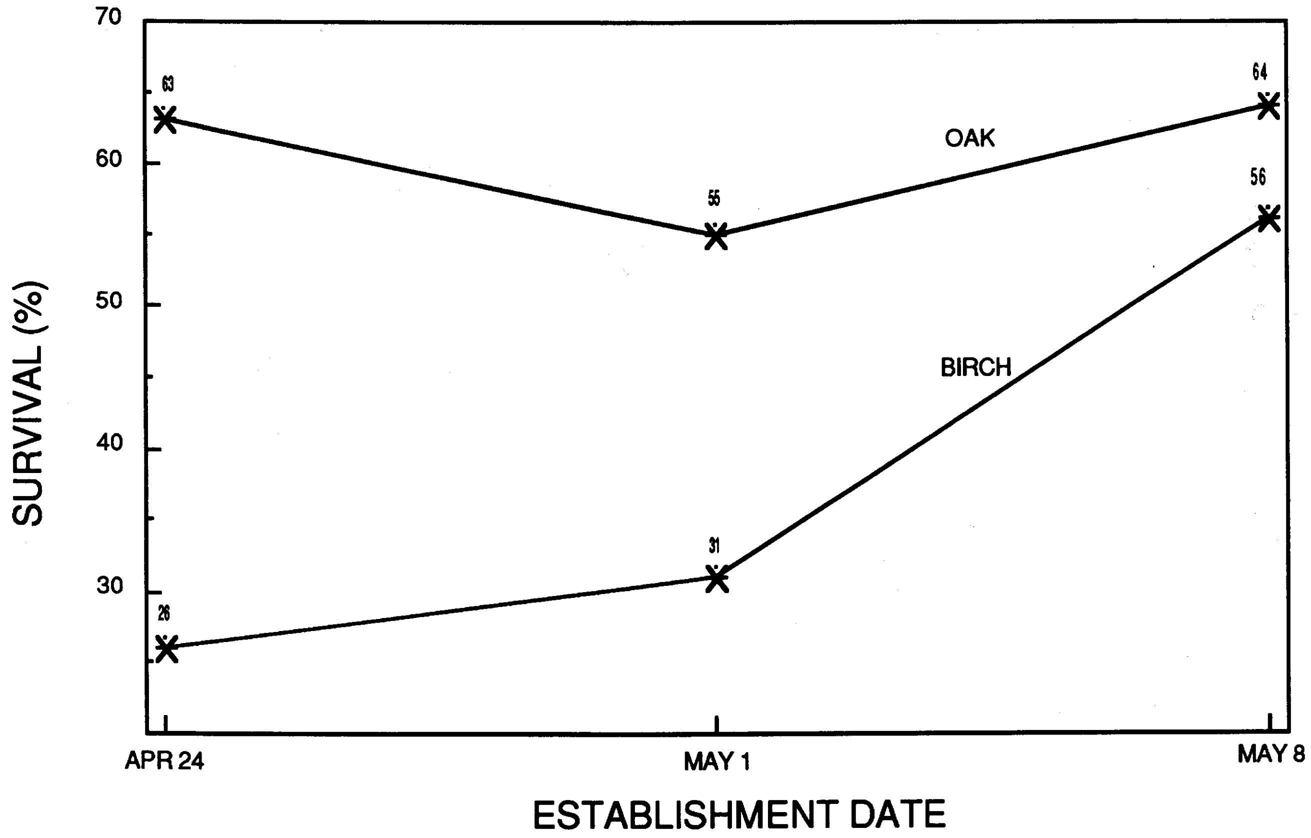

Figure 4. Survival of recently hatched larvae confined on black oak and grey birch foliage in the field on three dates.

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.

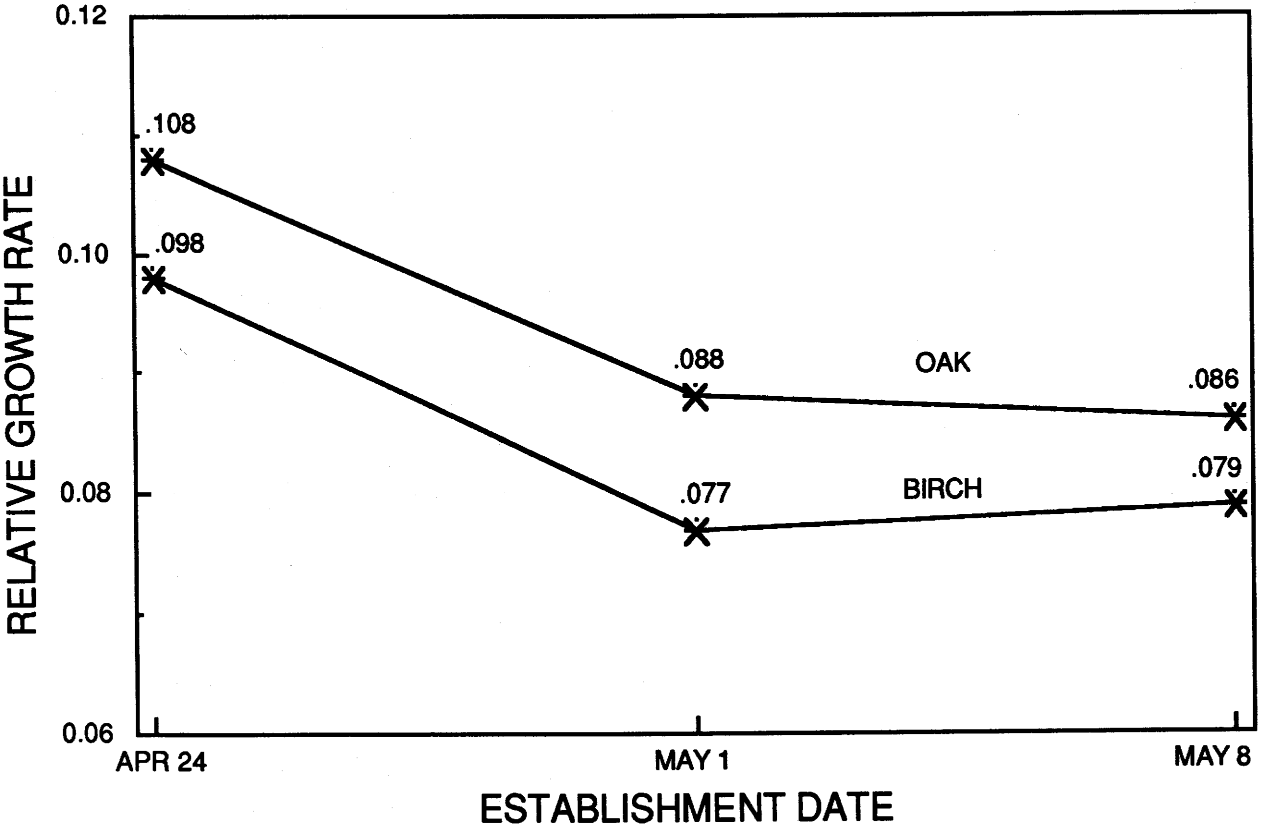

Figure 5. Relative growth rates (mg/mg/degree day) of 3rd - 4th instar larvae established on black oak and grey birch on three dates.

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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 preoutbreak 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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SAMPLING LOW-DENSITY GYPSY MOTH POPULATIONS

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ABSTRACT

The techniques and methodology for sampling gypsy moth, *Lymantria dispar* L., at low densities, less than 100 egg masses/ha (EM/ha), are compared. Forest managers have constraints of time and cost, and need a useful, simple predictable means to assist them in sampling gypsy moth populations. A comparison of various techniques coupled with results of recent habitat research studies indicates that a series of burlap banded trees can be utilized to monitor egg-mass density change over time. Egg masses beneath bands accurately reflect densities on unbanded trees, yet are easier to deploy and use as well as being less costly than other conventional methods. Habitat does not seem to be a major factor in determining the distribution of gypsy moth egg masses; however, forest stands selected for banding should have a major oak component. Predicting a 2-year lead time to outbreak is possible based upon two consecutive years with an increase of one order of magnitude or greater of egg-mass density beneath bands.

INTRODUCTION

Gypsy moth is capable of an increase of more than 1-1/2 orders of magnitude in a generation. The problem for managers in assessing egg-mass density counts is the inability to track increase trends and predict 1-2 years in advance the need for suppression. Successful forecasting of pest densities, whether for management or research purposes, relies on dependable sampling methodology. For the gypsy moth, *Lymantria dispar* L., we do not know enough about its dynamics to be able to predict outbreak occurrences. This has necessitated reliance on sampling, with a lead time of no more than one generation to provide the necessary information. For example, if gypsy moth is capable of increasing 1-2 orders of magnitude/year and if defoliation can occur at 10^4 egg masses/ha (EM/ha) or higher, then it is necessary to detect 10^{-1} to 10 EM/ha in order to predict defoliation during the next 2-3 year period. Trend prediction at low densities (<100 EM/ha) to detect population change requires more intensive sampling with inherent higher costs. The researcher has different demands for sampling than the forest manager and will utilize a technique or combination of techniques to suit the research. The forest manager, on the other hand, generally requires less detailed information, must assess populations over large areas of variable habitat, and sampling activity is constrained by economics. Several methods for population estimation have been developed but no consistent approach has been utilized by managers that permits comparisons and evaluation over a broad geographic region. Recent research indicates that such a procedure is feasible for the manager and may or may not be useful for the researcher.

For a sampling regimen to be acceptable to the forest manager as a successful forecasting tool, it must be simple, inexpensive, reliable and useful. A comparison of current sampling methods provides insights into their relative usefulness to meet these criteria. The comparative features of each method (Table 1) are based on specific studies (Kolodny-Hirsch 1986, Liebhold and Elkinton 1988, Wallner and others 1989, Wilson and Fontaine 1978) as well as our consensus assessment of their past performance and accepted use. Sensitivity reflects the ability to detect gypsy moth life stages at densities less than 100 EM/ha. Reliability of a method connotes its ability to consistently perform in measuring a life stage. The cost of methodology includes both deployment of the technique and subsequent observations, counting, and soon. Since the manager depends upon predictability for planning and allocating resources, a chosen sampling approach should provide not only insect density but also an assessment of defoliation prognosis. The greater the prediction in time (that is, N + 2, N + 3), the more useful the method.

The pheromone trap has consistently demonstrated the highest level of male moth detection sensitivity at minimal cost. However, it has not been possible to relate adult male capture to subsequent egg-mass and larval densities or defoliation. Hence, its use for population monitoring in generally infested regions is limited and is best suited for detecting and delimiting new, potential infestations. Sampling egg masses has been the most accepted method for expressing population densities, a luxury not provided by sampling adults or larvae. Additionally, egg masses can furnish information on fecundity, density change between generations, phenology, and levels of parasitism. Techniques such as fixed-radius and prism plots are most often used; their sensitivity and reliability are good, but high cost and use in predicting defoliation are limitations. Other means of quantifying egg masses such as timed walks and masses/stem are "quick fixes" lacking the necessary essentials such as sensitivity, reliability, and defoliation prediction. The larval stage is most difficult to sample at low densities and, with the exception of using burlap bands, tends to be costly and provide limited predictive information beyond the current year. Frass and head capsule counts are best suited to research on larval population dynamics because of cost of deployment, collection and evaluation, and lack of sensitivity at the lower density ranges of gypsy moth. From this comparison of methods, we conclude that egg-mass sampling is the method for predicting long-term population trends by managers but a new modification should be used.

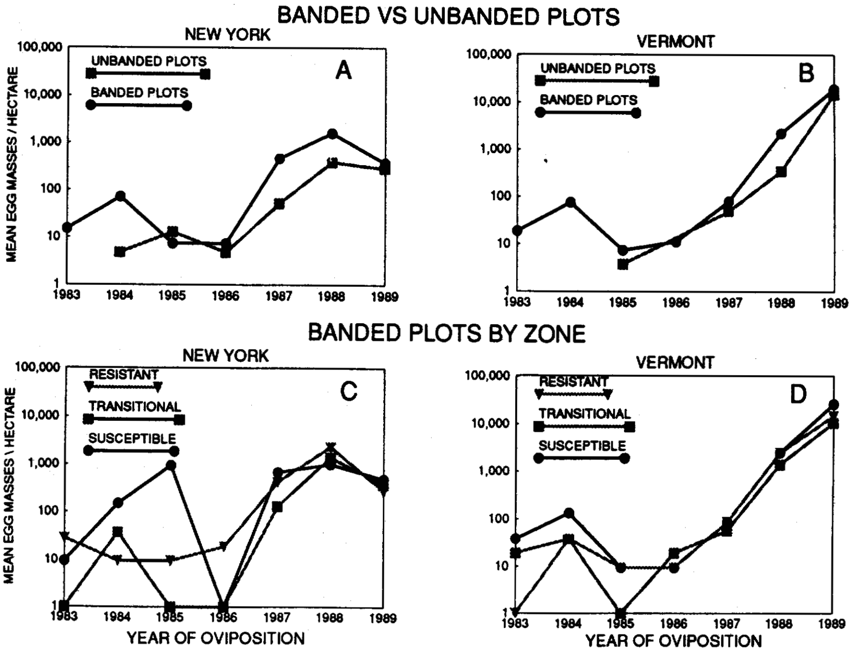

Figure 1. Mean egg-mass densities over time in burlap banded plots and adjacent unbanded plots (A, B), and mean egg-mass densities in susceptible, transitional, and resistant forests (C, D).

Table 1.--Comparison of techniques for sampling gypsy moth at low (<100 EM/HA) densities

Method	Sensitivity	Reliability	Cost	Predictability	
				Density	Defoliation
Pheromone traps	+++	++	+	+	+
Egg mass					
fixed radius	+++	+++	+++	++	+++
prism	++	+++	+++	+	++
burlap band	+++	+++	+	+++	++
stem	+	++	++	+	++
timed walk	+	+	+	+	+
Larvae					
burlap band	+++	+++	+	++	++
branch	+	+	+++	+	+
dislodgement	+	+	+++	+	+
head capsule	+	+	++	+	+
frass	++	++	++	+	+

Lowest = +; Moderate = ++; Highest = +++

During the past 6 years, we conducted collaborative research on low-density gypsy moth populations at the Harvard Black Rock Forest (New York), Bryant Mountain (Vermont), Cape Cod Military Reservation (Massachusetts), and North Stonington, Connecticut, which provided us with a new approach. It was essential that we quantify gypsy moth in different habitats at these sites to verify the dynamics of low-density populations. Forests can be classified based upon their susceptibility to defoliation by gypsy moth (Houston and Valentine 1977); we used this system in selecting and classifying our plots. Using a series of 15-m-dia burlap banded plots and adjacent unbanded plots, we measured density changes from less than 10 EM/ha in 1983 to greater than 10,000 EM/ha in 1989.

Burlap bands consistently mirrored egg-mass densities of unbanded plots. While bands tended to give higher values of masses/ha, they did accurately reflect density trends (Fig. 1A, B). Habitat potential (susceptible, transition, resistant forests) has been used to classify potential forest stand defoliation (Houston and Valentine 1977). Irrespective of habitat, equal numbers of egg masses were found in all habitats (Fig. 1C, D). Thus, burlap banded trees (> 7 cm) gave accurate, yearly estimates of egg masses and permitted us to predict defoliation in 1989 based on the dramatic increase in egg-mass density from 1986 through 1988. While we have not evaluated different sampling schemes for the manager, we believe that a series of burlap-banded oaks in clusters of 10 trees, with each cluster separated from the next by 100 m, can provide a reasonable estimate (<10% error). Arraying burlap-banded tree clusters on a square grid is recommended. This permits starting and ending at the same point, thus saving time and maximizing effort.

Figure 2 illustrates that larval densities beneath bands do not necessarily predict subsequent egg-mass densities. New York had a relatively consistent 10 mean larvae/tree from 1984 to 1989, yet egg masses and eggs/tree were extremely low in 1985 and 1986 but accelerated for two consecutive years in 1987 and 1988. Conversely, in Vermont the larval/egg-mass values appeared to track one another more closely. Explanations for these differences include larval immigration from adjacent infestations in New York and not in Vermont and differences, between sites in rates of predation or parasitism.

These same burlap-band counts of egg masses in New York and Vermont showed increases in density of more than one order of magnitude for two consecutive years. This presaged defoliation in 1989, which was forestalled only by an epizootic of *Entomophaga maimaiga*. We believe that managers can use this burlap banding of trees on a permanent basis to monitor density changes over time. Given two consecutive years of egg-mass density, increases of more than one order of magnitude should alert managers to expand sampling to other forested regions. It is not clear what role fecundity plays in such a prediction scheme. A simple method based on measuring the lengths of egg masses can be used to compute fecundity (Moore and Jones 1987). Our data suggest fecundity plays an important role at very low densities (<20 EM/ha) but may be unimportant as densities increase.

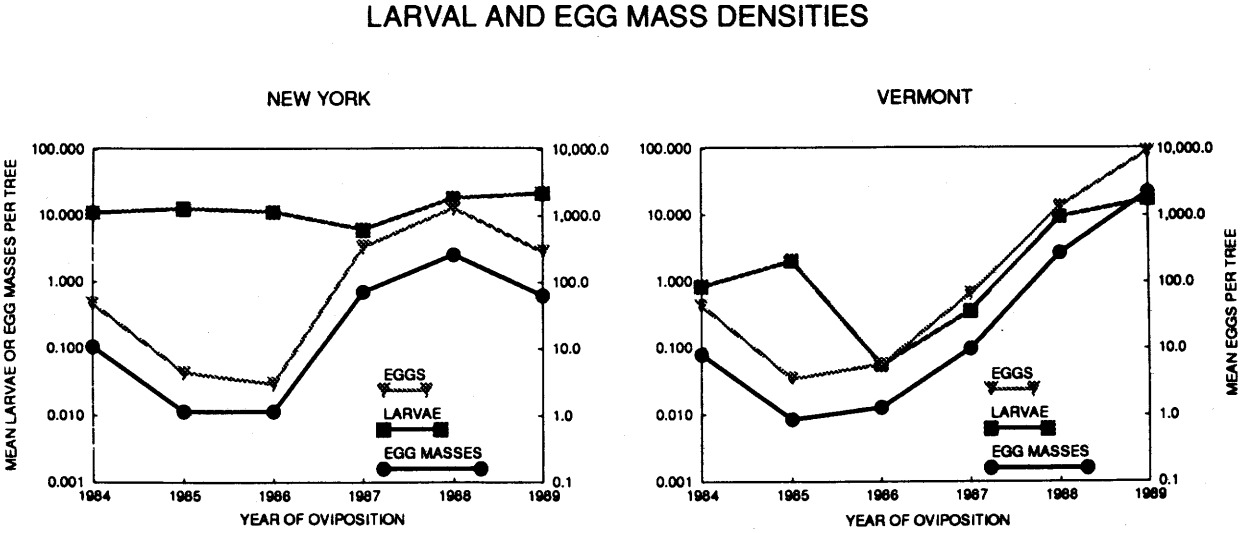

Figure 2. Mean number of eggs, larvae, and egg masses per tree for fifteen 15-m-dia plots in Vermont and New York for the period 1984-1989.

The possibility of using a series of individually burlap-banded trees (oaks, 20-30 m apart) or clusters of trees (20/cluster) on a permanent sentinel basis is suggested. The advantages of transects of individual trees is that it permits extensive sampling across heterogeneous habitat at minimal cost for set up and monitoring. It is not clear whether single-tree transects will be more efficient than transects containing clusters of trees. Egg-mass counts from the same tree clusters in Massachusetts, 15-m-dia plots in Vermont, and individually burlapped trees in New York have been used for several years with good success. However, we need to evaluate this further, not only in regions of general infestation but also in areas recently infested.

Past experience with egg mass density as a predictor of defoliation has been erratic. In most instances, samples were not taken in the same area year after year nor did they consider forest susceptibility to defoliation. The intent in using long term monitoring of egg masses under burlap banded trees is to detect shifts in density and predict the length of time before a defoliation event likely will occur. In our studies, the low-density equilibrium point is about 10 EM/ha. Campbell and Sloan (1978) state that at <25 EM/ha gypsy moth is in the innocuous phase and that once the population exceeds 25 EM/ha it is in the outbreak phase. We determined that gypsy moth was in an outbreak mode once densities exceeded 100 EM/ha. The outbreak was triggered when densities were 10 to 25 EM/ha. If we could identify more accurately the causal mechanism(s), our ability to predict outbreaks would increase. The most plausible explanation of the release mechanism is small mammal predators, which are important regulating mechanisms at low densities (Smith 1988). At the time when gypsy moth populations were lowest (1985-86, Fig. 2), small mammal densities were at a 20-year high for New England (Smith, personal communication). Certainly this relationship requires further clarification. However, we believe that managers should not delay using permanent burlap banded trees since they will provide useful information in assessing management decisions for gypsy moth.

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ENTOMOPHAGA MAIMAIGA PANZOOTIC IN NORTHEASTERN GYPSY MOTH POPULATIONS

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ABSTRACT

The fungal pathogen causing extensive mortality in gypsy moth larval populations during the 1989 field season has been identified as *Entomophaga maimaiga*. Identification was based on morphology and *in vitro* culture requirements, as well as results from allozyme and restriction fragment linked polymorphism analyses. *E. maimaiga* is well known to cause spectacular epizootics in Japanese gypsy moth populations but has not been reported from North America previously.

Entomophaga maimaiga was found in 7 contiguous states in the northeastern U.S. during late June and early July. Populations of late instar larvae in central Massachusetts sustained 60-88% mortality due to *E. maimaiga* in four forest stands. It is important that at the time of the panzootic, gypsy moth populations were increasing in the northeast and *E. maimaiga* caused significant mortality in low level as well as more abundant populations. In contrast, the commonly occurring nucleopolyhedrosis virus (LdMNPV) generally causes epizootics only in outbreak populations. The *E. maimaiga* panzootic was associated with high levels of May and June rainfall. We hypothesize that lack of adequate rainfall limited appearance of this pathogen in northern VT, NY, and NH. However, it is clear that *E. maimaiga* is not coextensive with the gypsy moth; in the southern and western areas of the gypsy moth distribution, which gypsy moth populations have colonized more recently, rainfall was abundant but *E. maimaiga* did not occur.

It is most likely that the presence of *E. maimaiga* in North America is due to biological control introductions made in 1910 and 1911 in the Boston area. This fungal pathogen may have escaped detection over the past 78-79 years, as it increased in distribution because (a) cadavers are similar in appearance to cadavers of LdMNPV-killed larvae, and (b) it is probable that this pathogen is not a major mortality factor every year. In conclusion, this panzootic had several major impacts: 1. extensive larval and pupal mortality occurred, 2. in many areas, defoliation was prevented, 3. large numbers of resting spores (the overwintering stage of *E. maimaiga*) were deposited in the environment, and 4. with the extensive activity of *E. maimaiga* in the northeast, there is great potential that this fungus increased in distribution even further.

GENERAL AND SPECIFIC GYPSY MOTH PREDATORS

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ABSTRACT

General larval predators of low-density gypsy moth, *Lymantria dispar* (L.), populations have been assessed by exposing caterpillars tethered by threads. Most mortality occurred on tree trunks and in leaf litter. Small mammals were responsible for 80% of the predation and brown wood ants of the *Formica fusca* group for the remainder. Almost all of the ant predation occurred in the litter. Predation accounted for practically all of the larval mortality. Predation by ants was investigated further because even slight increases in predation rates of low-density populations may influence gypsy moth numbers. Neonate larvae were seldom preyed upon, but first instars that had fed and 2nd instar larvae were especially vulnerable. These instars spend most of their time in trees, so ways of encouraging ants to climb trees should increase mortality of small gypsy moth larvae. It was found that ants could be induced to climb trees and attack gypsy moth larvae there by spraying sugar solutions on tree trunks, and this might be helpful for increasing control of the pest.

Investigations have also been carried out on predation by *Calosoma sycophanta* L., a large imported carabid beetle that is quite specific to the gypsy moth. Previous work shows that about 300 beetles per ha are able to produce enough progeny to destroy about half of gypsy moth pupae during an outbreak. Furthermore, adults disperse little, even though they are strong fliers. These characteristics suggest that small scale field releases of the beetle may be effective, and these have recently been done with some success. This beetle has a potential for being an important controlling factor of high gypsy moth populations.

IMPACT OF SMALL MAMMAL PREDATORS ON GYPSY MOTH

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ABSTRACT

Research in western Massachusetts, on Cape Cod, and on Bryant Mountain in Vermont conducted over the past decade has confirmed the importance of mortality during the late larval and pupal stages to gypsy moth population dynamics. Predation by small mammals is the dominant source of mortality during this period and the onset phase gypsy moth populations has been preceded by decreases in the density of *Peromyscus leucopus*. These findings support earlier theories concerning the importance of predation in the dynamics of the gypsy moth population system. Predation rates are affected by alternate food supplies. Additional experiments have explored whether predation is density dependent.

THE EFFECTS OF TREE SPECIES AND SITE CONDITIONS ON GYPSY MOTH SURVIVAL AND GROWTH IN MICHIGAN

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ABSTRACT

In 1987, we began a study to determine the relationships between gypsy moth growth and survival and forest site factors. The major objectives of this study were to determine the (1) relationships between gypsy moth survival and growth and different ecosystem conditions, (2) relationships among egg hatch, host phenology, and distribution of small larvae in the understory, (3) impact of leaf development age on gypsy moth growth and survival, and (4) role of host switching on gypsy moth growth and survival.

The research conducted in summer 1987 was to determine the variation in growth and survival of gypsy moth larvae on common understory plant species. Fourteen different understory tree and shrub species were studied at four different sites. Newly hatched larvae were caged on intact foliage in the field and survival and growth were determined by weighing larvae, recording mortality, and determining instar at 10 to 14 day intervals. Survival of small larvae and pupae varied greatly by tree species. Early larval survival was highest on witchhazel, paper birch, northern pin oak, and trembling aspen. Pupal weights varied considerably by sex and tree species, with female pupal weights 1.5 to 2 times larger on aspen than oaks. Relative growth rates varied by tree species; red oak decreased while white oak increased as the season progressed.

The effect of site on phenology of host tree and growth of gypsy moth larvae was emphasized in 1988. We studied the most common and most preferred host species: four oak species (red, white, northern pin, black) and two aspen species (trembling, bigtooth). In Michigan, there is up to a six week variation in date of leaf flush among aspen clones. Therefore, during 1988, detailed leaf phenology was obtained on eight sites for the four species of oaks and two species of aspen. During 1989, we continued gathering host phenology information for three species of oak and two species of aspen on six sites. The major experiments in 1989 were conducted on one site and emphasized: (1) the effect of host switching on gypsy moth growth and survival and (2) the impact of aspen leaf flushing dates (clonal variation) on survival and growth of gypsy moth.

The major results to date are: (1) survival and growth of gypsy moth larvae varied by tree species, year, and location, (2) the heaviest pupae were always produced on both aspen species, (3) drought has a major effect on overall pupal weights; pupal weights during the drought of 1988 were smaller for all species tested except red oak, which expressed no difference between the two years, (4) variability in insect growth and survival may be linked to the phenological development of individual trees, (5) phenological development of host plant varies by tree species and site, (6) red oak and trembling aspen had significantly faster leaf development than either northern pin oak, white oak, or bigtooth aspen, (7) host quality during the first two weeks of larval feeding has a major influence on overall size of mature larvae and pupae, (8) insects that fed on aspen during the first two weeks produced the heaviest larvae and pupae, no matter which host they were moved to, (9) all experiments involving gypsy moth growth and survival studies should use neonate larvae and natural hosts, because survival and growth during the first two weeks is extremely critical to understanding the interactions between gypsy moth survival and performance and host tree species, and (10) all experiments involving gypsy moth/host/tree interactions should consider host phenology, because host phenology has a major effect on gypsy moth growth and survival.

PERFORMANCE OF GYPSY MOTH LARVAE ON HOSTS FROM THE DEEP SOUTH: SURVIVAL, DEVELOPMENT AND HOST PREFERENCES

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ABSTRACT

Survival, development time and pupal weights of gypsy moth, *Lymantria dispar* L., which had fed on southern tree hosts were determined. Five species of oaks, *Quercus* spp.; sweetgum, *Liquidambar styraciflua* L.; and river birch, *Betula nigra* L., were found to be acceptable hosts. Survival and female pupal weights were significantly higher and development times were significantly shorter for larvae fed on water oak, *Q. nigra* L., than for any other species.

There were no clear host preferences by larvae in any instar among all possible paired combinations oaks and sweetgum. The inclusion of water oak in any pairing increased gypsy moth survival, reduced development time and generally produced heavier pupae, indicating that water oak is a superior host.

When lobolly pine, *Pinus taeda* L. was paired with hardwood hosts, gypsy moth larvae always fed c hardwoods. However, most larvae pupated in the pine foliage. When larvae were placed on loblolly pine at different developmental stages, first instars did not survive, second instar survival was 21 percent and survi instars 3-5 exceeded 95 percent. Development times (egg hatch to pupation) and pupal weights from larvae f pine were similar to those on most good hardwood hosts regardless of when they were transferred to the pin

It appears that the availability of acceptable hosts will not be a limiting factor for gypsy moth in the deep South. Loblolly pine stands with a high hardwood component may be at some risk for defoliation but pure pine stands probably will not be seriously affected.

DEVELOPMENT OF APPROPRIATE METHODOLOGIES FOR SAMPLING GYPSY MOTH POPULATIONS IN MODERATELY SIZED URBAN PARKS AND OTHER WOODED PUBLIC LANDS

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ABSTRACT

Egg mass survey data from operational gypsy moth (*Lymantria dispar* L.) management programs in five Maryland county parks and the Beltsville Agricultural Research Center (BARC) have demonstrated that improved survey protocols are needed to increase the precision and accuracy of the surveys. Despite an intensive 300-m survey grid, estimates of egg mass numbers within survey blocks containing at least 5 survey points had associated 90% confidence intervals ranging from 23 to 173% of the mean, with only 12% of the confidence intervals falling within 50% of the mean. Sampling of young larvae within the lower canopy shows promise as a supplementary survey tool on which to base management decisions.

LEADING EDGE GYPSY MOTH POPULATION DYNAMICS

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ABSTRACT

Leading edge gypsy moth populations have been the focus of several intervention programs (MDIPM, AIPM). Knowledge of gypsy moth population dynamics in leading edge area is crucial for effective management. Populations in these areas tend to reach outbreak levels (noticeable defoliation) within three to four years after egg masses are first detected. Pheromone traps have proven effective for detection and estimating population density in building populations. However, after populations have reached outbreak levels the utility of pheromone traps is decreased, primarily due to trap saturation. The emphasis of our research has been to investigate several aspects of gypsy moth biology with the objective of identifying characteristics that would be useful to monitor populations. We have focused on quantifying the impact of defoliation on several life history attributes.

Seventeen sites were studied during 1988 and 1989. These sites had a range of population densities and varying ecological characteristics (i.e., elevation, host species composition). Larval phenology was compared using a stochastic phenology model developed from estimates of instar occurrence and temperature data (in degree day form using a lower threshold of 7.65° C). Inspection of model parameters indicate there are no observable trends in larval development (faster or slower) due to density. However, parameters are not sufficiently consistent to suggest site conditions do not influence development. Pupae from sites with significant defoliation (90 - 100%) generally developed in fewer julian days. The most distinctive difference in phenology attributable to defoliation was a greatly shortened period over which pupation occurred (i.e., decreased variability).

Mortality was not explicitly measured, but field observations suggest mortality from NPV and starvation were the most significant sources of mortality. Regardless of the causes of mortality, high mortality is correlated with defoliation. Defoliation was found to have a significant effect on fecundity, but only if the level of defoliation exceeded 40%. High mortality and low fecundity, both defoliation related, were responsible for decreases in population density. Using larval density and estimates of total leaf weight per ha we were able to fairly accurately estimate if defoliation would exceed the 40% threshold. Sites with small egg masses (less than 300 eggs per mass), regardless of egg mass density, were lightly defoliated.

The spatial dynamics of gypsy moths in Virginia were also studied using defoliation coverages of the Northern District of the Shenandoah National Park and of the State of Virginia. Most areas tended not to be defoliated two consecutive years. Areas that were defoliated two consecutive years tend to be small patches the first year and part of large patches the second.

ANALYSIS OF SPATIAL DENSITY DEPENDENCE IN GYPSY MOTH MORTALITY

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ABSTRACT

The gypsy moth is perhaps the most widely studied forest insect in the world and much of this research has focused on various aspects of population dynamics. But despite this voluminous amount of research we still lack a good understanding of which, if any, natural enemy species regulate gypsy moth populations. The classical approach to analyzing insect population dynamics is the collection of a series of life-tables, stratified over several generations at the same location(s). This type of approach is valuable for detecting temporal density-dependent mortality and delayed density-dependence but recent theoretical studies have shown that the classical approach fails to quantify the relation of spatial heterogeneity in density and mortality and that this "spatial density-dependence" may have profound effects on the regulatory role of a mortality agent.

In this study we collected life table information that included estimates of gypsy moth survival and estimates of mortality due to specific causes. These life tables were spatially stratified within stands which facilitated the analysis for spatial density-dependence. These data were collected in stands where natural levels of spatial heterogeneity in gypsy moth densities existed and in stands where artificial gradients in density were created by introducing several million gypsy moth eggs into low-level populations.

Analyses of several natural populations indicated that mortality due to parasitoids and pathogens was largely independent of host gypsy moth density. In contrast mortality caused by three parasitoid species, *Cotesia melanoscela, Compsilura concinnata and Parasetigena silvestris,* appeared to be highly density-dependent in stands where artificial gradients of host gypsy moths were created. In these stands the spatial heterogeneity in gypsy moth densities was much greater than observed in any of the naturally occurring populations. Thus, these parasitoids probably operate in a significantly spatially density-dependent fashion only when spatial heterogeneity in host densities is great.

GYPSY MOTH LARVAL DEFENSE MECHANISMS AGAINST PATHOGENIC MICROORGANISMS

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ABSTRACT

We investigated the response of gypsy moth, *Lymantria dispar*, larval hemocytes to *L. dispar* nuclear polyhedrosis virus (LdMNPV) administered *per os* and by injection, and to injected hyphal bodies and natural protoplasts of some entomopathogenic, entomophthoralean fungi.

Light and electron microscope observations of gypsy moth larval hemocytes show seven distinct types of circulating cells: prohemocytes, spherulocytes, adipohemocytes, oenocytoids, plasmatocytes, granulocytes, and coagulocytes. Ultrastructural studies show that the latter three cell types predominate. Plasmatocytes and granulocytes engage in phagocytosis, and granulocytes and coagulocytes are involved in hemolymph coagulation. These events are integral components of nodulation, encapsulation and wound healing and together act to protect the host from microbial infection.

Phagocytosis of non-occluded and occluded LdMNPV took place, but it was an ineffective defense against viral infection. Viral replication was observed in hemocytes within 36 hours, and from then on, dramatic changes occurred in the blood system. During the course of nucleopolyhedrosis, infected larvae experienced significant decreases in total hemocyte count, in percentage of circulating granulocytes, in ability of the hemolymph to coagulate, and in time required for hemolymph to melanize. The blood volume per unit mass of infected larvae was significantly greater than that of controls and wound repair in infected larvae was accomplished in an altered manner.

Gypsy moth larvae were challenged with protoplasts of *Entomophaga maimaiga*, *E. aulicae*, and *E. grylli* and with hyphal bodies of the mite pathogen, *Neozygites* sp. and the Lepidopteran pathogen, *Erynia pieris*. Hemocytes responded to these entomophthoralean fungi in several different ways: these included melanization, phagocytosis, nodulation, encapsulation and lysis of fungal cells. The exact mechanism(s) implemented by the host varied with the fungus but in general, the walled cells of *E. pieris* and *Neozygites* sp. evoked the strongest cellular responses, while protoplasts elicited comparatively weak responses.

This study is an initial step in an investigation of the gypsy moth immune system and of the mechanisms by which this pest protects itself against pathogenic microorganisms.

TEMPORAL ANALYSIS AND SPATIAL MAPPING OF *LYMANTRIA DISPAR* NUCLEAR POLYHEDROSIS VIRUS TRANSCRIPTS AND *IN-VITRO* TRANSLATION PRODUCTS.

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ABSTRACT

The *Lymantria dispar* nuclear polyhedrosis virus (LdNPV) is being used as a biopesticide against the gypsy moth. We are attempting to enhance the potency of the LdNPV through recombinant DNA technology. As a prerequisite to genetic manipulation, we have characterized LdNPV gene expression in cell culture through the generation of transcription and translation maps. In addition, LdNPV polypeptides expressed in cell culture were identified.

To generate a genomic transcription map, northern blots containing RNAs isolated from 652Y cells 2, 7, 16, 24, 48, and 72 hours after infection with clonal isolate (CI) 5-6, were probed with labelled DNA fragments covering the LdNPV genome. Sixty-six viral transcripts were sized and mapped onto the genome. Fifteen viral transcripts were expressed early in infection, while most viral RNAs were initially detected from 16 to 24 hours post-infection (p.i.), and continued to be expressed until late in infection.

LdNPV CI 5-6 polypeptides, synthesized in 652Y cells, were identified after labelling with 35-S methionine and SDS-polyacrylamide gel electrophoresis. The expression of viral protein occurred in a sequential manner: 4 polypeptides were synthesized from 4 to 16 hours p.i., 24 proteins were initially detected from 12 to 20 hours p.i., and 5 polypeptides were initially detected at 24 hours p.i. These results are in good agreement with the study by J. McClintock et. al. (Virus Res., 5:307-322, 1986).

A translation map of LdNPV CI 5-6 was constructed. Six overlapping DNA fragments encompassing the CI 5-6 genome were used to hybrid select viral transcripts from RNA isolated from infected 652Y cells 7, 16, 24 and 48 hours p.i. The selected transcripts were translated in reticulocyte lysates in the presence of 35-S methionine, the protein products separated by SDS polyacrlyamide gel electrophoresis, and the labelled proteins visualized by autoradiography. The approximate genomic location of 89 LdNPV translation products were mapped. No proteins were detected using RNA hybrid selected from cells 7 hours p.i. *In-vitro* translation products were generated using RNAs from cells 16, 24 and 48 hours p.i. Eighteen proteins were expressed from 16 to 48 hours p.i., 5 proteins from 16 to 24 hours p.i., and 32 proteins from 24 to 48 hours p.i. Five proteins were detected only with RNA isolated 16 hours p.i., 22 proteins were specific to RNA isolated 24 hours p.i., and 7 proteins were specific to RNA isolated 48 hours p.i. The genes coding for proteins expressed late in infection were found to be dispersed throughout the LdNPV genome.

CONSTRUCTION OF A TRANSFER VECTOR FOR A CLONAL ISOLATE OF LDNPV

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ABSTRACT

Deoxyribonucleic acid from a clonal isolate of LdNPV (CI A2-1), obtained by *in vivo* cloning procedures, was used to construct genomic libraries in phage (lamda Gem 11) and cosmid (pHC79) vectors. Overlapping clones were selected to generate a restriction enzyme map. The restriction enzyme map, covering about 85% of the CI A2-1 genome, was determined. Efforts are underway to clone and characterize the missing regions.

A BglII fragment (10.5 kbp) containing the entire polyhedrin gene was subcloned into pUC18. This new plasmid was characterized for various restriction enzyme sites and the exact location of polyhedrin coding sequences. Several manipulations of the plasmid DNA were carried out which included: 1) deletion of a 6.2 kbp EcoRI fragment; 2) destruction of an existing HindIII site; 3) deletion of a 211 bp fragment containing sequence coding for N-terminal region of polyhedrin; and 4) replacing it with an oligonucleotide containing sites for NotI, HindIII, BamHI, SmaI, and ApaI enzymes.

The final product, pLdS1, was 6.6 kbp in size. It had 1.5 kbp region containing the promoter for polyhedrin gene and upstream sequences. Immediately following this were sites for NotI, BamHI, HindIII, SmaI and ApaI. The multiple cloning site was sequencially followed by 550 bp sequence coding for the C-terminal region of polyhedrin and 1.8 kbp sequences downstream from the polyhedrin coding region. Analysis of pLdS1 DNA suggests that this will be a suitable transfer vector for introducing foreign genes under polyhedrin gene promoter into CI A2-1.

A reporter gene, betagalactosidase, was subcloned into pLdS1 to produce pLdS1-Bgal. Both pLdS1 and pLdS1-Bgal will be tested by co-transfection experiments to determine whether pLdS1 can be used for introducing foreign genes into CI A2-1.

Using polyclonal antibodies, several cDNA clones corresponding to juvenile hormone esterase (JHE) were isolated from a lamda gt11 cDNA library constructed from poly(A) RNA from 5th instar, day 6 larval fat bodies. These are being analyzed to determine whether any contain the entire coding sequence for JHE. Meanwhile, these clones are being used as probes to isolate the JHE gene from a gypsy moth genomic library constructed in EMBL3 and labda Gem11 vectors.

REPLICATION AND INCLUSION BODY CHARACTERISTICS OF TWO *LYMANTRIA DISPAR* NUCLEAR POLYHEDROSIS VIRUS PLAQUE VARIANTS.

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ABSTRACT

Propagation of *Autographa californica* nuclear polyhedrosis virus in cell culture results in the generation of a mutant virus, termed few polyhedra. This plaque variant is characterized by a high budded virus titer, the formation of few polyhedral inclusion bodies (PIBs), and the production of PIBs exhibiting a low potency against its natural host. The isolation and study of a few polyhedra variant of *Lymantria dispar* nuclear polyhedrosis virus (LdNPV) could lead to a means of enhancing viral potency against the gypsy moth.

The replication characteristics of two *Lymantria dispar* nuclear polyhedrosis virus (LdNPV) plaque variants were studied in cell culture and *in-vivo*. In addition, the PIBs produced by the variants were characterized with respect to virion number, size, and morphology. The variants, clonal isolates (CI) A2-1 and 5-6, were found to exhibit differences in the number of PIBs generated, the titer of nonoccluded virus (NOV) produced *in-vitro*, the number of virions present within PIBs, and the potency of PIBs against the gypsy moth.

Infection of 652Y cells with CI A2-1 resulted in cells with an average of 51 PIBs per cell (ranging in number from approximately 3 to greater than 50 PIBs/cell), and with the variant CI 5-6, cells with an average of 4.4 PIBs per cell (ranging from approximately 1 to 12 PIBs/cell). The production of NOV in 652Y cells by the plaque variants was markedly different; CIs A2-1 and 5-6 exhibited TCID 50s six days after infection of 4.1 x 10-4 and 1.6 x 10-7, respectively.

The number of virions present, and size and morphology of PIBs generated by CIs A2-1 and 5-6, were analyzed through electron microscopic examination. CI A2-1 PIBs generated *in-vivo* contained an average of 11.6 virions per square micrometer of PIB surface area, in comparison to 0.09 virions/um-2 of PIB surface area within CI 5-6 polyhedra. In addition, larvae infected with clonal isolate A2-1 produced an average of 2.1 x 10-9 PIBs per larvae, ranging in size from 1.2 to 2.8 um in diameter, with an average of 2.0 um, while CI 5-6 generated an average of 8.6 x 10-7 PIBs per larvae, ranging from 1.9 to 5.8 um in diameter, with an average of 2.8 um. The shape of CI 5-6 and A2-1 PIBs produced *in-vivo* and of CI A2-1 produced *in-vitro* were round. In contrast, CI 5-6 PIBs generated *in-vitro* were primarily triangular, rectangular, or trapezoidal in shape. The potency of the variants against second instar gypsy moth larvae was investigated through bioassay. Preliminary data indicate that the LC-50 of CI A2-1 is approximately 1 x 10-3 PIBs per ml of diet. Incontrast, the LC-50 of CI 5-6 is greater than 1 x 10-6 PIBs/ml of diet.

The traits of CI 5-6: a high NOV titer, production of few PIBs, and the low potency of the PIBs are consistent with the classification of this virus as a few polyhdra variant. In contrast, the characteristics of CI A2-1: a lower NOV titer, production of many PIBs, and a wild type potency level are consistent with it being classified a many polyhedra wild type virus. The molecular basis for the few polyhedra phenotype of CI 5-6 is currently under investigation. There appears to be a correlation between potency and the number of virions present within PIBs. If such a relationship does exist these studies may yield insights into the process of virion occulsion and present a means of enhancing viral potency.

AUTOGRAPHA CALIFORNICA NUCLEAR POLYHEDROSIS VIRUS REPLICATION IN NON-PERMISSIVE *LYMANTRIA DISPAR* CELL LINES

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ABSTRACT

Autographa californica nuclear polyhedrosis virus (AcNPV) the prototypic group A baculovirus, has the widest reported host range of the baculoviruses and is considered to be one of the most virulent baculoviruses studied. The gypsy moth *Lymantria dispar* is not considered a natural host of AcNPV, however. To determine the factors regulating AcNPV restriction in *L. dispar*, *in vivo* and *in vitro* studies on AcNPV replication in gypsy moth cells have been initiated.

In vitro studies of AcNPV infection of *L. dispar* cell lines originated from egg, larval and pupal tissue sources revealed a variety of cell responses to infection. Cell susceptibility has ranged from permissive to non-permissive. Two cell lines, IPLB-Ld652Y and IPLB-LdFB have been shown to partially replicate AcNPV (semi-permissive cell lines) and thus are used to study at least one mechanism of AcNPV restriction in *L. dispar* larvae. Synchronous infection of these lines produces no budded virus nor viral occlusion bodies, however, distinct cytopathic effects are observed including nuclear hypertrophy, cell clumping (in IPLB-Ld652Y cells) and very condensed nuclear material (in IPLB-LdFB cells).

Growth rates and mitotic indices of infected cells are significantly inhibited, however, cell viability is not significantly affected initially. The kinetics of viral genome replication are normal (compared with viral DNA replication in permissive cell lines) as measured by DNA-DNA hybridization. Protein synthesis is drastically altered in both systems. Only a few of the early viral proteins are observed before there is a rapid total shut down of both viral and cellular protein synthesis. Analysis of transcriptional events in these systems reveal aberrant viral transcriptional regulation, however, cell translational processes appear normal.

Both *in vitro* systems are serving as models for events which are being monitored simultaneously *in vivo* and may give insight into *in vivo* AcNPV restriction mechanisms in *L. dispar* larvae.

RESPONSE OF GYPSY MOTH LARVAE TO HOMOLOGOUS AND HETEROLOGOUS NUCLEAR POLYHEDROSIS VIRUS

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ABSTRACT

The gypsy moth, *Lymantria dispar,* is not particularly susceptible to baculoviruses other than the nuclear polyhedrosis virus originally isolated from the species (LdMNPV). The multiple enveloped nuclear polyhedrosis virus of *Autographa californica* (AcMNPV), a very virulent baculovirus that replicates in a large number of Lepidopteran species, only rarely produces mortality in gypsy moth larvae regardless of the dose ingested.

We were unable to obtain a LC_{50} for AcMNPV in first instar gypsy moth larvae, and observed only occasional mortality among larvae fed concentrations of polyhedral inclusion bodies (PIB) exceeding 10^9 PIB per cup. This dose was more than six million times the dose required for a LC_{50} with the homologous virus.

The pathogenicity of AcMNPV for gypsy moth was not enhanced when PIB were produced *in vivo* in alternate hosts or *in vitro* in susceptible gypsy moth cell lines, or when PIB were fed to larvae in combination with inactivated homologous virus. Alkalai-disrupted AcMNPV PIB were not infectious *per os* or when injected into the hemocoel of gypsy moth larvae, although when injected into *Trichoplusia ni* larvae, 100% died of nucleopolyhedrosis.

Infections were readily established in gypsy moth larvae when extracellular non-occluded AcMNPV, produced in TN-368 cells *in vitro*, was injected into the hemocoel, but only low yields of PIB were obtained from cadavers and lethal times varied from 9 to 20 days.

The pathway of infection and histopathological effects of AcMNPV on *L. dispar* tissues were aberrant compared to what is observed during LdMNPV infection. Larvae infected with AcMNPV often had ruptures in the cuticle, presumably the result of dense accumulations of fibrous material that were observed in infected epidermal cells. Midgut cells, while not obviously infected, gradually degenerated and the midgut became grossly distended. Hemocytes became infected but little budding of non-occluded virus was seen. Other tissues in the body cavity were infected in a haphazard fashion. Pericardial and circumesophageal nephrocytes did not replicate AcMNPV, but accumulated electron-dense granules and underwent a significant color change. It is unclear whether the changes in nephrocytes are merely a form of necrosis due to an aberrant infection or whether these cells play a role in insect defense.

DETECTION OF LYMANTRIA DISPAR NUCLEAR POLYHEDROSIS VIRUS IN INFECTED LARVAE USING A DNA HYBRIDIZATION ASSAY

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ABSTRACT

The incidence of nuclear polyhedrosis virus in gypsy moth populations is currently measured by rearing field-collected larvae until death. Dead larvae then examined microscopically to confirm the presence of virus. Beside from being quite tedious, this method has several inherent difficulties and inaccuracies. In order to circumvent some of these problems, we have developed a DNA hybridization assay using radio- and digoxigenin-labeled viral probes to identify virus infected larvae using slot blot vacuum filtration and whole larval squashes. These methods are less tiresome and give more definitive results which are comparable with mortality data obtained from laboratory experiments as well as field collected larvae.

GENETICALLY-ENGINEERED BACULOVIRUS PESTICIDES AND THEIR ENVIRONMENTAL SAFETY

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ABSTRACT

Baculoviruses such as the *Lymantria dispar* nuclear polyhedrosis virus (LdMNPV) are ecologically attractive alternatives to chemical insect pesticides but have a slow rate of control. To overcome this we have developed and are field testing an environmentally acceptable strategy which can be used for the introduction and expression of pesticide-enhancing genes by baculoviruses. The field release data will be used to construct environmentally-safe, viral pesticides which have improved pesticidal properties and which will not persist in nature.

The model virus for this study has been the *Autographa californica* nuclear polyhedrosis virus (AcMNPV). Similar genetic constructions are being performed with the LdMNPV. Genetic alterations to the polyhedrin region of the LdMNPV will provide a phenotypic and genomic marker for release studies. The markers will provide a method to study the epidemiology of the LdMNPV in nature. In addition the genetic alterations are being made in such a way as to allow for the insertion and expression of foreign pesticidal genes.

An important ecological consideration involving the release of a genetically altered LdMNPV is the possibility of vertical transmission and persistent infections. In an effort to document and assess the extent of persistent virus infections, we have conduct experiments designed to induce productive LdMNPV replication in "persistently" infect gypsy moth larvae. A polyhedrin-minus mutant of the AcMNPV has been injected into gypsy moth larvae in an attempt to induce LdMNPV productive replication. We will report on the extent and nature of polyhedra produced in challenged, laboratory reared larvae.

KNOWLEDGE-BASED GEOGRAPHIC INFORMATION SYSTEMS ON THE MACINTOSH COMPUTER: A COMPONENT OF THE GYPSES PROJECT.

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ABSTRACT

GypsES, a decision-support and expert system for the management of Gypsy Moth addresses five related research problems in a modular, computer-based project. The modules are hazard rating, monitoring, prediction, treatment decision and treatment implementation. One common component is a geographic information system designed to function intelligently. We refer to this component as an intelligent GIS, (IGIS). The IGIS is incorporated in a prototype GypsES package on a Macintosh computer. The paper discusses the issues in the design and development of IGIS with regard to the hardware and software components, the nature of intelligence in the GIS environment and typical functions that IGIS will be called upon to perform by the various modules of GypsES.

An overall conceptual design of the GypsES project has been formalized giving IGIS a fundamental position underlying all other components and requiring communication with them. An expert system shell that the GIS and applications modules is being refined to exploit the window, icons, menus and pointing device capabilities of the Macintosh computer. The public domain GIS software, GRASS, developed by the Army Corps of Engineers, is being evaluated for suitability for basic GIS capabilities on the basis of its open, modular, C-language program structure. A hypertext prototype is now available to evaluate the user interface, determine flows of information in the decision-making process, and examine alternative output formats.

The intelligent functions of a GIS can be separated into three classes: user interface, knowledge base for GIS operations and knowledge base for application specific functions. The user interface guides an inexperienced user through the most efficient use of the system according to the stated needs of the user. A GIS knowledge base is necessary to permit the use of GypsES modules without comprehensive training in GIS technology. The application-specific knowledge base is part of a domain-specific expert system, e.g. Hazard Rating.

The experience of GIS experts and cartographers will be formalized in a knowledge base to assist in 1) map design, 2) terrain feature and cartographic feature extraction, 3) geographic database maintenance and 4) spatial analysis / geographic decision support. The knowledge bases will feature natural language interfaces and a facility for the explanation of reasoning behind decisions, i.e. the logic path is traced through the production rules to permit the user to determine the acceptability of the expert system outcome.

PHENOLOGY PREDICTION COMPONENT OF GYPSES

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ABSTRACT

Prediction of phenology is an important component of most pest management programs, and considerable research effort has been expended toward development of predictive tools for gypsy moth phenology. Although phenological prediction is potentially valuable for timing of spray applications (e.g. Bt, or Gypcheck) and other management activities (e.g. placement and removal of pheromone traps), we have had a difficult time effectively conceptualizing phenology prediction in GypsES. We have come to the realization that difficulties in representing phenology over a complex topographic landscape, such as is typical of many gypsy moth control areas, lies at the heart of the problem. Our current approach to phenological prediction, therefore, has two goals (1) representation of the complex landscape expression of gypsy moth phenology, and (2) reduction (or aggregation) of this complexity to a form that is useful in the management decision process. To meet these two goals, the problem of phenological representation falls into two catagories, Strategic Planning and Tactical Implementation.

Strategic Planning is the relatively static characterization of phenological attributes for a large management unit. In order to do this, it is first necessary to characterize temperature for the landscape in question. Sources of information for this characterization include, meterological weather stations, and the information in the USGS-Digital Elevation Model. From such information, it is possible to characterize (model) the thermal climate (on the order of a 30 yr. average)for a complex topography (c.f.: Russo et al., these proceedings). The thermal climate would be expressed as a 1-km grid, or at some other appropriate spatial scale. The next step is to run an appropriate phenological model for each grid cell in the management unit. Results of these simulations will be stored in rapid access, numerical form. Various specified gypsy moth management objectives, for example prediction of the maximum density of 2-nd larval instars, could then be easily determined for each grid cell. Since the phenological information is stored as a numeric data base, it would be a simple matter to change or test alternative objectives. Once management objectives have been stated, management constraints can be superimposed over these objectives. For example, the minimum difference in occurrence of a phenological event to be considered significant is constrained by tactical realities. A manager might decide that differences of less than 3 days between occurrence of the target event are not important. Such constraints provide the basis for aggregation. The convenient ability to test various combinations of management objectives and management constraints provide the capability of determining, through trial-and-error, an appropriate phenological resolution for tactical planning. The main things to be gained through Strategic Planning are: (1) reduction of a complex landscape to manageable terms (2) identification of areas (spray blocks) that can be treated as identical units with respect to management decisions such as spay application dates, pheromone trap placement, etc. (3) Improved delineation of spray blocks when phenology combined with other data layers through the IGIS capabilities of GypsES.

Tactical Implementation refers to the actual determination (prediction) of within season phenological events in order to better implement the tactical application of suppression or other management activities. The basic problem is phenological prediction that takes into account the inherent variability of seasonal weather patterns. This will require a combination of historical and predicted temperatures. Early in the season, the best predictor will be that obtained from the generalized phenological characterization that resulted from strategic planning. As the season progresses, observed temperatures can replace the 30-yr averages used in Strategic Planning, resulting in a improved target date. It would also be possible to incorporate both short and long

term seasonal temperature prediction into the model phenology predictions. All tactical applications require real-time running of the model to reflect seasonal phenological progression. Such applications will be possible **only** if the Strategic Planning procedure has resulted in a significant reduction in the complexity of landscape phenology. This capability remains an open research question!

In summary, the problem is not development of adequate phenological models for gypsy moth. In our opinion we already have good models. The real problem in phenology prediction for management application is not one of to little information, but one of too much information resulting in an information overflow. There is a pressing need for effective synthesis and aggregation of information to result in a useful management tool.

THE TREATMENT IMPLEMENTATION ADVISOR: A COMPONENT OF THE GypsES PROJECT

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ABSTRACT

The treatment implementation advisor is one of the knowledge based advisory modules of GypsES, a knowledge system environment for decision support in gypsy moth management. Its function is to provide detailed advice on intervention tactics for gypsy moth: e.g. aerial and ground application of insecticides and microbials, inundative or augmentative releases of parasitoids, mating disruption, genetic control and silvicultural management. The specific objectives of this project for 1989-1990 were as follows:

1) To design a knowlege based treatment implementation advisor .
2) To develop a prototype for early assessment by domain experts and potential users.
3) To begin linkage of the implementation advisor with the integrated tools of GypsES (GIS, DBMS, user interface, etc.).

GypsEX, a knowledge based module for aerial application of pesticides and microbials against gypsy moth (also operational as a stand-alone expert system), was refined considerably through verification efforts in June 1989 in Gettysburg, PA (with Ag-Rotors) and in August 1989 at Penn State University.

An initial knowledge engineering session in Hamden, CT, on August 1 stimulated three important suggestions: include a **treatment evaluation** section, a **tutorial** on the efficacy and safety of each major pesticide and ground vs aerial application, and **state-specific rules** layered on top of a fundamental rulebase for aerial application and other intervention methods.

GypsES research group meetings in August gave rise to the concept of the **treatment unit,** defined as an area within a management or administrative unit that is homogeneous with respect to treatment implementation. For example, a management unit which borders on water may have to be divided into two or more treatment units; those near water would not be recommended for aerial application of diflubenzuron.

A prototype for GypsES developed in the hypermedium SuperCard was presented in Providence, RI, on October 3 to several members of the United States Forest Service. The linkage of the implementation advisor to the other knowledge based advisors and integrated tools of GypsES is currently being conceptualized and is indicated in the prototype. Two major suggestions developed from this meeting: present a mix of **tutorials** on proposed **new technology** juxtaposed with **practical heuristics similar to current practice**, and include **algorithms to handle probabilities and incomplete information** whenever appropriate and possible.

The knowledge base for treatment implementation can be divided into choice of intervention method, aerial application of pesticides/microbials, and alternatives to aerial application. The subset of the knowledge base for aerial application can be further subdivided into choice of spray material during aerial application, spray timing, spray block prioritization, calibration, and characterization. Progress is presented on the design and software implementation of each subset of the knowledge base.

MONITORING COMPONENTS OF GYPSES

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ABSTRACT

The manager needs tools for assistance in planning and interpreting monitoring systems. We are building a system that designs sampling programs by interpreting data about Gypsy Moth, stand condition and management objectives. The system prioritizes areas within the management unit within budgetary constraints and defines the areas to be monitored. The system proposes monitoring procedures to guarantee an effective monitoring program. These tasks are accomplished by the following modules in the GypsES system: The Egg Mass Sampling Designer (EMSD), the Pheromone Trapping System Designer (PTSD), and the Defoliation Projector (DP).

The EMSD delineates the sampling area and proposes an adequate sampling plan. Currently, the area with pheromone trap densities above the sampling threshold are recommended to be sampled for egg masses. As in the Appalachian IPM project last year, the sequential sampling plan developed by Shelby Fleischer is proposed. The EMSD presents this underlying information, provides maps of the areas to be sampled and sampling plans.

We envision improving the design of egg mass sampling by incorporating more information. This can be the moth trend between last year and this year or the egg mass density of last year. Resident calls, observations of nearby infestations, and burlap bands are valuable indications that should be incorporated. Our system keeps track of these indications and will integrate them with more quantitative estimates of gypsy moth pressure. The threshold that defines what areas need egg mass sampling should be more comprehensive by making it dependent on the risk of the sampling unit. Egg mass sampling costs should be incorporated as well. With an estimate of the influence of the sampling plan, the size of the sampling area and the accessibility of the area on the sampling costs, the EMSD will support the manager in planning egg mass sampling under the constrained budget.

The PTSD delineates the sampling area where traps should be posted and proposes the pheromone trap distribution and pheromone trap type. With similar logic as in the EMSD only areas above a certain risk deserve greater monitoring efforts. Pheromone Trapping currently is mainly used in and before leading edge situations as an early warning system. Observations of lasts years pheromone traps and if available this years egg mass density are used to estimate GM pressure. With the PTSD the manager again has the opportunity to estimate the monitoring costs and compare them to his budget constraints.

The DP produces maps of the estimated level of defoliation. The hazard component of GypsES needs defoliation projections to estimate hazard ratings. Currently we intend to incorporate the algorithms developed by Gansner, Campbell and Montgomery into the DP. We anticipate more alternatives as we search through the available information and more researchers are focussing on this central problem in Gypsy Moth management. The uncertainty involved in the projection of the defoliation has to be considered in decisions based on defoliation projections.

With the components EMSD, PTSD, and DP of the GypsES system we want to build a system that can satisfy various needs of the forest manager: a guide for less trained personnel in planning monitoring systems and flexible compilation and display of data for the expert. It is a perfect vehicle to test new research results in field situations. Implementing scientific knowledge into forest management will no doubt improve understanding and generate new research questions.

HAZARD RATING FOR GYPSY MOTH ON A MACINTOSH COMPUTER: A COMPONENT OF THE GYPSES SYSTEM

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ABSTRACT

As gypsy moth expands into a new region, the threat of damage from its infestation is increasing greatly. The potential economic damage from the pest is extensive, considerably compounding the already substantial aesthetic damage and urban nuisance problems. One way to help forest managers deal with this threat is by providing them with a computer program which can help them determine how to set priorities for their forest lands by relative risk from gypsy moth. The program being developed, called GypsES, will serve as a surrogate "expert" on gypsy moth treatment, so it is referred to as an "expert system". The hazard rating module described here is one of several components of an integrated system.

Acceptance of working definitions of basic terminology was essential for progress in development of the hazard rating module. A management unit is defined as the smallest area having uniform management objectives, and may be subject to uniform silvicultural treatment. Susceptibility is the probability that a management unit may be defoliated by gypsy moth. Vulnerability is the probability that a management unit will sustain damage if defoliated by gypsy moth. Some trees or stands may suffer repeated defoliation (high susceptibility) without serious damage (low vulnerability), while other stands may suffer severe damage (high vulnerability) with only occasional defoliation episodes (low susceptibility). Risk is the probability that damage from defoliation will affect management objectives. Hazard is the probability that the objectives for a management unit will be affected by defoliation within a specified time period.

Hazard rating incorporates information about insect populations as surrogates for predicted defoliation. In a stand-alone mode, the module will require estimates of gypsy moth populations. As a component of GypsES, population data are obtained from the monitoring and prediction module. Hazard assessment produces the probable impact on the management unit, its importance to the management objectives, and an estimate of the economic effects. These outputs are to be used in the treatment decision module of gypses or on their own by a forest manager. Data from the associated insect population monitoring/prediction module being developed concurrently will be integrated into the Hazard Rating module. Probability of infestation combined with vulnerability of a management unit will allow this module to assess the likely severity of damage with regard to the management objectives for the unit. This assessment will produce an output of probable impacts on the stand, their importance to the management objectives, an estimate of the reliability of the predictions, and an estimate of economic effects. This output will be able to be used on its own by a manager, or can be used as input data for the next module within the system, that designed to aid in treatment decision-making. Data themes to be incorporated include stand composition, elevation, soils, roads and hydrology, management compartments, and land use types, among others.

MICROBIAL PESTICIDES

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ABSTRACT

Interest in the use of microbial pesticides has intensified because of public concern about the safety of chemical pesticides and their impact in the environment. Characteristics of the five groups of entomopathogens that have potential as microbial pesticides are briefly discussed and an update is provided on research and development activities underway to enhance the performance and use of microbial products. Emphasis is placed on viral and bacterial pesticides and their use in managing gypsy moth populations. The status of microbial pesticides registered by the Environmental Protection Agency (EPA) and regulations governing their use are reviewed

INTRODUCTION

The potential for utilizing microorganisms as an applied tactic to control pest insects was recognized in the 1940's when a species of bacteria, *Bacillus popillae,* was used successfully to control the Japanese beetle. Although many entomopathogens of insects have been isolated and described, probably only a few species have real potential as microbial pesticides. Interest in the application of microbial pesticides has accelerated since the 1960's for several reasons:

1) Environmental concerns associated with using chemical pesticides, including pollution of groundwater, the accumulation/biomagnification of residues and metabolites in the environment, contamination of food supplies, and direct effect on non-target organisms.

(2) Development of resistance in insects to chemical pesticides.

(3) Increased emphasis on integrated pest management (IPM) and low input sustainable agriculture (LISA).

(4) Recent developments in biotechnology.

Evidence of the interest in microbial pesticides is elucidated by the history of pesticide use in gypsy moth state/federal suppression programs (Fig. 1).

Since 1982, when about 90% of the acreage was treated with chemical pesticides, the use of Bt, the only commercially available microbial pesticide, has increased substantially. In 1989, Bt was used on over 50% of the 820,000 acres treated in 11 states; however the choice of chemical/microbial pesticides varies widely from state to state and is influenced by management philosophy and environmental pressures. Bt was used exclusively in Michigan and New Jersey whereas Dimilin was used on 74% of the acreage treated in Virginia, and on over 99% of the acreage treated in West Virginia.

The objectives of my presentation are to: provide an overview of the status of entomopathogens being developed as microbial pesticides; to highlight recent developments in those microbials that have been used against the gypsy moth; and to provide an introduction to the topics that will be addressed by the following speakers in this session and in the accompanying poster displays.

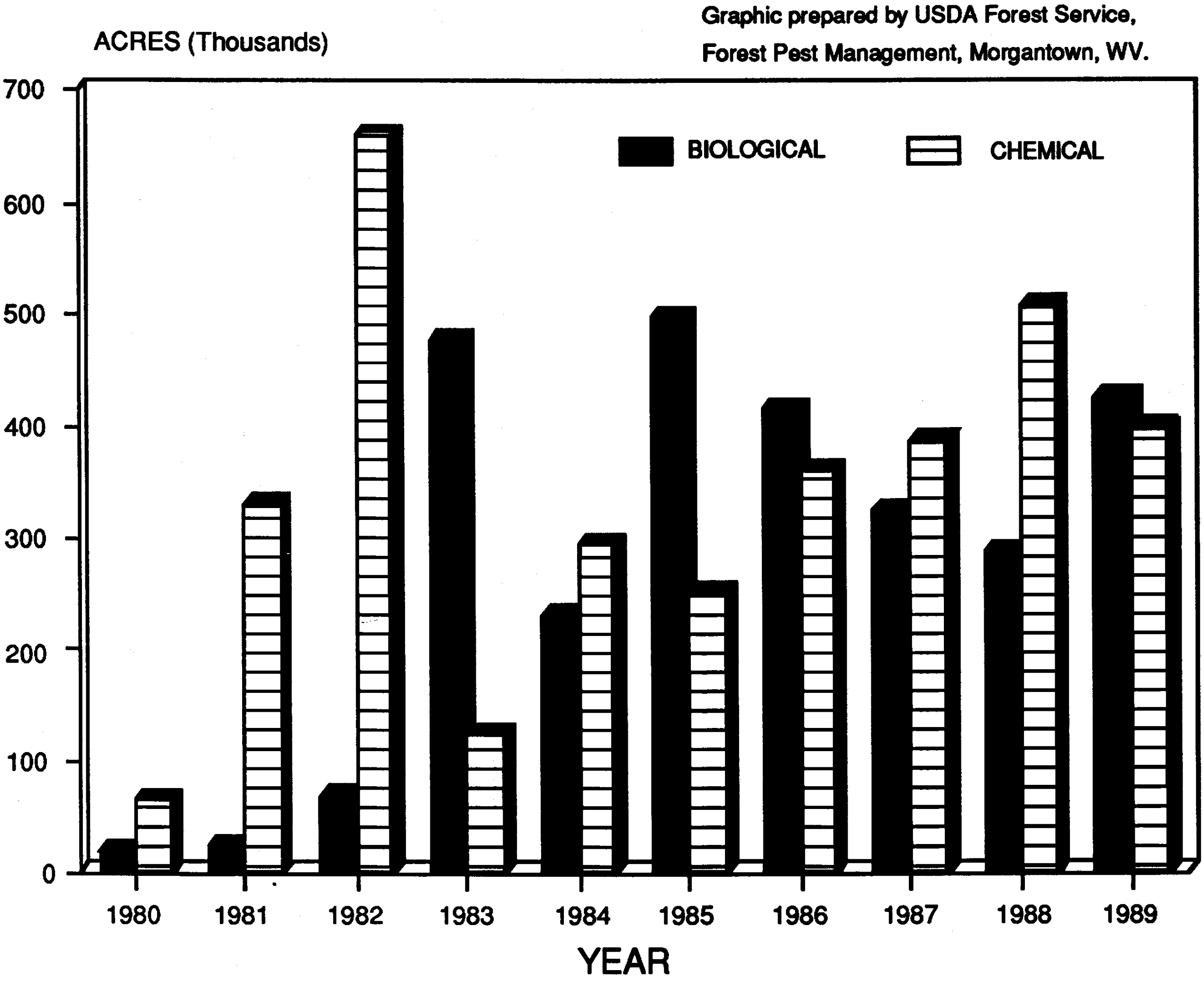

Figure 1. Insecticide use in State/Federal Cooperative Gypsy Moth Suppression projects (1980-1989).

ENTOMOPATHOGENS AND THEIR POTENTIAL AS MICROBIAL PESTICIDES

The Environmental Protection agency (EPA) defines a microbial pesticide as follows: any bacterium, fungus, alga, virus, or protozoan intended for preventing, destroying, repelling, or mitigating any pest, or intended for use as a plant regulator, defoliant, or desiccant. Although this is a very broad definition, it does not include nematodes which insect pathologists normally include within this category. Some of the general characteristics of entomopathogens that are used as microbial pesticides are listed in Table 1 and will be discussed in their respective sections. Emphasis will be directed at those organisms that have been or are being used against the gypsy moth.

Table 1. Some characteristics of entomopathogens used as microbial pesticides.

Pathogen	Mode of infection	Production requirement	Speed of Kill
Viruses	Ingestion	Cell culture Insect larvae	Slow
Bacteria (Bt)	Ingestion	Liquid culture	Stops feeding due to toxin
Fungi	Contact		Liquid/solid culture
Protozoa	Ingestion	Insects	Very slow
Nematodes	Search & penetration	Artificial substrate	Fast

BACTERIA (Bt)

Although many genera of bacteria infect insects, only species in the genus *Bacillus* have been commercialized and are being used as microbial pesticides. *Bacillus thuringiensis* Berliner (Bt) persists in nature worldwide and hundreds of isolates have been recorded (Kurstak and Tijssen 1982); Each strain of Bt appears to have its own specific spectrum of activity against insects.

Bt is a spore-forming bacterium that, when cultured under appropriate conditions, forms a crystalline parasporal inclusion body which contains the delta endotoxin. It is an ideal organism to produce in large scale commercial submerged culture systems using standard methods and fermentation equipment. The commercialization of Bt expanded dramatically in the late 1960's with the isolation and development of the HD-1 strain and its acceptance as the International Standard. This strain was found to have 15X the pesticidal activity of the earlier referenced standard.

In the past 10 years, the quantity of Bt applied annually against the gypsy moth and other forest defoliators in operational programs has varied considerably because of its inconsistent performance. In general, Bt applied once or twice against the gypsy moth provides good foliage protection but has not caused a significant reduction in larval populations; consequently, many areas need to be re-treated in subsequent years. However, substantial improvements have been made in commercial Bt formulations and methods improvement studies have demonstrated that the operational performance of Bt can be further improved through better application technology. This will be discussed later in this presentation.

Approaches to improve Bt performance

Interest and developments in Bt-related research have exploded in recent years due in part to: 1) the isolation of new strains that are toxic against a variety of insect pests, 2) the advent of biotechnology, specifically recombinant DNA technology, and 3) advances in formulation and application technology.

Isolation of natural strains. Isolation of new natural Bt strains worldwide is a continuing activity that has had a significant impact on the industry. *Bt* var. *israelensis* was found to exhibit a high level of insecticidal activity against larvae of mosquitoes and black flies. It has been used successfully against both pests in Africa, Germany, and in abatement districts in the United States, and is considered to be a significant component in public health programs. Other strains such as *Bt*. var *tenebrionis* and *Bt* var. *San Diego* are active against species of Coleoptera; these isolates are currently being developed by industry and evaluated against several pests such as the Colorado potato beetle, elm leaf beetle, and the yellow mealworm.

In 1981, a new strain of Bt was isolated from diseased larvae of the spruce budworm that exhibited 3-4 X toxicity against the gypsy moth and other species of Lepidoptera (DuBois and others 1988). This strain, labeled NRD-12, was commercialized by Sandoz Inc. as Javelin® for use against species of *Spodoptera* and more recently has been marketed as SAN 415® for use against the gypsy moth and other forest defoliators. It differs from the HD-1 strain in its DNA sequence of the toxin genes and their expression, and in its spectrum of insecticidal activity. It has been determined that the increased insecticidal activity is attributed to the 135 KDa protein that makes up the bipyramidal crystal. Discovery of these natural strains has stimulated the continued search for new and more potent Bt strains that may be effective against a range of pest insects.

Biotechnology-Genetically Altered Strains. Genetic engineering technology is capable of producing recombinant organisms such as *Pseudomonas fluorescens* and *Escherichia coli* that express the delta-endotoxin of Bt. This is currently a wide open and fiercely competitive field that involves large chemical and pharmaceutical firms and venture capital companies, as well as public and private laboratories. Certain strains can be induced to produce large quantities (25-30X) of delta endotoxin, while other strains may possess toxic proteins that decompose more slowly in the environment. Since 1984, the EPA has reviewed at least 12 genetically modified microbial pesticides that include organisms with genes inserted or deleted, induced mutants, and transconjugants. Many scientists suggest that eventually, molecular biologists will be able to produce a Bt product that will be specific to most of our major insect pests.

Formulation and Application Technology. Microbial pesticides such as Bt consist of small particulates that are formulated as wettable powders or flowable concentrates and applied as water suspensions. Except for fungi, microbials must be ingested by the target pests; therefore they must be applied to a substrate (i.e. foliage) and retain their viability for several days. This is no easy feat since exposure for less than 24 hrs. to wavelengths below 500 nm (UV spectrum) inactivates Bt spores and crystals and degrades the protein structure of viral polyinclusion bodies (PIB's). Since microbials are most active against early larval instars, the window for their application is very narrow and finite: because of these limitations the successful utilization of microbials is considered to be both an art and a science.

Bt formulations have undergone an evolution in the past five years and for the most part have been improved substantially. Oil formulations have given way to aqueous formulations and adjuvants such as stickers, ultraviolet screens, and humectants have been added to increase their persistence in the environment. Several novel formulations have emerged. Mycogen Inc. has developed an insecticidal delivery system for the delta endotoxin, called MCAP®, whereby the toxin is encapsulated within a non-viable cell of *Pseudomonas fluorescens*, a soil inhabiting, plant colonizing, non-pathogenic microbe. This system affords greater field persistence of the toxin. ARS scientists have also developed a system whereby Bt spores and crystals are encapsulated along with a UV screen within a starch matrix. This formulation retained 50% of its toxicity for up to 12 days in the field.

The difficulties associated with applying microbial pesticides were elucidated at an NSF-USDA sponsored workshop that was held in Gainesville, Fla. in 1978. Microbials are still being applied with conventional application systems that were designed for contact chemical pesticides and it was emphasized at that meeting that radical modification of equipment and ideas regarding application is needed. The erratic performance of Bt since that time has been blamed on weather, poor application, or poor timing of application. However, prior to 1985, studies had never been conducted to relate spray deposit on foliage to efficacy. Since then, we have learned much about the effect of droplet diameter, density of droplets, and their distribution in the forest canopy on the efficacy of Bt against the gypsy moth (Bryant and Yendol 1988; Yendol and others 1989).

Much of the credit for generating interest to improve the aerial application of Bt and other microbials can be attributed to the Northeast Forest Aerial Application Technology Group (NEFAAT), an ad hoc group of scientists and practitioners from the Forest Service (FS), Animal and Plant Health Inspection Service (APHIS), Agriculture Research Service (ARS), Pennsylvania State University, and the University of Connecticut. This group meets several times each year to identify and prioritize research needs, and then jointly conducts laboratory and field studies designed to improve the performance of Bt. The NEFAAT group also provides technical assistance and training to user groups by conducting workshops on the operational aspects of aerial spray programs. .Another major activity involves acquiring data sets on spray deposit, meteorology, and canopy geometry that are needed to validate and enhance spray models such as FSCBG and AGDISP that have been developed by the Forest Service. These models have utility for standardizing and improving aerial spray technology. The NEFAAT group represents the only concerted effort to address the aerial application problems that were identified over 12 years ago.

Recently two other committees have been established to improve the coordination of activities related to the application of microbial pesticides. A Bt Technical Committee was formed in 1986 consisting of representatives from the FS, APHIS, ARS, Industry, Academia, and affected states. This committee meets annually in the Fall to review the performance of Bt in operational programs and field and pilot studies, and then identifies research needs and methods improvement studies.

In 1988, the Forest Service established a series of National Steering Committees for Aerial Application of Pesticides to address problems associated with eastern forest defoliators, defoliators of western conifers, insect pests of seed orchards, and vegetation management. Each Committee meets annually to review data and progress of field and pilot tests, identifies needs for improving application systems and strategies, and assigns priorities for field and pilot studies to be conducted in the following year. The joint Committees also developed badly needed guidelines for conducting field and pilot studies, the intent being to better standardize the design of experiments and acquisition of data so that results submitted from various investigators can be compared.

Although the role of these coordinating groups may be perceived as duplicative or overlapping, it in fact is not since each group functions differently and satisfies various needs among the agencies and within the user community.

VIRUSES

General

More than 20 groups of viruses are known to be pathogenic for insects, however most interest is directed toward the nuclear polyhedrosis virus (NPV's) and to a lesser degree to the granulosis viruses. Both of these groups are placed in the family Baculoviridae and are called baculoviruses; they are more restricted in their host range than other viral groups.

Diseases caused by viruses are usually fatal, though infected larvae may not die until 6 to 10 days after first symptoms appear. Epizootics causes by viruses are quite dramatic and frequently cause total collapse of gypsy moth and other forest insect populations. The virions or infectious agent are cylindrical, rod-shaped structures that are enclosed within an inclusion body that is polyhedral in shape, protein in nature, and is a late viral gene product. The polyhedral inclusion body (PIB) protects the infectious virions much like a protective spore, is resistant to desiccation, and under optimal conditions can be stored for years. In gypsy moth populations, the PIB's are released from dying and dead larvae and then passively dispersed in the environment and horizontally transmitted to other larvae, thus attributing to the sometimes rapid development of epizootics. The persistence of PIB's on environmental surfaces contributes to the vertical transmission of the virus in subsequent generations (Murray and Elkinton 1989, Woods and others 1989).

There is a tremendous interest in developing viruses as microbial pesticides because of their host specificity, safety to non-target organisms, and lack of persistence in the environment. Conversely, their specificity limits their potential marketability since incentives for industry to embark on commercial production revolve around predictable and expanding markets. Thus, while Sandoz Inc. registered Elcar® as the first viral pesticide for control of *Heliothis* sp. in 1975, the last three viral products that have been registered for control of the Douglas Fir Tussock Moth, gypsy moth, and European pine sawfly, were developed and registered by the Federal Government.

The potential role of biotechnology in developing and enhancing utilization of baculoviruses is unlimited. Recombinant DNA technology offers many avenues to improve the pathogenicity and effectiveness of baculoviruses; scientists are exploring the possibility of inserting toxin or hormone genes into the viral genome to either amplify toxicity, alter behavior, or arrest the development of insects. However, most commercial interest to date has been directed at using baculoviruses as expression vector systems to produce massive amounts of protein in a short period of time. It's estimated that over 150 laboratories are using baculoviruses for this purpose, one important application being for producing AIDS vaccine for human trials in the U.S.

Gypchek - The Gypsy Moth NPV

Gypchek,® the gypsy moth NPV, was registered by the EPA in 1978 and recently re-registered in 1988. It is not commercially available because, like all baculoviruses, it must be produced *in vivo*, which is a labor-intensive, costly process; furthermore, the specificity of the virus to the gypsy moth and the periodic, eruptive nature of its outbreaks somewhat limits the market potential for a viral pesticide.

Since its registration, Forest Service Research has been producing Gypchek® in collaboration with the APHIS Methods Development Center in quantities sufficient to conduct methods improvement studies annually in cooperation with the FS-Forest Pest Management Group in Morgantown, W.VA. Prior to 1986, the field efficacy of Gypchek® against gypsy moth populations had been erratic at best and varied with the dosage applied and the density of the population. In 1986, excellent control was attained when the dosage of Gypchek applied was increased to 5 X 10" PIB's/acre (100 million potency units) and a new sunscreen, Orzan LS® was added to the tank mix. Aerial tests conducted in 1987-88 confirmed that two applications of Gypchek® at that dosage with Orzan LS provided excellent foliage protection and resulted in ca. 90% reduction in egg masses in the treated blocks. These results stimulated a renewed interest by industry in both in-vivo and in-vitro production of Gypchek® as a viral pesticide.

Approaches to Improve Gypchek® Performance

Interest in Gypchek® has been intensified not only because of its improved performance in aerial field studies but because of environmental concerns about the impact of aerially applied Bt on non-target Lepidoptera, and recent developments in biotechnology and in cell culture production of viruses. Consequently, several initiatives are being pursued simultaneously that are designed to ameliorate both the activity and availability of the gypsy moth virus.

Strain Selection. Gypchek® is produced from a wild type isolate (LDP-67) that apparently contains several genotypic variants. Shapiro and others (1984) reported that a natural isolate of the gypsy moth virus, the Abington strain, demonstrated 5-10X activity against gypsy moth larvae in laboratory bioassays. This strain is currently being evaluated along with Gypchek® in a comparative field study on small plots in Maryland. There is also more recent evidence that isolates cloned from Gypchek® also demonstrated increased activity (5-20X) when bioassayed against gypsy moth larvae, suggesting that more virulent isolates do exist in nature and that cloned isolates may provide a better source of inoculum for future production of the virus.

In vivo production. Significant advancements in rearing technology have been realized at the Otis Methods Development Center, resulting in the production of better quality insects at a lower cost per unit. Additionally, improvement in the processing of viral-killed cadavers at the FS Ansonia facility has resulted in more efficient recovery of viral PIB's and production of a better physical product. Undoubtedly, both rearing and processing could be further improved through mechanization. Theoretically, an alternative strain of gypsy moth could be developed that is specifically adapted for producing virus rather than for producing quality adult insects; similarly a less-expensive, modified diet might be developed that would be adequate for rearing larvae for virus production. Many of these options are being pursued by ESPRO Inc. which has a technology transfer agreement with the FS to produce Gypchek® and is pursuing commercialization of the gypsy moth virus.

In vitro production. ARS scientists have made major advancements toward producing gypsy moth virus in cell culture systems. The feasibility of producing virus in cell culture has been improved by utilizing a new fat body cell line along with the Abington strain, and by reducing the cost of culture media. ARS has entered into a cooperative research and development agreement with IGB Products Ltd. to develop the technology for scaling up a cell culture system for producing gypsy moth NPV. The availability of a cell culture system would eliminate the need for an expensive in-vivo production facility and would promote the production of a more standardized viral product.

Genetic Engineering. As stated earlier, scientists believe that there are unlimited opportunities to improve baculoviruses such as the gypsy moth NPV using gene deletion/insertion techniques, or by producing chemically induced mutants. Many of these alternatives are being pursued at the FS laboratory in Delaware, OH., and at the Boyce Thompson Institute (BTI) in Ithaca, NY. Scientists at BTI are creating a polyhedrin-minus mutant thereby providing a genetic marker than can be used to follow the dissemination of aerially applied virus in space and time. This would be the initial step leading up to replacing the polyhedrin gene with foreign genes designed to enhance activity of the virus or disrupt the development of gypsy moth larvae.

Formulation and Application Technology. Gypchek®, like other viral preparations, is readily degraded by ultraviolet light and therefore must be formulated with a good UV protectant along with other adjuvants needed to improve its stability and persistence in the environment. Now that the field efficacy of Gypchek® has been demonstrated, there is a need to develop a Bt-like formulation for Gypchek® so that we can eliminate use of the current tank mix. This mixture, which includes water, Orzan LS, molasses, a sticker, and Gypchek®, is not practical for use in operational programs. Methods improvement studies are being conducted to identify even better sunscreens or additives that magnify either larval feeding or viral activity. Investigators are also evaluating encapsulated formulations for viruses that would effectively extend their field persistence.

To date, little or no effort has been directed toward optimizing the aerial application of Gypchek®, that is determining the best dose, application rate,and delivery system needed to provide adequate deposit and repeatable efficacy. Although there is much to be done, studies of this nature should not be conducted until an acceptable formulation for the virus is developed, since the physical characteristics of a formulation will greatly affect it's atomization, dispersal, and deposit on foliage.

FUNGI

Pathogenic fungi are unique among the entomopathogens used as microbial pesticides because they infect insects directly through their cuticle and therefore need not be ingested. However, the micrometeorological conditions (temperature and relative humidity) that are required for germination of spores and infection are critical and seldom realized in field applications. There are about 750 species of fungi that are known parasites or pathogens of arthropod pests; more than 30 have been tested as biological preparations, and several are commercially available in foreign countries. According to Weiser (1982), the reason for the lack of widespread use of fungi is that there are too many variable conditions which make their application unreliable, thus requiring that proper conditions would have to be established for each combination of fungus and pest.

Fungal epizootics can be very dramatic and occasionally will decimate pest populations. Hajek (this proceedings) reported on a panzootic in gypsy moth populations caused by *Entomophaga maimaiga*. This was the first recorded fungal epizootic affecting the gypsy moth in the U.S., though fungal epizootics apparently are more common among Japanese gypsy moth populations (Aoki, 1974). Although the species was introduced into New England from Japan in 1910 or 1911 (Speare and Colley 1912) it has never been reported in the literature as a mortality agent in gypsy moth populations. It should be noted however that fungal-infected larvae appear similar to virus-killed larvae, therefore it is very likely that incidents of fungal mortality were heretofore overlooked.

There has been a concerted effort by industry in the U.S. and abroad to develop *Beauvaria bassiana* as a microbial pesticide for use against a wide range of insect pests. However, when *B. bassiana* was applied against the gypsy moth in Slovakia, it caused less than 5% mortality in the population. (Novotny 1988). Fungi probably are not candidates for use as a microbial pesticide against the gypsy moth, but should be used in inoculative releases to effect permanent biological control.

PROTOZOA

Among the Protozoa, the only group considered to have potential as microbial pesticides is the microsporidia. Microsporida are known to infect over 100 species of mosquitoes and several major forest defoliators such as the spruce budworm, gypsy moth and forest tent caterpillar. One species, *Nosema locustae*, is registered in the U.S. as a bait formulation for grasshopper control.

Microsporidia generally produce chronic rather than acute disease in insects, consequently, their effect on populations is not as dramatic as the epizootics caused by bacteria, viruses, or fungi. However they do cause debilitating effects on individuals such as prolonged development, reduced fecundity, and, in some cases, behavioral changes. Microsporidia are reported to act as a stressor in insect populations thereby predisposing individuals to attack by other pathogens such as viruses. Some species are vertically transmitted transovarially to subsequent generations, thus exhibiting a desirable attribute not common to other entomopathogens.

At least seven species of microsporidia have been described or reported from European gypsy moth populations and several species are recognized as having a significant effect on the dynamics of populations in Eastern Europe (Weiser and Novotny 1987). Five species were isolated from gypsy moth populations in Europe and returned to the U.S. for evaluation and potential introduction (McManus and others 1989). One species, *Nosema* N. sp., from Portugal, was introduced into an isolated gypsy moth population and persisted for at least three generations at low levels (Jeffords and others 1989). This species is being recommended as a candidate for general inoculative releases into U.S. gypsy moth populations.

Although Czechoslovak scientists have successfully used a species of microsporidia, *Nosema lymantriae*, as a microbial pesticide (Novotny 1988), there is no intent to use these organisms other than for classical biological control in the U.S. Studies are underway to evaluate the interaction of various isolates with the gypsy moth NPV and to screen other isolates for potential introduction.

NEMATODES

Entomogenous Nematodes occur naturally in soils and possess a wide host range. They are relatively easy to mass produce and apply, however their persistence in soil is limited to a few weeks. The soil environment is a complex medium for nematodes; their efficacy as pathogens is affected by soil moisture, pH, texture, and antagonistic organisms.

Since nematodes are classified as macroparasites, they have been exempted from EPA registration requirements. Several species are being evaluated and actively developed by industry as a control alternative for several insect pests, particularly soil inhabiting species. Novel delivery systems are being evaluated that include desiccated nematodes mixed with baits, and nematodes and seeds encapsulated together within an alginate matrix.

Nematodes have been recovered from gypsy moth populations in Japan, Austria and the Soviet Union. Several species were introduced into U.S. gypsy moth populations during the USDA Accelerated R&D Program (1975-78), however infected larvae were never recovered. In 1984-85, several studies were conducted to evaluate application of *Neoaplectana carpocapsae* against late stage gypsy moth larvae; nematodes that were applied directly to burlapped trees or sprayed on foliage within alginate capsules failed to cause infections among resident gypsy moth larvae. It was concluded that applications of nematodes are not feasible to control foliage-feeding insects like the gypsy moth.

REGULATORY ISSUES

Microorganisms intended for use as microbial pesticides are subject to the Federal Insecticide Fungicide and Rodenticide Act (FIFRA) which has oversight of experimental use, sale and distribution of pesticides. Guidelines for the testing of microbial pesticides, referred to as Subdivision M, were initially published in 1982 and updated in 1989. Data requirements for microbial pesticides (40 CFR Part 158) were published in 1984. There are currently 15 microbial pesticides that are registered for use against insects (Table 2.)

Table 2. EPA Registered Microbial Pesticides (As of 4/19/90).

Microorganism	Year Registered	Pest Controlled
Bacteria		
Bacillus popilliae / B. lentimorbus	1948	Japanese beetle larvae
B. thuringiensis Berliner	1961	moth larvae
Agrobacterium radiobacter	1979	*A. tumefaciens* (crown gall)
B. thuringiensis israeliensis	1981	mosquito larvae
Pseudomonas fluorescens	1988	*Pythium, Rhizoctonia*
B. thuringiensis San Diego	1988	coleopterans
B. thuringiensis tenebrionis	1988	coleopterans
B. thuringiensis EG2348	1989	gypsy moth
B. thuringiensis EG2371	1989	lepidopterans
B. thuringiensis EG2424	1990	lepidopterans / coleopterans
Viruses		
Heliothis Nuclear Poly-hedrosis Virus (NPV)	1975	cotton bollworm, budworm
Tussock Moth NPV	1976	Douglas fir tussock moth larvae
Gypsy Moth NPV	1978	gypsy moth larvae
Pine Sawfly NPV	1983	pine sawfly larvae
Fungi		
Hirsutella thompsonii	1981	Mites
Phytophthora palmivora	1981	citrus strangler vine
Colletotrichum gloeosporioides	1982	northern joint vetch
Trichoderma harzianum/ Trichoderma polysporum	1989	wood rot
Protozoa		
Nosema locustae	1980	grasshoppers

A statement of policy on microbial products of biotechnology and non-indigenous microorganisms, was issued in the Federal Register in June, 1986. Microbial pesticides are distinguished from conventional chemical pesticides by their unique mode of action, their low-use volume, and target species specificity. Each new variety or strain of microbial pesticide must be evaluated and may be subject to additional data requirements. Genetically altered organisms used as pesticides will be subject to additional data on a case-by-case basis, depending on the organism, the parent organism, and the proposed use pattern. The EPA has reviewed 12 submissions of genetically modified microbial pesticides since 1984, 6 of which have been insecticides. The EPA is currently reviewing its policy of including non-indigenous organisms in the same category with genetically-altered microorganisms. This action would be welcomed by insect pathologists since the current policy hinders the introduction and evaluation of exotic entomopathogens that may have potential utility in inoculative releases for permanent biological control.

Microbial pesticides can play an important role in pest management systems either as a principal or supplementary control tactic. However, they are not a panacea and should not be considered as such. There is a need to promote foreign exploration for new and more virulent strains of entomopathogens that can be developed as microbial pesticides or used in inoculative releases to augment classical biological control.

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INTERACTIONS BETWEEN NUCLEAR POLYHEDROSIS VIRUS AND *NOSEMA* SP. INFECTING GYPSY MOTH

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ABSTRACT

Nuclear polyhedrosis virus (NPV) is the only entomopathogen that plays an important role in the natural regulation of North American gypsy moth populations. Recent European studies suggest that populations of gypsy moth in Eurasia are regulated primarily by the interactions between NPV and several species of microsporidia. Researchers have proposed that the introduction and permanent establishment of microsporidia into North American gypsy moth populations may reduce the frequency, duration, and severity of population fluctuations.

Microsporida are obligate, intracellular protozoan pathogens that typically cause chronic disease of many insect species. Their low virulence allows high persistence within populations. However, the coinfection of microsporidia and NPV in host tissues suggests the potential for interaction is high. The purpose of this study is to determine the nature of the interactions between NPV and a microsporidian species in the genus *Nosema.*

A reproducible bioassay procedure was developed to provide second-, third-, and fourth-instar larvae known doses of NPV and *Nosema* within a 24-h time period or less. Simultaneous, sequential, and separate pathogen treatments were performed at these larval stages.

The results of these studies show that NPV LD_{50}s were not affected by simultaneous, pre-existing, or subsequent infection by *Nosema.* NPV LT_{50}s were reduced significantly be the presence of *Nosema* infection. The pathogen interaction at the population level can be described as independent in terms of mortality and synergistic in terms of lethal time. However, quantification of infective units by each pathogen produced on a dry weight basis suggest that production of polyhedral inclusion bodies may be antagonized by pre-existing *Nosema* infections. This competition was positively correlated with *Nosema* dosage. This is being studied further using transmission electron microscopy. The short lethal time of NPV also antagonized *Nosema* pathogenesis by preventing the production of large numbers of mature spores in individuals with dual infections.

EVALUATION OF THE ABINGTON ISOLATE OF THE GYPSY MOTH NUCLEAR POLYHEDROSIS VIRUS AGAINST A FORMULATION OF GYPCHEK IN SMALL FIELD PLOTS

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ABSTRACT

The "Abington" isolate of the nuclear polyhedrosis virus (NPV) of the gypsy moth (*Lymantria dispar* L.) was compared with a formulation of Gypchek against a natural gypsy moth population in the Swallow Falls State Forest in Garrett County, MD. The materials were applied from the ground using hydraulic equipment to 1/100 ha (5-8 trees) plots. Thirty-five such plots were spaced at least 100 m apart along roads in forests with moderately high (500-2000 egg masses per ha), healthy (large egg masses) populations of gypsy moths. Each material was applied at three dosages: 2.5×10^{10}, 2.5×10^{11}, and 2.5×10^{12} polyhedral inclusion bodies (PIB's) per ha, each to five replicate blocks, and there were five untreated control blocks. Rhoplex B-60A sticker (Rohm and Haas, Philadelphia, PA) was added (2% vol./vol.). Twenty larvae were taken from each plot one day pretreatment and one, four, and seven days posttreatment. Larvae were returned to the laboratory and held, ten to a cup, until death or pupation. All dead larvae were examined by light microscopy and the cause of death was determined. The presence of PIB's in the cadavers was taken as evidence of death due to NPV.

Mortality from NPV (combined for the three posttreatment dates) indicated that the Abington isolate killed more larvae at all doses than the Gypchek formulation (36%, 38%, and 58% versus 13%, 17%, and 31%, respectively, low to high dose). Mortality from NPV in the control plots was less than 1%. Interpretation of these data is confounded by high levels of larval mortality due to spore-forming and nonspore-forming bacteria that affect the results in unknown ways.

GYPCHEK® USE PATTERN REALITIES

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ABSTRACT

Gypchek® is the gypsy moth *Baculovirus* product developed by the U.S. Forest Service and registered with the U.S. Environmental Protection Agency in 1978. It has since been reregistered (1988) as a minor use pesticide.

The product was originally intended as a gypsy moth suppression tool whose value would be maximized in those situations where environmental concerns precluded the use of either broad-spectrum chemical, or microbial, pesticides.

Recent refinements in formulation have improved product performance and Gypchek® is now viewed by many resource managers as a "substitute" for either *Bacillus thuringiensis* (Bt) or Dimilin products. Under certain conditions Gypchek® may be an adequate substitute, but the innate biological and physical characteristics of the present product, coupled with high costs associated with its production and application, must temper the urge towards "all-purpose" use.

Promising research with new virus strains and with formulations that provide enhanced foliar persistence, portends well for the eventual expansion of Gypchek's® use pattern. While awaiting this, resource managers can rely upon this "specialty" product, available in limited quantities, for use in situations where no environmental insults from broad-spectrum pesticides can be tolerated.

CURRENT RESEARCH EFFORTS WITH *BACILLUS THURINGIENSIS*

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ABSTRACT

The bioassay of 260 strains of *Bacillus thuringiensis* (Bt) and 70 commercial preparations show that regression coefficient estimates may be as critical as LC_{50} estimates when evaluating them for future consideration. Also most of the last group of 81 Bt strains present in the NRRL-HD culture collection, have been bioassayed. The results of this massive evaluation of all Bt strains available from such a large collection will be discussed. The proteins, coded from the cryIA(a), cryIA(b) and cryIA(c) genes of both the HD-1 and NRD-12 strains of Bt differ in their insecticidal activity against second instar gypsy moth. Finally, field efficacy of Bt appears to be optimized by use of high viscosity and specific gravity formulations applied at high dose and volume rates. Results of 1989 field studies indicate that a healthy and increasing pest population can be consistently reduced to less than 50 egg masses per acre.

SUMMARY OF THE BLACKMO 88 SPRAY EXPERIMENT

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ABSTRACT

The Blackmo 88 spray trial experiment was conducted for two primary purposes: To quantify the effects of local micrometeorological processes, in and near the canopy, on the deposition patterns of aerially applied BT in a mature oak forest; To generate a data set containing simultaneous measurements of spray deposition and detailed micrometeorology, in a canopy of known structure, that could be used to verify the FSCBG spray deposition and penetration model in oak forests.

The experiment was a cooperative venture between the Pesticides Research Lab at Penn State, the forest meteorology research project at UCONN, APHIS and the FPM AIPM project. The sampling and measurement of spray deposition patterns were conducted by the Penn State Lab personnel and the micrometeorology measurements were conducted by the UCONN personnel. Eighteen single swath runs were made with an APHIS ag-truck when the spray deposition and canopy penetration and the micrometeorological conditions were monitored.

The experiment was conducted in a fully leafed, 20 m tall, oak forest in the Black Moshannon State Forest near State College, PA. Canopy photographs during the 1988 experiment were used to calculate the leaf area density at that time. Then, during the following summer (1979) extensive follow-up measurements of vertical leaf area profiles were made. Data and preliminary results from the experiment are given in four other papers in this meeting. Verification analyses of the FSCBG model are now being conducted. The results of this experiment have led to plans for a similar follow-up experiment in the spring of 1990 shortly after leaf bud break, during the gypsy moth first instar. This second experiment will be aimed at determining the conditions necessary to deliver spray materials to the early spring understory vegetation.

GYPSY MOTH MANAGEMENT PROGRAM FOR MODERATELY SIZED URBAN PARKS AND OTHER WOODED PUBLIC LANDS

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ABSTRACT

Specialized gypsy moth (*Lymantria dispar* L.) management programs were developed for moderately sized, high-valued forested public lands. Intensive egg mass sampling, monitoring of aerial applications, and modified treatment thresholds were employed, and multiple applications of *Bacillus thuringiensis* (B.t.) were used where appropriate. The programs were implemented on five Maryland county parks and the Beltsville Agriculture Research Center. Larval mortality averaged 69, 86, and 93% under one B.t., two B.t., and diflubenzuron (Dimilin™) applications, respectively. No noticeable defoliation occurred in blocks treated with diflubenzuron or 2 B.t. applications, and defoliation was noticeable on less than 4% of the acreage treated once with B.t. A computer-based decision support system is being developed to facilitate technology transfer.

VERMONT MANAGEMENT IN FOCAL AREAS

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ABSTRACT

Following the 1979 outbreak of gypsy moths *Lymantria dispar* L. in Vermont, state personnel began monitoring a number of focal areas for signs of increase in gypsy moth populations. In 1986 data from this early warning system indicated an incipient outbreak. We took advantage of this increase to test an experimental management technique. Would disruption of increasing gypsy moth populations at focal sites forestall further expansion of those populations? Four foci were selected, and at each one four one kilometer transect lines were established; one in each cardinal direction, with a 7.5 m radius plot every 100 meters. To better understand and delineate population distribution we set up over 150 additional plots. *Bacillus thuringiensis* was applied to approximately 500 acres on two of the four sites in the spring of 1988. Egg mass and larval density surveys have been conducted at all sites since September, 1987.

Egg mass counts from the fall of 1988 showed that eradication of egg laying females from within the spray block at Brigham Hill was completely successful. Egg masses that remained in the site the year of treatment did not appear to serve as reservoirs for the 1989 population, though there was a unilateral increase in population density. No defoliation occurred at Brigham Hill, in contrast to Arrowhead Mtn., the accompanying check, which was 100% defoliated. Rocky Pond, the check in the central region, was also 100% defoliated, while Perch Pond, the treated area, only had spots of heavy defoliation. The egg mass density in the largest spray block at Perch Pond, which was most effectively contained by treatment in 1988, is now as high as the population at Rocky Pond. It remains to be seen whether the populations at both sites will collapse this coming year.

NPV and *Entomophaga maimaiga* have been positively identified from three of the focal areas used in this study. Incidence of disease was highest at Rocky Pond. Comparison of control and treated sites is continuing to determine the following; whether treatment prolongs the outbreak phase by temporally impeding epizootics, and whether increasing populations outside of a treated area will re-invade the original focal area. The research reported will clarify the significance of the focal area concept for management use, and will determine the value of disrupting gypsy moth outbreaks in susceptible forests before widespread outbreaks occur.

Data collected in the fall of 1988 indicated that two of the three spray blocks at Perch Pond had continued to increase in egg mass density, but the largest one was held to pre-spray population levels. This trend was reversed by the fall of 1989; the population in the largest spray block doubled, but declined in the other two.

SUMMARY OF EXPERIMENTAL RELEASES OF EXOTIC MICROSPORIDIA: CONCLUSIONS AND RECOMMENDATIONS

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ABSTRACT

During a 1985 European expedition, 5 species of microsporidia were obtained from gypsy moth collected in Portugal Czechoslovakia, and Bulgaria. From 1986-1989, we released all 5 species of these microsporidia into gypsy moth populations in isolated woodlots in Maryland. This presentation is a summary of the conclusions and recommendations based on the results of our experimental releases.

Nosema sp persisted in gypsy moth populations in the same woodlot for 3 years. *Vavraia* sp spread horizontally through the gypsy moth populations but did not persist from one season to the next. All three *Vairimorpha* species were slow to spread horizontally through gypsy moth populations and only persisted at very low levels from one season to the next.

Based on our experimental releases we have concluded that: 1) the egg mass method is suitable for introducing most species of gypsy moth microsporidia, 2) synchronizing the batch of contaminated and feral egg masses is critical, 3) the number of spores per egg mass is critical and is different for each species, and 4) *Nosema* sp from Portugal appears to be the most suitable biological control candidate.

Our research recommendations are: 1) conduct detailed taxonomic studies on all species of gypsy moth microsporidia, 2) obtain additional gypsy moth microsporidian isolates from Eurasia, 3) clarify the regulatory requirements for permanent establishment of exotic microsporidia, and 4) experimentally introduce gypsy moth microsporidia into high-density gypsy moth populations.

REGULATION OF DISPARLURE TITER IN GYPSY MOTH FEMALES: EFFECTS OF MATING AND SENESCENCE

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ABSTRACT

In the gypsy moth (*Lymantria dispar* L.), mating causes a decrease in the titer of the sex pheromone. This process appears to be regulated by a two step mechanism. A rapid, but transient, initial decrease is mediated by a mechanical signal associated with mating. A long term decrease in pheromone production is mediated by the presence of viable sperm in the spermatheca. Despite a prompt decrease in pheromone titer, mated females remain receptive and remate readily when courted by males. This receptivity is terminated when oviposition begins. Interestingly, all three aspects of mated behavior (i.e. decline in pheromone titer, oviposition and loss of sexual receptivity) were also observed to occur in senescing virgin females.

ISOLATION AND CHARACTERIZATION OF JUVENILE HORMONE ESTERASE FROM GYPSY MOTH (*LYMANTRIA DISPAR*).

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ABSTRACT

Insect metamorphosis is under precise hormonal control. During the last larval stadium, the degradation of juvenile hormone by juvenile hormone esterase (JHE) is essential for the initiation of pupation. Therefore, we have targeted this system for disruption with a strategy to produce a recombinant gypsy moth virus which expresses JHE. In order to clone and insert the JHE gene into the virus, purification of the enzyme, amino acid sequence information, and polyclonal antibody were needed.

Developmental analysis of JHE activity revealed a single major peak during the last larval stadium and another peak of JHE 3-5 days after pupation. JHE was purified from larval and pupal hemolymph by classical procedures. The specific activity of the purified enzyme approached 1000 units/mg. Gypsy moth JHE was found to have an apparent size of 62 kilodaltons, was insensitive to diisopropylphosphofluoridate, and was activated by polyethylene glycol. Partially purified enzyme displayed two closely-spaced bands on SDS PAGE. Polyclonal antiserum raised against the larval enzyme also reacted with the pupal JHE. This antiserum did not cross-react with hemolymph JHE from other Lepidoptera by western blot analysis. Two forms of JHE, JHE-A and JHE-B, were isolated by reverse-phase HPLC. Both appeared similar in size, had very similar amino acid compositions, were indistinguishable by HPLC tryptic peptide mapping, and had an identical N-terminal amino acid sequence. Since JHE-A and JHE-B are structurally very similar, these two forms may reflect minor differences in post-translational modification of the gypsy moth enzyme. Whether these forms differ with respect to their function remains to be determined.

Comparison of the gypsy moth enzyme with that from other Lepidoptera showed that they were antigenically distinct. In addition, the N-terminal and peptide amino acid sequences revealed marked differences in the structures of JHE from different Lepidoptera. Whether these enzymes also differ in their properties remains to be determined.

USING RESPIRATION RATES OF SINGLE EGGS TO DETERMINE GYPSY MOTH PRE-DIAPAUSE DEVELOPMENTAL RATES

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ABSTRACT

Gypsy moth (*Lymantria dispar* L.) egg phenology has been described as being comprised of three phases: pre-diapause morphological development, diapause, and post-diapause morphological development. Despite a large amount of published information on the temperature-time requirements of egg hatch there exists no robust model of the process(es) involved. This may be largely due to an inability to distinguish the phases of development (Rubstov 1938[1], Lyons and Lysyk 1988[2]). This inability has necessitated that the observed (dependent) variable in egg phenology studies be the temperature and duration of the final incubation period leading to egg hatch, despite the fact that treatments may have been applied to eggs in a diapause, pre-diapause, or post-diapause phase. Respiration rate has previously been unusable as a distinguishing characteristic due to the requirement of using hundreds of eggs in each measurement. This has prevented accurate estimation of temperature-time requirements for each phase, and obscured variability within the population.

This paper proposes a three phase model to describe gypsy moth egg phenology, and presents a novel technique for determining the temperature requirements of the pre-diapause phase, and preliminary estimates of population variability in those requirements.

Respiration rates of individual gypsy moth eggs were determined under temperature conditions ranging from 4°C to 38°C using an infrared gas analyzer. Among individuals of equal physiological age, temperature had a significant effect on respiration rate. Among individuals reared at constant temperatures, respiration rate was observed to increase with time and then decline rapidly to a steady rate of approximately 50% of each maximum. This rapid decline was interpreted as the completion of pre-diapause development.

A non-linear development rate curve was fit to the inverse of the median development time for each temperature. Population variability in pre-diapause temperature requirements was described by a three parameter Weibull function fit to the normalized development times.

This technique has the important ability to distinguish developmental phases on the basis of an accepted physiological parameter. Using appropriately designed experiments, this technique can be used to determine the uniqueness or commonality of the phases, the relationships between developmental phases, and the developmental rates of each unique phase.

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USE OF MOLECULAR PROBES TO DETECT PARASITES AND RETROTRANSPOSONS IN GYPSY MOTHS

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ABSTRACT

Retrotransposon screen: Gypsy moth families containing straggling and nonstraggling individuals were divided into categories of straggling, medium, and nonstraggling individuals, from which DNA was extracted. Four families were tested by southern hybridization and probing with ribosomal sequences designed to detect R1 and R2 retrotransposon insertions. Results showed no differences between stragglers and nonstragglers in the proportion of insertions in their ribosomal genes. The average proportion of insertions was 30%.

An initial screen from one family indicated that an amplification of ribosomal genes had occurred among stragglers; however, this was not observed in the other three families. It can be concluded that variable expression of R1 and R2 retrotransposons is not a likely cause of straggling in Gypsy Moths. Experiments were performed to test the effectiveness of the *Compsilura* total genomic probe for detecting parasitization in gypsy moths by that fly parasitoid. For one experiment, 3rd instar and 4th instar larvae were exposed to *Compsilura* females until stung. These were then shipped (1-2 days) to the Werren laboratory. Samples were divided into three groups. One was frozen immediately at -70 C, the second group developed on media for one day (25 C) prior to freezing, and the third group developed for two days. These were then individually homogenized and probed using radionucleotide labelled *Compsilura* total genomic DNA. Forty individuals were used in each group. Approximately 73% of third instar larvae yielded parasites and approximately 78% of 4th instar larvae yielded parasites. Most of these produced 1 parasite per larva, although multiple parasites did emerge in a few cases.

DNA probing results closely match rearing results for larvae which had fed for 1-2 days post stinging. However, there was a significant drop-off in detection of parasites in 3-4 day post stung larvae. There are two possible explanations for this drop-off. First, parasite larvae may be growing less rapidly than the gypsy moth larvae, resulting in a "dilution" of the parasite DNA below the level of sensitivity of the particular probe. A second explanation may be that shipping of samples caused some lethality of parasites within the hosts, and that decreasing detection with time represents degradation of parasite DNA.

So far, results are very promising that a simple molecular probe can be used to detect parasitization of gypsy moths. However, issues relating to sensitivity of the technique for detecting parasitization need to re resolved.

THE BACKCROSS STERILITY TECHNIQUE

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ABSTRACT

The sterile insect technique (SIT) and the induced inherited (F_1) sterility technique have been investigated for a number of lepidopterous pests, including the gypsy moths. Another technique, backcross sterility, which could potentially prove as or more useful for control of pest species has been developed for the control of only one lepidopteran species, *Heliothis virescens*. This genetic technique has several theoretical advantages over both SIT and the F_1 sterility techniques. In contrast to F_1 sterility, backcross sterility can persist indefinitely once introduced into a population. Because fertile females are continuously backcrossed to target males, the strain becomes increasingly genetically similar to the target species. The backcross strain should also be behaviorally similar to the target species and there are no radiation-induced effects on competitiveness.

Because of these potential benefits, approximately a year and a half ago we initiated a project to screen for backcross sterility with the gypsy moth and other closely-related lymantriid species. The first species we selected was *Lymantria obfuscata*, a species from India. To date we have hybridized *L. dispar* and *L. obfuscata* and are in the process of making the appropriate backcrosses. At this time, it is too early to determine the outcome of these particular crosses. We plan to continue to screen additional *Lymantria* species to determine if backcross sterility can be developed and applied as a technique for use in the management of gypsy moth populations.

OUTCROSSING COLONIES OF THE OTIS NEW JERSEY GYPSY MOTH STRAIN AND ITS EFFECT ON PROGENY DEVELOPMENT

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ABSTRACT

The Otis New Jersey gypsy moth (*Lymantria dispar* L.) strain is considered the "white rat" of gypsy moth research. This strain has been laboratory reared for 34 generations. It currently consist of 35 subcolonies or cohorts that have been genetically isolated from one another for several generations. Usually, larvae that hatch at the same time develop synchronously; however, in recent years this strain has been plagued by periods of asynchronous larval growth (straggling) and other performance abnormalities. These abnormalities are now collectively called *Abnormal Performance Syndrome* (APS).

It was hypothesized that APS may be caused by the intense inbreeding within subcolonies. During 1989, the Otis Rearing Facility made outcrosses between subcolonies placed into cold storage in adjacent weeks. The progeny from the outcrossed lines were compared to those of the pure bred lines to determine if outcrossing had any influence on the incidence of APS and/or survival in the G_1 generation.

APS was not detected in either the outcross or pure lines and therefore we could not determine if outcrossing would have had any effect on the incidence of APS in the G_1 generation. Parents used to produce these crosses had a high incidence of APS, indicating that APS is probably not caused by genetic factors but by environmental, nutritional and/or microbial factors that affect the parental generation but are not expressed until the G_1 generation, or affect the G_1 eggs shortly after they are deposited.

Outcrossing did not have any influence on survival of G_1 generation insects. Both the outcross and pure lines had greater than 90% pupation and adult emergence. This high survival rate also indicates that APS was not present in the G_1 generation.

PUPAL ABNORMALITIES AMONG LABORATORY-REARED GYPSY MOTHS

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ABSTRACT

Gypsy moth cohorts from 10 near-wild strains (one to six previous generations in culture), six wild strains (field-collected egg masses), and the standard "New Jersey" lab strain (34th and 35th generation in culture) were reared on Otis wheat germ-based artificial diet, in a constant environment. Rearings were begun with newly-hatched first instars; pupae were later collected daily, sexed, and weighed. Pupal lengths and maximum body widths were measured for some lab strain females. Collected pupae were classified as morphologically "normal" or as possessing at least one of seven types of morphological abnormalities, then reared individually to adult eclosion.

Less than 25% of near-wild, wild, and lab strain female pupae were classified as normal. "Banding" was the most common female abnormality; banded pupae possessed a light-colored, poorly-sclerotized cuticular band located ventrally between thorax and abdomen. Pupal abnormalities were infrequent among male pupae of all strains; most (>85%) were classified as normal. For both sexes, frequencies of occurrence for various pupal abnormalities varied little among strains.

Banded female pupae were significantly heavier, longer, and wider than normal female pupae. Normal pupae tended to experience longer larval stages, though mean larval development times for banded and normal pupae were not significantly different.

Pupal deformity patterns for lab-reared females were compared to those for feral and lab-strain females reared on oak foliage or artificial diet in an outdoor insectary. Most foliage-reared female pupae were normal; less than 5% exhibited banding compared to 70% or more of the lab-reared females. Diet-fed female pupae reared outdoors exhibited intermediate banding levels. Foliage-reared pupae were smaller, averaging ca. 1.22 g in weight, while lab-reared female pupae exhibited mean weights greater than 2.25 g. Thus, the occurrence of banding among female pupae appears associated with the larger sizes and, perhaps, more rapid development connected with artificial diet and laboratory rearing conditions. However, a direct abnormality-inducing role for the artificial diet or its constituents remains a possibility.

Banded female pupae successfully eclosed adults as frequently as normal pupae; only females with "gross abnormalities" yielded adult less successfully. Male pupae exhibiting morphological abnormalities produced adults less often than normal pupae. However, these reduced male eclosion rates are likely to have a minor impact, if any, because of the infrequent occurrence of malformed males.

Ongoing and future experiments will further quantify the impacts of pupal deformities on adult eclosion and egg mass production rates in the mass-rearing operation, and will address specific mechanism(s) responsible for the occurrence of pupal abnormalities.

VARIATION IN GYPSY MOTH, WITH COMPARISONS TO OTHER *LYMANTRIA* SPP.

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ABSTRACT

Specimens of gypsy moth, *Lymantria dispar* (L.) *sensu lato* were displayed in museum trays. Many specimens were quarantine laboratory reared during the 1989 season to provide samples (wing venation, frozen adults, prepupal haemolymph, larval feeding behavior, egg mass hair color, head capsule coloration and larval development) for various studies. Material reared was from HOKkaido, HONshu, and KYUshu, JAPAN; BEIjing, CHINA; Sibenik, YUGOSLAVIA; Queen Annes, MARYLAND (QAMD); and our standard BIRL culture. All (except HON) were individually reared (60 specimens each) in the first rearing using prepared diet. Varying numbers of additional specimens were reared on diet or *Betula* leaves in multiple larval containers. All were examined daily.

Specimens were used first to satisfy the various study needs. Remaining specimens were frozen and subsequently mounted. Reared adults illustrate the intraspecific variation present in L. dispar, sensu lato. Most striking was the HON strain with very dark brown males and females with a dark wash to the general color and unusual large size in both. Maximum male forewing length was 32 mm in HON compared to only 23 mm in QAMD. Maximum female wing length was 43, 41, 38, 32, 32, 29, and NA mm in HON, KYU, HOK, BEI, YUG, BIRL and QAMD respectively (flight impossible in the latter three). Ability for flight was demonstrated in gravid females for HON, HOK and BEI but not in YUG. Morphological comparisons between these two functionally polymorphic forms illustrated the degree of wing reduction in the non-flying forms. HON pupae weighed nearly twice as much as the representative North American forms since maximum female pupal weight was 5.43 g for HON but only 2.47 g in QAMD. Maximum egg production in the three largest HON females was 1550, 1482, and 1375 eggs while the maximum was 1028 eggs per QAMD female. Two black-backed larval mutants appeared in YUG samples. In summary, size (expressed either as forewing length, pupal weight or female egg production), body color, and female flight capability clearly differed among the samples reared. As we will repeat these rearings in 1990, and we intend to incorporate several Russian samples, we expect to see even more evidence of intraspecific variation in gypsy moth.

Specimens of congeneric species, *mathura* Moore, *monacha* L., and *sakaguchi* Matsumaura (all from Japan) and *atemeles* Collenette (Thailand) were displayed to illustrate the similarities of these species to *dispar*. These permitted a comparison of the differences between intraspecific and interspecific variation.

A MONITORING SYSTEM FOR GYPSY MOTH MANAGEMENT

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ABSTRACT

Within the last ten years considerable research has been directed toward the development of a gypsy moth monitoring system for project planning at a regional level and for making control decisions at a local level. Pheromones and pheromone-baited traps have been developed and widely used and several egg mass sampling techniques have also been developed. Recently these sampling techniques have been combined into a pheromone trap-based monitoring system which uses pheromone trap results to assist in prioritizing areas to received egg mass samples. This approach has also made extensive use of graphical presentations using geographic information systems. This paper describes the status of monitoring tools and systems for determining gypsy moth densities for management purposes and areas in need of continued research.

INTRODUCTION

As late as 1984, major management units (states or areas of similar geographic scale) in the United States used a wide variety of methods for making gypsy moth control decisions. These methods focused primarily on egg mass sampling using an underlying assumption that egg mass density is related to defoliation in the subsequent larval generation (Ravlin et al. 1987). Several studies have found a significant relationship between egg mass density and defoliation (Gansner et al. 1985, Wilson and Talerico 1981, Montgomery in press). However, the question of how to arrive at precise and/or accurate estimates of egg mass density for management purposes within the constraints of pest management programs has only begun to be explored. Questions related to when in the gypsy moth population cycle to begin egg mass sampling, how many samples to collect, how to spatially distribute those samples, and how to present the results from these samples to determine treatment areas have also been only recently been addressed. The objective of this paper is to present developments in sampling and monitoring technology and how they have or have not addressed these questions.

THE BASIS FOR MAKING CONTROL DECISIONS

The Relationship Between Egg Mass Density and Defoliation

The basis for control decisions in gypsy moth management programs is an assumed relationship between egg mass density and defoliation. The question is whether or not a given level of defoliation will occur as a result of the subsequent larval population. Consequently, it is necessary to only specify whether or not to treat based on a threshold egg mass density. The earliest thresholds mentioned in the literature were published in "The Comprehensive Gypsy Moth Management System" study where Etter discusses 250, and 1,000 egg masses per acre as possible action thresholds (Appendix K-9, National Gypsy Moth Management Board 1979). These thresholds have continued to be used by most gypsy moth management programs through the 1980's (Ravlin et al. 1987) even though there are no studies which provide economic or biological reasons for their use. Nevertheless, they have provided managers with a decision criterion.

Egg Mass Density Estimates

In 1981 the so-called "compendium" (Doane and McManus 1981) was produced and with it came a wealth of information for researchers and managers. The title "Research Toward Integrated Pest Management" was very appropriate because it was clear that many components of an IPM system were ready for implementation or were being used but a functional "system" had not been delivered to the manager community. Monitoring tools such as pheromone-baited traps, hazard rating models, knowledge of gypsy moth population cycles, and chemical and microbial controls were available for use on a day-to-day basis. The concept of how these components might be integrated was also presented but it was still clear that one of the weak links in the chain of management activities was an approach to predict the amount and spatial extent of defoliation based on egg mass density. Wilson and Fontaine (1978) developed the fixed- and variable-radius sampling method that could generate egg mass densities with any desired level of precision, given infinite resources, and this method was promoted throughout both the research and management communities. It became clear that the fixed- and variable-radius method was not suitable for most management situations because of their time-intensive nature and limited spatial coverage. In 1983 Eggen and Abrahamson devised a method which simply required field personnel to walk through areas of interest for five minutes, count all egg masses, and then relate the counts to absolute egg mass densities using regression models. However, Eggen and Abrahamson state that "More accurate surveys must be conducted when densities are at or near egg mass treatment thresholds". In other words, the technique is useful for gross categorization of populations and not a precise sampling tool. There are several variables that contribute to variability in density estimates based on five-minute walks. Bellinger et al. (1989) showed that the distribution of gypsy moth egg masses is affected by proximity to an "edge". Here edge is defined as the change from one habitat to another, such as where roads are cut through continuously forested areas or pastures. In the Bellinger et al. study an edge effect was so prevalent that significant differences occurred between the "edge side" of trees and the "forest side" of trees. Depending on the side of the tree that one walked by, different egg mass density estimates would be obtained using the timed walk method. In a study done by Fleischer et al. (unpublished manuscript) the timed walk method was compared to 1/40 acre fixed radius plots. Analysis of variance of these data showed that significant amounts of variability could be attributed to location, habitat, the agency responsible for taking the data, and the individual taking the samples. Thus, the five minute timed walk method does not produce consistent egg mass density estimates and cannot be relied upon for treatment decisions.

In an effort to simplify and reduce the time spent taking fixed- and variable-radius plot samples for the Maryland Gypsy Moth IPM Pilot Project Kolodny-Hirsch (1986) compared fixed- and variable-radius plot sampling (Wilson and Fontaine 1978) with fixed-radius plots. His findings were that 1/40 acre fixed-radius plots far exceeded the other methods tested in terms of relative net precision[1]. Using 1/40 acre sampling as the sample unit, Kolodny-Hirsch developed a sequential egg mass sampling protocol for making treatment decisions, although implementation and validation data were not presented. Sequential sampling protocols are dependent on the underlying statistical distribution (e.g., poison, negative binomial) of data used to develop protocols and the amount of error that decision makers are willing to accept. Statistical distributions of gypsy moth egg mass samples are a result of the number and physical size of a sample unit and the spatial pattern of egg masses which, in turn, is dependent on habitat. Kolodny-Hirsch used randomly distributed 1/40 acre samples taken from 14 oak/sweetgum woodlots in urban/suburban Maryland. These woodlots were in flat terrain and had not experienced outbreak gypsy moth populations. Thus, it cannot be assumed that factors affecting the underlying egg mass distribution will stay constant for other types of populations, habitats, and terrain. Making this assumption, Fleischer et al. (unpublished manuscript) developed sequential sampling protocols from several data sets

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[1] Relative net precision (RNP) is defined by: $RNP = [1/(C_s)(RV)]100)$ and relative variation (RV) is defined as $RV = (SE/x)100$ (Pedigo et al. 1972).

collected in northwestern Virginia in continuously wooded areas. This resulted in the development and validation of four sequential sampling protocols used in the Appalachian Gypsy Moth Integrated Pest Management demonstration project (AIPM).

USE OF PHEROMONE-BAITED TRAPS TO PRIORITIZE AREAS FOR EGG MASS SAMPLING

The Moths per Trap Model

Egg mass sampling is expensive and methods for prioritizing areas to receive egg mass samples are essential to working within budgetary constraints. There are no universal methods for prioritizing areas and research conducted during the last five years has sought to address this problem through the use of pheromone-baited traps for male gypsy moths. Pheromone-baited traps have been universally used in gypsy moth detection, eradication, and management programs in the United States (Ravlin et al. 1987). However, decision-makers have not had models that relate pheromone trap results (moths per trap) with the density of other gypsy moth life-stages, particularly egg masses. Thus, management programs are forced to expend more of their resources on expensive egg mass sampling without the benefit of using pheromone trap results to assist in the process of prioritizing areas to receive egg mass samples.

For gypsy moth management programs it would be useful if the number of pheromone trap-captured moths could be used to estimate one or more of the following parameters: egg mass density, egg density, the probability of occurrence of an unacceptably high population (i.e., exceeding a treatment threshold), or be used to trigger and target egg mass sampling for more precise population estimates. Regression techniques for determining if a relationship exists between moths per trap and egg mass density have been described for the Douglas-fir tussock moth (Daterman 1978, Shepherd et al. 1985) and the spruce budworm (Allen et al. 1986). Regressions have been performed on gypsy moth data taken from the Maryland Integrated Pest Management Pilot project, Shenandoah National Park, and plots distributed throughout Virginia. In all cases there are significant regressions between moths per trap and egg mass density. But, like the tussock moth and budworm, there were differences between locations and years with the proportion of variability explained ranging from 30 to 80%. While there is some utility in these relationships, data from Massachusetts do not always support them (Elkinton, 1987). Reasons for this are not known. Many factors affect the dynamics of pheromone trap/moth interactions and the relationship between trap catch and egg mass density. Male moth dispersal and behavior are particularly important. More importantly, because male moths move away from the location from which they emerged it is not reasonable to assume that there will always be a good relationship between moths and egg masses when data are taken from a single location. Developing relationships over larger areas (e.g., a radius 250-500 m) may provide more insight into this problem. Another approach to this problem is to stratify egg mass and moth data into density categories and determine the probability of exceeding different egg mass densities (Table 1). This approach has the advantage of providing managers with a measure of risk and alleviates the need to project egg mass densities given moth counts.

Table 1. Probability of exceeding a given egg mass density based on the number of moths captured in a pheromone-baited trap.

	Moths Captured per Trap		
Egg Masses / Acre	0 - 500	501 - 1000	>1000
0 - 250	0.88	0.40	0.10
251 - 500	0.00	0.20	0.05
501 - 1000	0.00	0.10	0.25
>1000	0.12	0.30	0.60

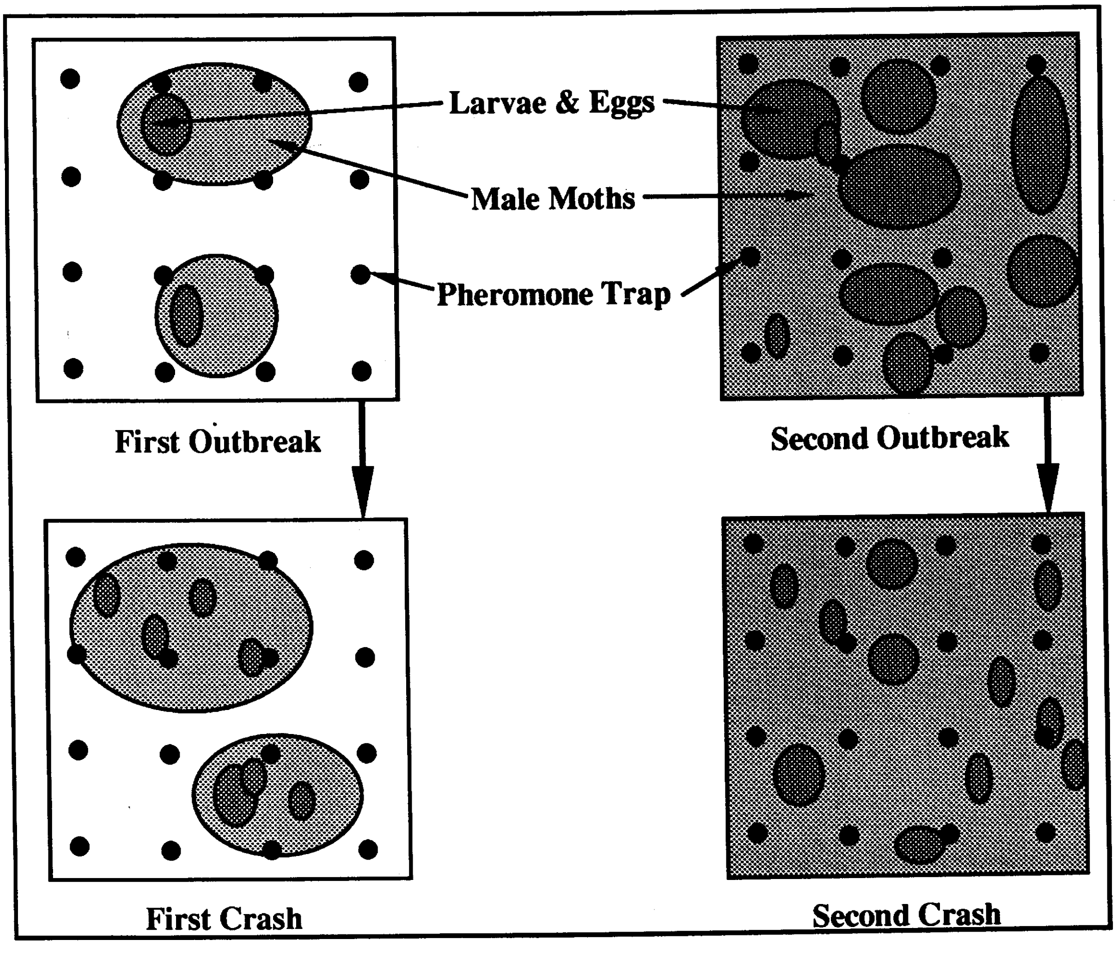

Figure 1. Hypothetical spatial pattern of eggs, larvae and male moths during and after the first two outbreak episodes in a leading edge area.

Other factors contribute to variability in the egg mass density-moths per trap relationship. Elkinton (1987) has shown that the standard gypsy moth milk carton-type pheromone trap decreases in efficiency after about 400 moths have been captured (i.e., increasing numbers of moths enter but subsequently leave traps). Also, traps that have accumulated water often contain rotten moths and presumably, volatiles from these rotting moths can decrease trap efficiency independent of the number of moths caught. Finally, it is not uncommon in the northeastern states (e.g., Massachusetts) to completely fill pheromone traps with male moths and yet fail to find egg masses or other life-stages in the immediate vicinity of the trap (Elkinton 1987). It may well be that the dynamics and/or spatial distribution of populations may contribute to this discrepancy. In theory, when populations first invade new areas their distribution tends to be highly aggregated (Fig. 1, top left) and it is not until after one or more outbreaks (defoliation episodes) that isolated populations begin to coalesce and become more generally distributed (Fig. 1, bottom left). The result would be male moths emanating from several sources creating a "cloud of moths" over the entire area even when other life-stages are highly aggregated and at low density (Fig. 1, right top and bottom).

The Male Wing Length Model

Use of a density index independent of the number of pheromone trap-captured moths would, in part, circumvent some of the problems listed above. Leonard (1968) reported that there was a relationship between body size and density of the gypsy moth and Hinckley (1970) suggested that male moth size, as measured by wing length, varied inversely with the level of defoliation. It follows that egg mass density should be directly related to larval density however, the relationship between defoliation and larval density is less direct. Wilson and Talerico (1981) and Gansner et al. (1985) found a relationship between egg mass density and defoliation, but there is significant variability in these relationships presumably due to population, site characteristics, and sample method. Despite the tenuous nature of these relationships we might expect to find a correlation between male moth size and population fecundity (eggs per unit area) based on the assumption that density dependent stress and defoliation will produce populations of smaller individuals. In 1984, field observations in the Shenandoah National Park indicated that the size of male gypsy moths and egg mass density were correlated and that some measurement of male moths might be used as an index of egg mass density and eggs per mass. We began a study to examine the relationship between male moth wing length and other population parameters. Data were collected in the Shenandoah National Park in Virginia and throughout Maryland. Male wing length and eggs per mass were correlated (r = .70) and wing length and egg mass density were also well correlated (r = .72) (Bellinger et al. in press). Additional research has found that moths falling into the smallest size classes may be produced only after larvae experience a defoliation episode (> 40% defoliation). The relative frequencies of small (< 19 mm) and large (> 19 mm) moths may then predict an egg mass density category but not necessarily an absolute density estimate (Carter et al. unpublished manuscript)

INTEGRATION OF PHEROMONE-BAITED TRAPS AND EGG MASS SAMPLING

Figure 2 describes how pheromone trap results and egg mass sampling can be combined with other variables to determine areas requiring more intensive sampling. The basis for this system is an area-wide grid of pheromone traps, the results of which, serve as a trigger for initiating egg mass sampling at the local level. Research into methods for delimiting egg mass sample blocks and treatment blocks has been conducted primarily through AIPM methods development and has been described by Fleischer et al. (these proceedings);. Geographic information systems play an essential role in the spatial representation of male moth data, egg mass distributions, and subsequent treatment areas. Using the results of male moth surveys to determine egg mass sample areas requires that point data from pheromone traps be converted to a continuous surface and lines of constant moth density (contours) determined. For the AIPM project, this was done using the ARC/INFO geographic information system. At this point a male moth threshold for egg mass sampling was determined by managers based on the probability of exceeding an egg mass treatment threshold (Table 1) and the risk associated with not sampling (treating) a location. Following the selection of a male moth threshold and generation of contours, a 1 km grid was overlaid on areas to be managed and all 1 km grid cells that were intersected by a contour line greater than or equal to the moth threshold were candidates for egg mass sampling. Other factors that influence the selection of areas for egg mass sampling are last year's egg mass density, population trend (previous moths/current moths), susceptibility, accessibility of sites for sampling, and political and economic considerations. All of these factors can be combined using a geographic information system to produce a composite map used in conjunction with USGS topographic maps and other relevant information (Fig. 3).

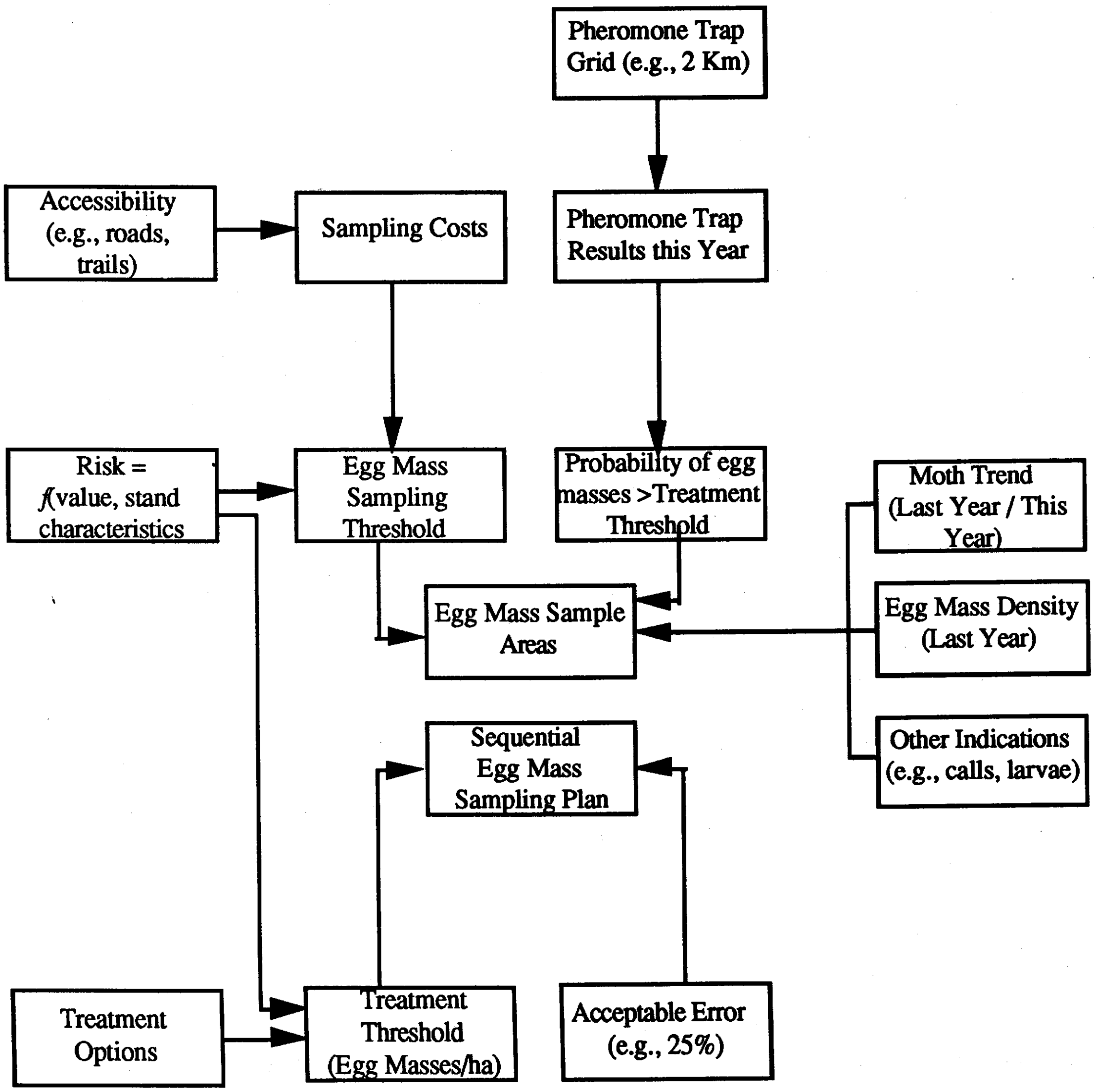

Figure 2. Sequence of events and flow of information to determine the location and number of egg mass samples to be taken for a given geographic area (figure by L. Schaub).

Once an area has been targeted for sampling, sequential egg mass sampling schemes can be generated based on treatment thresholds and sampling error selected by managers. Treatment thresholds should be determined on the basis of expected levels of defoliation (e.g., Montgomery in press) and the efficacy and cost of treatment options (e.g., diflubenzuron vs *Bacillus thuringiensis* (Berliner)). Methods for implementation of sequential egg mass sampling schemes are described in Rutherford and Fleischer (1989). Treatment blocks can then be delimited based on egg mass density, landscape features, and management objectives. For AIPM this threshold was 200 moths in 1988 and 500 in 1989. Results of egg mass surveys can be analyzed similar to pheromone trap results to produce treatment blocks.

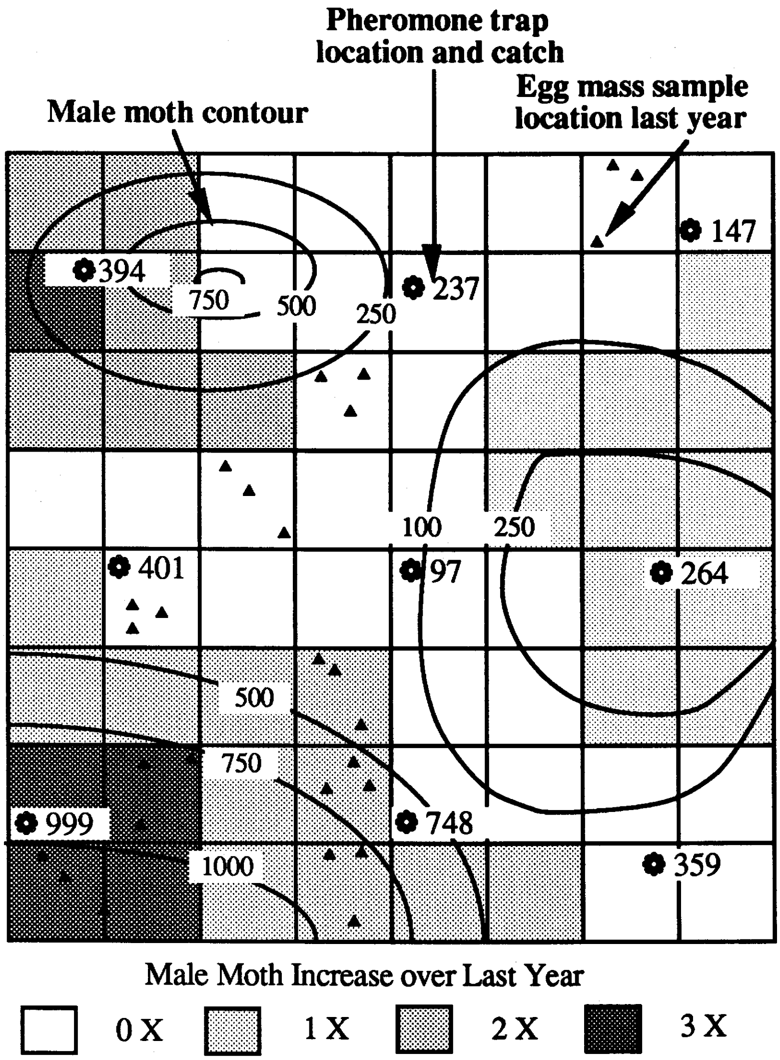

Figure 3. Map used for determining egg mass sample areas in the Appalachian Gypsy Moth Integrated Pest Management demonstration project.

SUMMARY AND CONCLUSIONS

Several problems remain in the development of gypsy moth monitoring systems. As yet, the pheromone trap-based system described above can be used only in areas which are not generally infested (i.e., at or in front of the leading edge). Problems with trap saturation and lack of a reliable moth-to-egg mass relationship prohibits its use in northern Virginia and areas to the north and east. We now have a sequential egg mass sampling scheme that has been field tested and appears to produce the best results to date, but cost remains a constraint to sampling large geographic areas. Systems to access land-use and habitat-related variables could reduce the number and size of areas requiring egg mass sampling. Thus, the cost of this approach would also be reduced. Alternative egg mass sampling approaches need to be developed. These approaches may include stem counts which relate the proportion of stems with egg masses to the probability of exceeding treatment thresholds. This approach would satisfy the need to cover large areas of land and provide decision makers with an estimate of the risk associated with not treating a given area. Stratified sampling in residential situations may also provide risk and density estimates while reducing the cost of intensive searches around houses and man made objects. Burlap bands placed around trees to collect larvae, pupae, and egg masses may also generate useful information.

No matter what type of systems are developed, they must be evaluated in a variety of management situations including leading edge populations and generally infested areas with endemic and increasing populations. The idea that only one monitoring system needs to be developed must be challenged. Yet, standardized protocols need to be put in place to allow good interpretation of data and a wide area perspective of data collected from adjoining geographic regions. One approach may be useful in generally infested areas but may not be appropriate for leading edge populations or data may not lend themselves to spatial presentations essential to making good treatment decisions over large land areas. Evaluation criteria for monitoring systems must include accuracy and precision of population estimates, ease of use, and cost effectiveness. The entire process of data collection, data base management, and data presentation must also be considered before making global sampling recommendations to the gypsy moth manager community.

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HISTORY OF RESEARCH ON MODELLING GYPSY MOTH POPULATION ECOLOGY

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ABSTRACT

History of research to develop models of gypsy moth population dynamics and some related studies are described. Empirical regression-based models are reviewed, and then the more comprehensive process models are discussed. Current model- related research efforts are introduced.

Software that models the life system of gypsy moth (*Lymantria dispar* L.) is described. The gypsy moth life system model (GMLSM) is designed to simulate the dynamics and interactions of gypsy moth, its hosts and natural enemies, in a forest stand over a number of years, with or without human intervention. Working hypotheses of gypsy moth researchers can be synthesized. The purpose and objectives of model construction, the history of model development, model structure and subsystems, and plans for testing and additional developments are described.

INTRODUCTION

The range and extent of damage by gypsy moth, *Lymantria dispar* L., in North America have been increasing since 1869 when it was imported and inadvertently released in the Boston area. The gypsy moth has nearly reached its northern limits but is continuing to spread west and south. It has been suggested that the gypsy moth may find suitable habitat farther north as it continues to move west. The insect is a naturally occurring pest in Eurasia. With its spread in North America, research and attempts to control the gypsy moth have expanded and intensified, and more recently, increased emphasis has been placed on mitigating the effects of this pest.

The U.S. Department of Agriculture initiated accelerated and expanded funding of gypsy moth research in the 1970's. Much of this work is summarized in *The gypsy moth: research toward integrated pest management* (Doane and McManus 1981). Since that time, the Gypsy Moth Research and Development Program in the Northeastern Forest Experiment Station has been one of the leaders in organizing and supporting research on this insect.

Researchers have applied the modelling approach to understand many facets or components of the gypsy moth-mixed hardwood ecosystem. Here, I review the history of gypsy moth population modelling research; describe the gypsy moth life system model (GMLSM), and discuss plans for development and testing of the GMLSM and related models.

HISTORY OF MODELLING RESEARCH

Sheehan (1989) published a review of most of the currently available literature on models dealing with gypsy moth in North America. In a recent article, Elkinton and Liebhold (1990) described a few of these models and discussed factors that should be considered in models of specific portions of the life system, such as phenology.

Sheehan (1989) partitioned her review into two major sections: the first covers models dealing with specific components such as fecundity or mortality sources, and the second covers those whole-population models that deal with year-to-year changes in population numbers, and primary factors that determine density or trend. She further partitioned her review of population models into the regression-based empirical models and process-based system models. I will concentrate on whole-population models and discuss some of the work on component models that I believe to be particularly significant to overall population ecology.

Regression-based empirical models

These models predict the number or proportional change in number of gypsy moth from year to year based on statistical methods such as correlation or regression. They are used to ascertain the relationship between population parameters and other relevant factors, but not necessarily in ways that directly describe the biological processes that give rise to the relationships. Such models specify independent variables such as past temperature or precipitation regimes, previous gypsy moth density, forest type or forest condition. These models assume that all remaining influences on the dependent variable can be and are absorbed into a normally distributed error term about the model.

There have been a number of models developed that predict trend, egg density, or egg-mass density. Using data from the Melrose Highlands and the Forest Service's Intensive Plot System, Campbell and Sloan (1978a) used multiple regression to fit log transforms of annual trend to a polynomial of log transforms of prior egg density and the coefficient of variation of the log transform of egg density. In a second regression model they fit log transform of egg-mass density to precipitation in June, log transform of prior year's egg-mass density, and the square of the coefficient of variation of the log transform of prior egg-mass density. Later they published (Campbell and Sloan 1978b) additional linear regression models fitting log(annual trend) to the cube of the log transform of egg-mass density.

Earlier, Campbell (1967, 1973a) produced three equally complex polynomial models for predicting trend or density. Biging et al. (1980) developed a regression model using log transformed data from the Melrose Highlands (Campbell 1973b), predicting plot egg-mass density from 3 prior year's egg-mass density and 2 prior year's temperature and precipitation. They applied the model to Wisconsin forests using weather data from that state and found that there is potential for maintaining gypsy moth populations throughout the entire state for protracted periods of time. To predict egg density, Znamienski and Liamcev (1983) used the proportion of oaks in the stand; average temperatures for May-August and July-August, minimum temperature for May and its departure from an average for the prior 10 years; egg-mass density, eggs/mass, and egg weight for the previous generation. Three sets of stand data were tested separately and a final model, where egg weight was not included in the model, was developed using all stands.

Only one developed by Campbell and Sloan (1978b) and those developed by Znamienski and Liamcev (1983) have been tested, and only the latter was tested successfully on independent data.

There are generally three problems with models such as these that are based on correlation rather than on the underlying biological principles or mechanisms that give rise to the behavior that is exhibited. First, to provide confidence in predictions, large data sets are required to build such models; second, models of this type rarely apply well outside the range of data on which they were built; and third, indicator variables chosen as independent variables for analyses may not always correlate with processes that give rise to the variability being analyzed. Campbell and Sloan (1978a) describe one such problem as follows: "...intrapopulation influences on the dynamics of gypsy moth populations probably include occasional switches in key factors over time...Specifically, we infer from these results that neither multiple regression models such as those in Campbell (1973a) nor any other models can possibly provide accurate projections of the natural maintenance of area wide gypsy moth outbreaks unless these intrapopulation phenomena are accounted for."

Problems can be overcome and additional valuable information can result from follow-up studies. For example, existing relations can be tested or strengthened by collecting additional data in other years or at new sites. Models can be extended to include additional variables. This often requires recollecting initial data and can be expensive. Again, Campbell and Sloan (1978b) state: "We infer from these differences [between areas] that one or more of the truly major mortality (or natality) factors that govern this life system may differ substantially from one area to another or from one time to the next." While Campbell and his coauthors have provided many extremely valuable results, too often people attempt to apply such results without heeding the caveats.

It should be noted that many of the same procedures that produce empirical models are used in the development of process models.

Process simulation models

Process models are designed to synthesize biological hypotheses and to provide a means to understand their interactions. Such models are not meant to predict exact futures, but may elucidate relationships and provide a holistic understanding by integrating many hypotheses. I will briefly review six published process models.

Picardi's (1973) model was designed to investigate management policy associated with gypsy moth population dynamics. Pheromone control and pheromone in combination with insecticide at high densities were proposed. He did not specify a particular spatial resolution and no stand model was developed BUT the basis for population density was on a "per available oak leaf surface area" that included production and death rates for this substrate. It did have a well-developed population dynamics section that included stage specific mortality from predators, parasites, and disease, as well as the effects of management actions.

Morse and Simmons (1979) developed a model to examine possible results of management actions taken against colonizing populations in Michigan forest. The purpose of this model was to describe year-to-year forest/gypsy moth interactions and the effect of gypsy moth on forest growth and mortality, and to examine control policies and propose alternatives to an eradication policy. Large tracts of land are represented by average units of 1 square mile. Each unit is simulated as a product of terms: number stems/unit, average tree diameter, ratio of host/non-host, average foliage per tree of the given diameter. A single tree growth equation was combined with mortality based on three site classes and three classes of defoliation. Gypsy moth population dynamics were constructed from three life stage mortality rates with three additional random number multipliers. Additional virus mortality resulted when population density was sufficiently high for 2 or more years. No results of inter-site spatial patterns or interactions were reported.

Valentine (1981) designed a model to assess the influence of gypsy moth on an even-aged oak forest stand. The dynamics of a number of individual trees were simulated through difference and differential equations. Gypsy moth and foliage dynamics were built in continuous, differential equation models within each year on each tree. This model was given the most thorough sensitivity analysis but only limited calibration tests. Only one host species, red oak, was used in the sensitivity analysis.

Etter (1981) developed simulation models for use in development and analysis of a comprehensive gypsy moth management system. Two differential equation models were designed to show interactions of gypsy moth density with NPV in a policy analysis setting. He does not include stand or natural enemies except for a uniform foliage growth equation and fixed mortality rates for all factors other than NPV. In the discussion of the more complex model that is not actually presented, he describes expanding the 15 equation model to 130 equations by partitioning a population by sex and life stage, and by adding more detailed accounting of NPV and non-NPV mortality rates and feedbacks.

Brown et al. (1983) used two simulation models to examine the effects of *Ooencyrtus kuvanae* (Howard) parasitism on gypsy moth populations. A discrete model of gypsy moth populations and an extension of Picardi's model with modifications were developed. They analyzed simulation results and compared outputs to field data. The study is the most comprehensive in terms of modelling the biological processes of the gypsy moth life system. They include mortality factor formulations, using functional, numerical, and density dependent relationships. They compared simulation results to two field data sets using ANOVA to obtain measures of effectiveness of *Ooencyrtus* mortality. No foliage or stand interactions were modeled or discussed in this publication.

Byrne et al. (1987) developed a model that was built around Johnson's (1977) model of forest succession in the North Carolina Piedmont. The objective was to determine the effects of gypsy moth outbreaks on forest succession and to evaluate the sensitivity of forest management practices. Their conclusions were made relative to managed or natural succession on the Piedmont. Using the distribution of 12 forest types described by Johnson, Byrne et al. refined the stand development stage distribution of each type. The 12 forest types were then grouped into three food preference categories. Gypsy moth larvae were classified as either small (L_1-L_3) or large (L_4-L_6) with no distinction of sex until pupation. Feeding was considered only for large larvae; daily mortality rates were fixed along with dispersal mortality rates. They did not model any spatial or multi-year temporal dynamics but uniformly projected a single outbreak population pattern for each food preference group for the entire Piedmont.

CURRENT POPULATION MODELING RESEARCH

There are a number of model-related studies being pursued at present. Mike Foster at The Pennsylvania State University is working on the NPV virus-pathogenicity-interactions with host foliage phenolics as exhibited in gypsy moth feeding, infection, and mortality rates. The landscape ecology of gypsy moth in the northeastern United Sates and southeastern Canada is being studied by Andrew Liebhold and Joel Halverson of the USDA Forest Service, in cooperation with Gregory Elmes and Jay Hutchinson of West Virginia University, in an attempt to understand the large-scale spatial and temporal dynamics of gypsy moth populations. Jesse Logan and David Gray of Virginia Polytechnic Institute and State University are developing a three-phase temperature-dependent model of gypsy moth egg phenology that utilizes temperature thresholds and thermal requirements specific for each of the three phases, and includes possible developmental constraints imposed by a preceding phase. Joseph Russo and John Kelly of Zedx Inc. and Andrew Liebhold of the Forest Service are developing a mesoscale landscape model of gypsy moth phenology by using high-resolution climatological data and the Gypsy Moth Phenology Model (GMPHEN) (Sheehan[1]) within a geographic information system to produce high spatial resolution of the average gypsy moth development for selected days in the northeastern United States.

Modelling of a very different sort is being done by Mark Twery of the USDA Forest Service, Mike Saunders and Mike Foster of The Pennsylvania State University, Bill Ravlin and Jesse Logan of

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[1] Sheehan, Katharine A. GMPHEN: a gypsy moth phenology model. 52 p. Unpublished manuscript.
Sheehan, Katharine A. User's guide for GMPHEN: a gypsy moth phenology model. 38 p. Unpublished manuscript.

Virginia Polytechnic Institute and State University, and Gregory Elmes and Charles Yuill of West Virginia University. They are developing the Gypsy Moth Expert System (GypsES). A full section of these proceedings is devoted to this topic. This system will have models imbedded within it and there are plans to allow communication between the expert system and other models, particularly the GMLSM and the Stand Damage component of the GMLSM.

The stand damage subsystem can be executed independent of the rest of the GMLSM when defoliation in a stand is known or assumed. In Morgantown, we are also working on development of synoptic models that will capture the major features of the gypsy moth life system in a compact form that can be more readily explored for asymptotic behavior and stability. This work is being carried out in cooperation with Dr. Xu Rumei of Beijing Normal University, Peoples Republic of China (currently a visiting scientist at West Virginia University).

GYPSY MOTH LIFE SYSTEM MODEL

As discussed above, a number of models have been constructed to simulate various aspects of the population dynamics of the gypsy moth in North America (Elkinton and Liebhold 1990, Sheehan 1989). Each of the simulation models described by Sheehan was designed to investigate a specific set of circumstances and specific management implications. The gypsy GMLSM was designed to capture, as much as possible, all of the current hypotheses related to gypsy moth population dynamics, its natural enemies, and its host trees, representing a gypsy moth susceptible stand as the basic ecological unit. As a stand-based model, there are phenomena that will not be addressable using this model.

In 1983, the Gypsy Moth Research and Development Program sponsored a series of workshops to begin development of a model system that would provide a comprehensive framework for research development, synthesis, and testing. This initial development relied heavily on prior research (Doane and McManus 1981, Campbell et al. 1978). The GMLSM development was initiated under contract with ESSA Adaptive Environmental Assessments Inc.[1] Three workshops were scheduled to gather a variety of experts on the gypsy moth and related topics and to gather advice on the ecological system. This version of the model was turned over to the Forest Service late in 1983. Between then and now the model has undergone extensive revisions and considerable extensions in complexity and scope. We are now completing the final revisions and initial tests of the model.

Recent work has relied heavily on published literature (e.g., Elkinton and Liebhold 1990, Fosbroke and Hicks 1987) and on the cooperation of many individual researchers of state and federal agencies in and near currently infested areas (e.g., Smith 1989). Agencies and institutions cooperating in the construction of the Gypsy Moth Life System Model are:

- United States Department of Agriculture
  - Forest Service
    - Northeastern Forest Experiment Station
    - Appalachian IPM Gypsy Moth Demonstration Project
    - Northeastern Area Forest Pest Management

  - Agricultural Research Service
    - Beneficial Insects Research Laboratory

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[1] McNamee, P.J.; Bunnell, P.; Jones, M.L.; Marmorek, D.R. 1983. Final report of a project to identify and evaluate important research questions for the gypsy moth life system, August, 1983. Unpublished report on file at USDA Forest Service, RWU-4507, PO Box 4360, Morgantown, WV 26505. 182 p.

Animal and Plant Health Inspection Service
Otis Methods Development Center

Institutions
Connecticut Agriculture Experiment Station
Dartmouth College
Hammermill Paper Company
Illinois Department of Energy & Natural Resources
New Jersey Department of Agriculture
North Carolina Department of Agriculture
Pennsylvania Bureau of Forestry
Pennsylvania State University
State University of New York
University of Connecticut
University of Massachusetts
University of Rhode Island
University of New Hampshire
West Virginia Department of Agriculture
West Virginia University

Background

Initially, the purpose of this modeling effort was to serve as a research planning tool that could later be extended and expanded into a facility for research entomologists, foresters, and economists. With the model, investigators could test and develop working hypotheses, and evaluate means for developing management-oriented tools. It was envisioned that the model would: integrate existing research information and understanding of the gypsy moth life system, identify areas where information was incomplete, identify research needs, and provide a vehicle for evaluating alternate hypotheses. The modelling exercise integrates existing information, understanding, and hypotheses; the model provides a means to view working hypotheses within the framework of the stand. In this context, hypothesis testing and sensitivity analysis provide mechanisms for identifying needs and setting priorities, including impacts on human use and management objectives. Dynamics that might be very impractical or impossible to capture in field studies may be simulated, providing a means to explore and develop understandings of the gypsy moth/forest ecosystem. It has already served as a research evaluation and planning tool and will, in the future, serve to analyze factors or relationships that might show promise as management tools, that is, to evaluate relative consequences of alternate scenarios.

Between 1984 and 1988, Sheehan and others did considerable work to develop and expand the model (Sheehan 1988). The first version was near completion when Sheehan left the project at the end of 1988. Documentation of the model structure and formulation was drafted except for one subsystem. Considerable work was required during the 1984-88 period to transform the code from a nonstandard FORTRAN to ANSI-77 Standard FORTRAN and complete additions and enhancements proposed by researchers.

Model Design

General structure.--The current model is composed of four major subsystems that are driven by weather. The stand subsystem incorporates the effects of damage by the gypsy moth into annual tree diameter and height growth as well as tree mortality. These calculations are modified by ambient heat (degree-days) accumulated each calendar year. The stand subsystem can be run independently as a stand-alone model. Gypsy moth growth and portions of the predator-parasite subsystems are driven by accumulated ambient heat (degree-days) on a much finer scale.

The gypsy moth subsystem follows insect growth in each cohort, partitioned into a number of insects per cell (host species and canopy strata), and larval movements between cells. The predator and parasite subsystem follows several natural enemy guilds and species that have been determined to be significant mortality agents of the gypsy moth; detailed feedback relationships are provided for natural enemy populations where sufficient information is available. The pathogen subsystem follows naturally occurring nucleopolyhedrosis virus (NPV), and introductions of both NPV and *Bacillus thuringiensis* (Bt) as insecticides. The pathogen subsystem operates from initial conditions and feedback from infected gypsy moths. This subsystem models distribution of NPV in the environment and in infected gypsy moth.

Scope and Scale.--The spatial scope of the model is a single forest stand. No spatial coördinates of trees are needed, but the model does use vertical stratification of the tree canopies. The stand is partitioned by tree species and diameter class for calculation of tree growth, tree mortality, and foliage biomass. Stand variables are updated once each year; these updates include stand management prescriptions imposed by the user.

Foliage, gypsy moth, and natural enemies are followed on a finer time scale within each calendar year. After sufficient degree-day accumulation, foliage begins to grow and gypsy moth eggs begin to hatch. As long as the current generation of gypsy moth exists, each accumulated 30 degree-days produces another simulation step. Following the completion of an insect-generation cycle, annual summary accounts and links to the stand model are completed for a year, and another year produces another generation. These routines operate on a spatial scale that aggregates among the diameter classes for each tree species present. Four strata are distinguished: (1) overstory trees, (2) understory trees, (3) boles of overstory trees, and (4) a shrub and ground layer.

Weather Subsystem

Both the stand and gypsy moth are affected by ambient temperature and the gypsy moth model by rain (rain data are not required); such physical parameters in turn affect gypsy moth development rates and foliage growth rates. Daily maximum and minimum temperatures are required to derive degree-day accumulation for each Julian day. The average of the daily minimum and maximum temperatures, less the lower threshold, are accumulated into 30 degree-day steps; or the sine wave method (Allen 1976) is available. The user can alter the number of degree-days that are accumulated each cycle or step. The stand model uses only annual total accumulated degree-days. The user can provide known or expected daily temperature regimes. Weather data can be introduced in any of three formats. A stochastic weather generator is available as is default weather data for several years at a few sites.

Stand Subsystem

The stand model is fashioned after JABOWA (Botkin et al. 1972) and the FORET model (Shugart and West 1977). There are parameters for 20 tree species (Table 1); up to 6 species can be included in a single simulation. Tree establishment, growth, and mortality are simulated. This is a distance-independent diameter class model. Thus, a stand is assumed to be spatially homogeneous. The user can stipulate the number and size of diameter classes.

To describe a stand, the user specifies tree counts by species and diameter class and provides one of three soil-moisture categories for the stand. Annual ambient heat accumulation (day-degrees) is required for each year. An average for the site may be used in place of annual data.

Table 1. Tree species that can be simulated in the Stand Model.

Tree species Common Name	Species	Host food preference[a]
white oak	*Quercus alba*	1
scarlet oak	*Quercus coccinea*	1
chestnut oak	*Quercus prinus*	1
northern red oak	*Quercus rubra*	1
black oak	*Quercus velutina*	1
eastern white pine	*Pinus strobus*	1
quaking aspen	*Populus tremuloides*	1
basswood	*Tilia americana*	1
paper birch	*Betula papyrifera*	1
sweet birch	*Betula lenta*	2
yellow birch	*Betula alleghaniensis*	2
American beech	*Fagus grandifolia*	2
black cherry	*Prunus serotina*	2
hickory spp.	*Carya* spp.	2
red maple	*Acer rubrum*	2
sugar maple	*Acer saccharum*	2
striped maple	*Acer pensylvanicum*	3
yellow-poplar	*Liriodendron tulipifera*	3
white ash	*Fraxinus americana*	3
flowering dogwood	*Cornus florida*	3

[a] Host food preference:
1 = most preferred food for gypsy moth larvae;
2 = not particularly favored but upon which a small portion may develop;
3 = unfavored as food of gypsy moth, larvae are not able to complete development.

Each year, tree height is used to calculate potential resting sites for gypsy moths. Potential foliage biomass is calculated as a sum, over species and diameter class counts, of species-specific allometric functions of class midpoint diameters. Diameter growth of trees is calculated as a reduction from maximum potential growth. Reductions due to relative stocking (a measure of tree crowding), shading, temperature, and defoliation are calculated. Base tree mortality rate is altered according to reduced growth, gypsy moth defoliation, and other stresses. Following mortality calculations, tree growth is updated for the residual stems by moving trees between diameter classes; new stems are recruited to the smallest class for each species that has been included in a particular simulation. Recruitment is species specific and decreases as stocking increases.

The stand is stratified by tree species and size to provide foliage and resting site information to the gypsy moth subsystem. Defoliation is returned by the gypsy moth subsystem or entered by the user when the stand subsystem is run as an independent model to assess growth and mortality losses.

Gypsy Moth Subsystem

The egg population starts the cycle. Egg parasitoids and other mortality agents that affect eggs between the time they are laid in late summer of the previous year and they hatch in late spring are taken into account. Once sufficient heat has accumulated, eggs begin to hatch. As many as 10 cohorts result from eclosions; the user can stipulate what portion of the population hatches at each step. Within each cohort, each sex is followed separately. Larvae go through five or six instars and then pupate. This period of growth and feeding is modelled in detail.

During each 30 degree-day step: foliage grows; eggs hatch (first 10 steps); larvae age; larvae move to feeding sites between hosts and canopy strata; nocturnal foliage consumption and destruction or dispersal occurs if no food available; larvae grow (both biomass accumulation and stage transition); if appropriate, suppression mortality is accounted for; natural enemies attack; move to resting sites to spend the daylight hours (large larvae only); natural enemies attack; and gypsy moth survivorship is tallied.

When all gypsy moth have reached the adult stage, the population cohort vector is collapsed to a single variable. Mating and egg laying take place to complete the generation. Larval stages can be affected by chemical or microbial pesticides; adult mating and reproduction can be disrupted by pheromone trapping, confusion (pheromone disruption), or release of sterile eggs. Indirect effects on gypsy moth may be simulated through stand management such as removal of preferred hosts.

Natural Enemies

There are a number of naturally occurring factors that keep the gypsy moth in check. Besides the natural factors that exist in North America, researchers are looking for natural enemies in Europe and Asia where the gypsy moth occurs naturally. Promising natural enemies might be introduced into North America. At present, we are modelling all natural enemies that are thought to play significant roles in the gypsy moth's population ecology in North America. Those natural enemies that are currently incorporated or under consideration for incorporation are:

PREDATORS:
Insects
*+[1] *Calosoma sycophanta, C.* spp.
* Birds
Small mammals
* white footed mouse *Peromyscus leucopus*
shrews *Sorex* spp., *Blarina brevicauda*
PATHOGENS:
Virus
* nucleopolyhedrosis virus
Bacteria
Streptococcus faecalis
Serratia marcesceus
*+ *Bacillus thuringiensis*
Fungi
Beauvaria bassiana
Paecilomyces farinosus
\+ Microsporidia spp.
PARASITES:
Diptera (flies)
*+ *Parasetigena silvestris*
*+ *Compsilura concinnata*
*+ *Blepharipa pratensis*
\+ *Exorista larvarum*
Hymenoptera (wasps)
*+ *Cotesia melanoscelus*
\+ *Phobocampe dispar*
*+ *Brachymeria intermedia*
\+ *Monodontomerus aureus*
*+ *Ooencyrtus kuvanae*
\+ *Anastatus dispar*
Itoplectes conquisitor

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[1] * = modeled now, + = introduced species

Predator and Parasite Subsystem.--Arthropod, avian, and mammalian predators and a number of insect parasitoids are simulated. Where sufficient information is available, functional or numerical responses to gypsy moth numbers are simulated by density-dependent recruitment of predators and parasitoids to gypsy moth prey. Probabilities of encounter, and of successful and unsuccessful attacks, are included. When parasitized, gypsy moth populations are followed until the parasitoids emerge and the gypsy moths die. Parasitized gypsy moth progeny continue to be at risk to superparasitism, predation, disease, or starvation. Inter- and intra-specific competition of parasitoids within gypsy moth can be determined by the sequence of attacks. It is possible to simulate the probability of a predator or parasitoid actively avoiding previously parasitized individuals, because the parasitized proportion of each cohort is known.

Pathogen Subsystem.--The pathogen subsystem follows polyhedral inclusion bodies of NPV and infectious particles of Bt on the foliage and in other strata. The probability that gypsy moth larvae will encounter sufficient quantities to become infected is used to predict viral or bacterial infections in the population. Virus propagation through the gypsy moth population is modelled; that portion of each cohort that becomes infected with lethal concentrations of the virus is followed and the virus polyhedral inclusion bodies produced become available to other gypsy moths through cadaver ruptures. Both virus and Bt must be ingested to affect the gypsy moth. The half-lives of NPV and Bt are used to simulate the degradation rates of these pathogens under ultraviolet light exposure or other causes of deactivation.

Input Data Files and Output Tables and Files

There are default inputs for all required data, and minimal outputs are generated under the default inputs. Four input data files are required and three others are optional. These provide the users with maximum flexibility in controlling the model. There are a number of tables and plain ASCII text files that can be generated upon request; the latter are designed for use as input to graphic packages or for use in statistical analyses.

Inputs.--The first required file is used for general information and includes controls for further input or output. The second contains all of the data for the stand subsystem, and provides a vehicle for the user to manipulate many of the growth parameters and to assign the initial stand tree counts by species and diameter class. An optional data file can be used with the stand model to provide defoliation data when the stand subsystem is run separately, without the detailed gypsy moth and natural enemy subsystems. This independent version of the stand model has been referred to as the Damage Model. The weather data file can be provided in any of three formats. An optional file of precipitation data can be included. A large portion of the parameters (for example, rates and coefficients) and all of the initial conditions for the gypsy moth subsystem are located in the third required data file. Finally, a natural enemies file containing all parameters and initial conditions for these mortality agents can be manipulated by the user. Default files are provided for all required data.

Outputs.--There are 10 different output tables describing the gypsy moth and its natural enemies that users may request; parallel to 9 of these are summaries as formatted ASCII data files. There are 2 stand summary tables for viewing and 4 ASCII data files. These 13 data files are designed for use in other software packages such as graphics or statistical analysis programs.

The life table is the basic output of the gypsy moth subsystem. It provides the breakdown of mortality source for each life-stage age interval through each year. Annual summary tables of gypsy moth population attributes or mortality sources can be requested; these can also be broken out by host species. A direct control summary provides information on timing and efficacy of NPV, Bt, or chemical applications. Population attributes can further be broken out by degree-day interval. There is a phenology summary. Finally, mortality information can be summarized annually or be requested in detail for each 30 degree-day interval.

The stand table gives summary input and parameter information as well as annual summaries of tree growth, mortality, and stand volume. A separate defoliation summary can be requested for review of data inputs or transferred from the gypsy moth subsystem. Stem counts, basal area, volume, and diameters for each simulated year also can be output in ASCII text file format.

Current Status and Future Plans

The model is running on MS-DOS® and Apple® Macintosh™ microcomputers and on Data General® minicomputers. Coding of the model is complete, and analysis and testing of the model have been initiated. Only cursory examinations of state variables and intermediate calculations have been made. We are reviewing and structuring the code and beginning detailed analyses, including comparisons with field data. We are using USDA Forest Service watershed growth and yield research plots to examine stand growth and tree mortality in the absence of gypsy moth. Plots throughout Pennsylvania, designed to assess damage, will be used to assess the effects of defoliation on growth and tree mortality, within stands of various age, structure, and defoliation histories. Additionally, we are in the process of completing user-oriented documentation for the model and a design for a user-friendly input/output control system to be written in C. These will provide access for researchers and other potential users who are not computer specialists.

CONCLUSIONS

Empirical statistical models and process oriented simulation models have been shown to provide insights into the dynamics of the gypsy moth life system. However, to date, none of these models have been shown to be useful as predictive tools. Researchers have suggested that models might be useful for predictive purposes and, too often, people have come to expect more than can be delivered. I strongly doubt that models will ever be able to answer questions such as "When will gypsy moth become a problem here?" or "When will this outbreak subside?" with any fine degree of accuracy.

Just as we cannot predict the weather total accuracy, we cannot expect to make exact predictions about the gypsy moth. That does not mean that there are not significant gains to be made from the use of models. Models have been able to assist us in organizing and analyzing available information. The use of GIS to obtain long-term trends for spread and expert systems surely will play a positive role in answering questions that are appropriate to their design. We have been able to elucidate significant biological processes and relationships in useful contexts. Models have been shown to provide useful information to both researchers and managers.

Process models usually require that a number of empirical relationships be fitted, that is, the same statistical procedures that are used to develop empirical models are used to develop relationships within process models. Thus, process models **can** contain all the drawbacks of empirical models and more, because of their complex design. By watching our own development process carefully and involving sufficient biological review on a continuing basis, we hope to avoid this. Any model is only as good as the basis on which it is built. As mentioned above, we are in the process of extensively testing the models we are developing. This testing should provide us with information on model applicability. We will develop documentation that describes what we think will be appropriate and inappropriate uses of the models. We will be working with many of you to find concerns and ways to improve the system as it is being further developed.

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PHEROMONE DISPENSER FORMULATIONS FOR USE IN GYPSY MOTH MANAGEMENT PROGRAMS

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ABSTRACT

The sex attractant pheromone, disparlure, is utilized in several aspects of gypsy moth (*Lymantria dispar* L.) management programs. These include detection of new infestations, assessment of population levels of existing infestations, and disruption of mating communication in control efforts. Each of these applications requires the development of an effective and commercially feasible dispensing system. In 1989 efforts were undertaken to biologically and chemically evaluate 11 different controlled-release pheromone dispensers from 7 commercial firms for use in the detection traps deployed by the Animal and Plant Health Inspection Service. In addition, results were obtained on dose/response in 3 population levels using a new PVC dispenser containing 1 ng to 10 mg of disparlure. A new ARS dispenser was found to be equal to the preferred commercial dispenser for detection. A 1 µg PVC dispenser was selected for additional study in monitoring established populations.

DEVELOPMENT OF A PHEROMONE-BAITED TRAP TO MONITOR GYPSY MOTH POPULATIONS

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ABSTRACT

The standard milk carton trap baited with 500 µg of (+) disparlure has worked very well in detecting populations of gypsy moth in regions where it is just becoming established. However, it has not been useful in New England or anywhere within the area generally infested by gypsy moth. In such areas, the traps fill up with males even in populations of extremely low density. Repeated sampling of such traps during the flight season is neither practical nor advisable. We have explored several strategies for modifying the trap to reduce the number of males captured. These are: 1) baiting the trap with racemic disparlure, 2) baiting with a low release rate (+) disparlure dispenser and 3) modifying the trap so that it is difficult for males to get into. We have explored whether traps based on any of these modifications would be correlated with other estimates of local population density (egg mass counts or pupal counts under burlap). Other experiments and behavioral observations have aimed at elucidating the factors which influence trap catch.

MONITORING, AND MAPPING GYPSY MOTH DATA IN AIPM: THE PROCESS AND PROBLEMS OF IMPLEMENTATION

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ABSTRACT

The Appalachian IPM program (AIPM), due to its size (12.8 million acres), location along the leading edge, and use of new technology, will influence the development of gypsy moth management programs. This paper reviews the data collection, management and mapped display of the adult male and egg mass life stages in the AIPM project. Data are field-collected using optically-scanned forms and managed using database management and geographic information systems. Maps showing population density, trend in density, extent of infestation and proximity to other infestations are delivered to land managers.

Male moth data are collected from ca. 9,000 pheromone traps in a 2 or 3 K systematic survey. Sentinel traps (ca. 3% of the traps) are checked weekly towards the end of the season to establish the end of moth flight and initiate egg mass surveys. A small proportion of traps along the northern edge of the project have been filling and this problem is projected to increase. Progress of trap placement and service visits are mapped weekly to aid in personnel management. Moth catch and trend in moth catch are modelled into surfaces. Male moth maps at the same scale and size as USGS 7.5 minute topographic maps display male moth trend as shaded polygons, moth catch as contours and postings, and last year's egg mass point data. Computer programs which automate this procedure are in place. About 100 minutes of computer time is currently necessary to produce and plot each map, and ca. 130 quads were produced in 1989 by the USFS in Atlanta.

Egg mass data (1/40th acre fixed-radius plots) are collected where male moth data suggest positive counts are likely. The number of egg mass samples between the two years is increasing dramatically. A sequential sampling plan was established in 1989 to help increase precision in the face constrained sampling resources. This problem is projected to continue, and additional sampling plans are needed. Due to the resolution, spatial distribution, and spatial dependence of the egg mass data, surface models easily produce artifacts at locations distal to collection sites. To prevent this, mapped displays are restricted to within 250 m of collected data by creating a polygon that defines the area within 250 m of any sample, and restricting the display of all surfaces to fall within this polygon. Defoliation data are also included on egg mass maps.

LANDSCAPE ECOLOGY OF GYPSY MOTH IN THE NORTHEASTERN UNITED STATES

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ABSTRACT

The gypsy moth was accidentally introduced to North America near Boston by E. Leopold Trouvelot in 1869. Since that time, the range of the gypsy moth has slowly spread and the generally infested region presently extends as far as Ohio, West Virginia, Virginia and North Carolina. A separate isolated but expanding population exists in Michigan. The goal of this study was to quantify the process of gypsy moth spread through North America and relate the process to other landscape features. The ultimate purpose of this research is the development of sound predictions of future gypsy moth spread.

The past spread of the gypsy moth in North America was quantified from historical quarantine records. Since the enactment of the Domestic Plant Quarantine Act of 1912, the federal government has designated certain parts of the United States as officially "infested" by the gypsy moth. Though there has been some variation in detection methods used to make this designation, it is the only record we have of past gypsy moth spread. We compiled these historical records to designate the yearly infestation status of each county in the United States and similar records that designate the status of each census district in Canada. We used the IDRISI geographical information system (GIS) to manage these data. County and census district coordinates were imported from the SAS system and were used to define the geographical boundaries of historical infested areas.

We used the historical spread data from 1966 to 1986 to model a county's time to infestation as a function of its minimum distance from the generally infested region and the county's mean minimum January temperature. The minimum distance was calculated using the GIS and minimum temperatures were interpolated from 30 year historical weather station data collected through out the area. Both distance and temperature contributed statistically significantly to the model. Extremely cold winter temperatures can kill overwintering gypsy moth egg masses and this is the most likely explanation of the effect of January temperatures on spread. When we applied the spread model that was developed from 1966-1986 data to the 1900 data, it greatly over-estimated the rate of spread from 1900-1950. This indicated that the rate of spread over the last 20 years has been much greater than it was during the earlier part of the century. There are many possible reasons for this change and we are currently attempting to incorporate this process in an improved model.

MODELING GYPSY MOTH SEASONALITY

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ABSTRACT

Maintaining an appropriate seasonality is perhaps the most basic ecological requisite for insects living in temperate environments. The basic ecological importance of seasonality is enough to justify expending considerable effort to accurately model the processes involved. For insects of significant economic consequence, seasonality assumes additional importance because management decisions are often based on seasonal timing. In gypsy moth management, timing of BT applications and determining an efficient sampling interval for placement of pheromone traps are two such applications. We are, therefore, in the process of developing models required for representation of gypsy moth seasonality. Model representations currently under consideration are those for egg diapause and embryogenesis, and larval phenology.

The conceptual basis for our diapause model is founded in two generally accepted first principles. These are (1) there are two important temperature dependent rate related processes that define diapause, that of diapause development and that of embryogenesis, (2) the relationship between these two temperature dependent rate processes results in arrested development that is the outward manifestation of diapause. We differ from traditional interpretations, however, in that we conceptually allow the relationship between these two phases to be more flexible than conventional models. In particular, we acknowledge that the relationship may allow concurrent phase development as well as the more traditional strictly sequential progression through phases. Larval phenology is modeled by a flexible modeling paradigm developed by Logan (1988). The empirical foundation for this model resulted from a reevaluation of data published by Casagrande *et al.* (1987).

Linking the models of egg diapause with that of within season dynamics results in a composite representation of seasonality. The resulting model allows long-term representation and analysis of gypsy moth seasonality. In this paper, we discuss: (1) the structural detail of the two modeling approaches (2) coupling of the models to produce a composite model that links one year to the next, and (3) implications, both basic ecological and applied, of long-term simulation experiments with the seasonality model.

MESOSCALE LANDSCAPE MODEL OF GYPSY MOTH PHENOLOGY

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ABSTRACT

A recently-developed high resolution climatological temperature data base was input into a gypsy moth phenology model. The high resolution data were created from a coupling of 30-year averages of station observations and digital elevation data. The resultant maximum and minimum temperatures have about a 1 km resolution which represents meteorologically the mesoscale.

The GMPHEN phenology model was used to simulate the seasonal development of gypsy moth. The model predicts the timing of male and female gypsy moth stages based on degree-day thresholds. As daily maximum and minimum temperatures are input into the GMPHEN model, the simulated insect population passes through a succession of phenological stages according to accumulated degree days.

Weekly averages of daily high resolution climatological maximum and minimum temperatures for two areas, one in western Pennsylvania and the other centered on West Virginia, were input into the GMPHEN model. The resulting model output were displayed as landscape maps overlaid with county boundaries. Beginning with January 1, the weekly landscape maps depict the average seasonal development of gypsy moth starting with egg and ending with the adult stage. By viewing the succession of maps, one can follow the progression of gypsy moth development both temporally and spatially. The series of maps provide a strategic tool for anticipating the seasonal date of a particular gypsy moth stage at a given location.

BEHAVIOR OF THE GYPSY MOTH LIFE SYSTEM MODEL AND DEVELOPMENT OF SYNOPTIC MODEL FORMULATIONS

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<u>Aims of the research</u>. The Gypsy moth life system model (GMLSM) is a complex model which incorporates numerous components (both biotic and abiotic) and ecological processes. It is a detailed simulation model which has much biological reality. However, it has not yet been tested with life system data. For such complex models, evaluation and testing cannot be adequately accomplished comparing the outputs with life systems data. Our strategy is to combine structural and functional analysis of the ecological processes within the GMLSM with development of synoptic models that incorporate the fundamental ecological processes, gradually increasing their complexity and reality.

Ultimately, we hope to achieve the following results: A. for the GMLSM: 1. Improve our knowledge of the life system, discover the weak points of present hypotheses and their linkages via parameter sensitivity and structural analysis, and thus direct further experimentation and modelling; 2. By evaluating and improving the GMLSM, we hope to provide a standard and clearly documented model which can be widely used, providing means to investigate optimal strategies for gypsy moth management under specific local conditions. B. for the simplified models: 1. Understand mathematical behavior and stability of models with regard for formulations, parameter values, and initial conditions; 2. Understand biological and ecological processes and parameters and how they should be most appropriately incorporated in models, i.e., how they should best be expressed in model formulations; 3. Understand how the mathematical characteristics of simpler models compared with the more detailed GMLSM and help us understand what in the GMLSM gives rise to the major stability and behavioral characteristics of the GMLSM.

<u>Scheme of the research</u>. The general scheme of our research is to parallel the work on the analysis of the GMLSM with construction of simple model formulations that provide means to explore major components of the ecosystem. These two approaches can be very complementary.

For structural analysis of the GMLSM, we have constructed flow charts to elucidate the basic components and interactions of the system model and each submodel. Computer diagnostic tools have a mechanism for step-by-step examination of calculations being performed. This process has already allowed us to uncover obscure behavioral problems and to correct inappropriate component interactions.

But is it structured on a sound biological basis, and is it interpreted correctly in mathematical terms and computer program representation? The most fundamental procedure is to evaluate the functional behavior of the basic ecological processes. This approach can be very helpful for constructing simple model systems. On the other hand, constructing and operating simple model systems in correspondence with the GMLSM can very efficiently detect errors in the GMLSM.

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[3] Due to personal problems, Dr. Xu had to return to China; with the time required for international communication and the need to balance this work against other obligation, we do not expect this work to progress as fast as originally scheduled.

HAZARD RATING FOREST STANDS FOR GYPSY MOTH[1]

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ABSTRACT

A gypsy moth hazard exists when forest conditions prevail that are conducive to extensive damage from gypsy moth. Combining forest hazard rating with information on insect population trends provides the basis for predicting the probability (risk) of an event occurring. The likelihood of defoliation is termed susceptibility and the probability of damage (mortality, growth loss, reduced aesthetics, etc.) is called vulnerability. Hazard rating systems are usually developed by making empirical observations of forest stands that are exposed to a gypsy moth outbreak and formulating a prediction model that can be used to estimate susceptibility and/or vulnerability of other stands.

The value of hazard rating is in forecasting where the problem is likely to be most severe and how severe it is likely to be. Using this information, forest managers can target gypsy moth population monitoring in stands that have high hazard and high value. When potentially damaging population levels are detected, the manager can then deploy one of several intervention strategies in the appropriate stands.

INTRODUCTION

The term hazard is given several definitions in the dictionary, but the one which most closely approximates my use of the word in pest management is "something causing danger, risk, or peril". Risk can be further defined as "the degree of probability of loss". Thus hazard rating helps establish conditions where a damaging event is most likely to occur and how extensive the damage is likely to be (Hicks and others 1987). Risk assigns a probability to these likelihoods and is determined by the dynamic relationship between forest conditions and insect population levels. For example, a high hazard can exist in combination with a low risk when insect populations are absent or low. This situation is particularly appropriate to an introduced pest like gypsy moth as it moves into previously unexposed areas.

When a defoliator like gypsy moth consumes the leaves of a tree, the direct effect is a lowered amount of total photosynthesis for the tree, thus less carbohydrate is available for metabolism and storage. Heavy defoliations trigger a refoliation response of trees which further depletes starch reserves from the roots. This physiological stress results in lowered vigor. Multiple years of defoliation tend to compound the problem and defoliation coupled with any other stresses that are normally experienced by trees (drought, heat, cold, shade) often predisposes trees to attack by secondary organisms such as two-lined chestnut borer and *Armillaria* root disease. Either of these organisms directly causes tree mortality (Fig. 1). Because defoliation *per se* doesn't directly cause tree death and because not all trees are equally likely to be defoliated or to die, hazard rating systems to predict "susceptibility" (likelihood of defoliation) and "vulnerability" (likelihood of death or damage) to gypsy moth have been developed (Campbell and Standaert 1974; Valentine and Houston 1979; Herrick and others 1979).

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[1] Funding for this research was provided to West Virginia University by the USDA, Forest Service, Northeastern Forest Experiment Station.

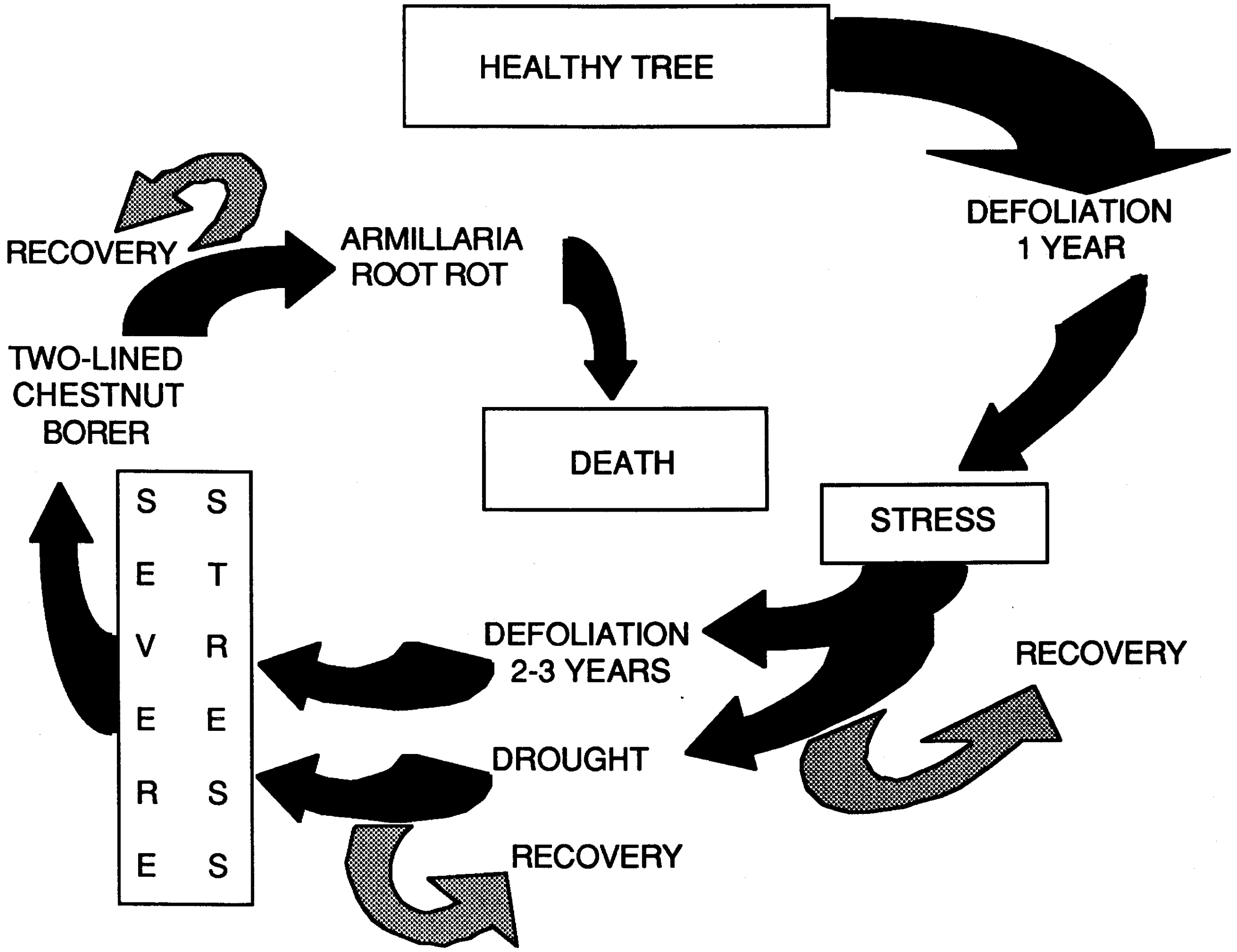

Figure 1. Mortality spiral for trees defoliated by gypsy moth (after Manion 1981).

Insect hazard rating is widely promoted among researchers as a means of targeting activities such as survey and detection, intervention and insect suppression. Unfortunately, many forest managers are slow to implement insect hazard rating as a normal component of their management activities, even though hazard rating systems are available that require standard inventory data, and in some cases have been integrated into total management packages such as SILVAH (Marquis and others 1984). It is the purpose of this paper to develop an appreciation for and an understanding of gypsy moth hazard rating and to illustrate how it can be used in an integrated forest management program.[1]

Developing a Hazard Rating System

Researchers attempting to understand the functioning of natural systems usually have some sort of conceptual model of the system. In the case of gypsy moth hazard rating for vulnerability, that model might be expressed as: Gypsy moth defoliation results in stress to trees which in turn predisposes them to secondary mortality agents; the magnitude of stress can be quantified using measurable variables.

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[1] For more on hazard-rating terminology, see "The Revelation" that follows the conclusion of this paper.

Jeffers (1982) refers to this as a "word model". He further discusses "diagram models" which help to organize the problem into a structured form. I have adapted Manion's (1981) "disease spiral" to this purpose (Fig. 1). A primary purpose of modelling is predictions,in this case to forecast hazard or risk of an event happening. Thus to facilitate prediction, some type of quantitative model is required. The dependent variable is some measure of hazard or risk and the independent variables are measures of the state of the system. For example, if we assume that a stressed tree is more susceptible to mortality than a healthy tree, the independent variables we choose should be those that directly or indirectly affect or measure the impact of stress. The variables measured should also be things that are measurable and precise. For example, xylem moisture potential may meet the criterion of being indicative of stress and may be measurable at any point in time, but due to the dynamic fluctuations of tree water balance, it may change drastically in a short period of time and therefore would not be a useful variable for hazard rating. Soil moisture or monthly rainfall, although not direct measures of drought stress would be related to potential for drought stress and could be more useful than the direct measure of xylem water potential.

Once a list of dependent and predictor (independent) variables has been selected, a sampling scheme must be developed. No matter how conscientious one is about sampling, at best only a very small proportion of the total area can realistically be sampled. For example, our study of gypsy moth mortality involves some 400 tenth-acre plots in southwestern Pennsylvania, western Maryland and eastern West Virginia (roughly a circle containing 5 million acres). That works out to about one acre sampled per one hundred twenty thousand acres or a sampling intensity of 0.0008%.

The population of samples should include plots representing the principal forest cover types and sites and should include both defoliated and undefoliated forests. In our study we divided the sample plots roughly evenly between the Appalachian Plateau and Ridge and Valley physiographic provinces since these provinces represent clearly different environments (forest types, soils, geology and climate). It is also important to accurately record the defoliation history of plots since stands receiving different levels of defoliation would be expected to respond differently even when other factors are equal. After a sufficient post-defoliation time period has elapsed for the effects of defoliation to be manifested, tree mortality, growth, development of understory, etc. should be assessed. These are the dependent variables to use in subsequent analyses.

The final step in the model development process is the generation of a mathematical model. Since such sample data generally contain a good deal of variation, the appropriate technique is one which produces a "best fit". Examples are multiple regression and stepwise discriminant analysis. The goal of a model is prediction. In the case of hazard prediction, it can be accomplished as the classification (or probability of classification) of individual trees in a particular state (e.g. dead v. alive). Discriminant analysis or logistic regression are useful techniques for accomplishing this (Valentine and Houston 1979). Predicting hazard for a stand of trees in terms of such dependent variables as number of dead trees or percent dead basal area, etc. can be accomplished by using multiple regression or automatic interaction detection (Herrick and others 1979).

Testing and validation is an often overlooked aspect of model development. Certain techniques can be employed using the sample data. For example, an independent data set can be withheld from the analysis (regression, etc.) and the model developed from the other data can be applied to the independent set to see how well the model predicts. Another statistical validation technique which allows the use of the whole data set for model development is the leave-one-out method. Each observation (plot, stand, tree) is systematically excluded from the data set. The model is developed using all the others and tested against the one left out. These statistical procedures are useful as far as they go, but the true test of a model is whether or not it will work on other stands, in other environments and at other times. Such validation is an on-going and necessary process to determine where, when and if a model provides acceptably reliable predictions.

Applying Hazard Rating.

Hazard rating is a component of integrated pest management and IPM is a component of forest resource management. All too often, the tendency to become specialized makes us myopic and so it is with forest pest managers. Although outbreaks of forest pests like gypsy moth become the proverbial "tail that wags the dog" it is still necessary for pest management to be kept in perspective as a component of forest resource management. Figure 2 is a diagram from Gansner and others (1987) outlining an example of how IPM decisions are made. Hazard rating is a key element in this process which enables the manager to target many of the subsequent activities.

Application of hazard rating, as with all forest management, requires knowledge about the forest. The fundamental unit of management is the stand. Once stands have been delineated, data needed for hazard rating can be collected. In many cases the data needed for hazard rating are the same as needed for other facets of forest management (e. g. tree species, site quality, tree size, crown condition, etc.). Programs like SILVAH (Marquis and others 1984) may facilitate stand data collection and processing.

We have been engaged in gypsy moth hazard rating at the West Virginia University (WVU) Forest during the last year and this experience has been helpful in identifying some of the problems of hazard rating. We selected two compartments at the WVU Forest, each of approximately 450 acres (Fig. 3). Stands were located from point samples taken on a 1 x 2 chain grid using a 10 BAF prism. We used the Society of American Foresters cover type designations and descriptions to define the cover types and set a minimum of 10 acres for stand size (smaller stands became inclusions in surrounding stands). The stands identified in these two compartments are indicated in Figure 3. An interesting adjunct to this is the fact that using student labor, the cost of stand mapping and collection of stand data for the two compartments was accomplished at about $1.15 per acre.

We applied several hazard rating equations and methods to the stand data. Table 1 compares the results of these ratings for Compartment 4 of the West Block. The most striking aspect to these numbers is how much they differ, both in magnitude and in relative terms. For example, the equation of Gansner and Herrick (1984) produced very low estimates of percent mortality. Looking at their equation it is apparent that percentage of trees with poor crowns (> 50% dead limbs) is the most important driving variable for predicting mortality. Trees with poor crowns are manifesting pre-existing stress and defoliation simply adds to the stress state of the tree until some threshold is exceeded that allows secondary agents to gain a foothold. Since Gansner and Herrick's sample data were collected from the Pocono Mt. region of Pennsylvania, it is easy to visualize how trees may be under stress in this droughty and poor site region. However, at the WVU Forest where annual rainfall averages about 55 inches and oak site index averages around 72 ft., it is not surprising that the percentage of trees showing poor crowns is generally below 5%. The question is; Does Gansner and Herrick's equation accurately project the rate of mortality that might be expected due to 3 years of heavy defoliation at the WVU Forest? My guess is that it doesn't because we have observed very high levels of mortality in stands that were similar to those at the WVU Forest after heavy defoliation. In-other-words, pre-existing stress may hasten the mortality of trees, but the stress threshold for secondary organism attack can be achieved by defoliation alone. Looking farther at Table 1 reveals that the equation of Crow (1985) gives predicted mortality rates of 20-30%, which is fairly consistent with average rates of mortality we have observed in the Ridge and Valley and Appalachian Plateau of western Pennsylvania and Maryland. However a stand mapped as northern red oak type had a lower projected rate of mortality than one mapped as Yellow-poplar-red oak-white oak. When examining Crow's equation, it can be seen that presence of oaks in the white oak group tends to increase the projected rate of mortality while oaks other than white oaks tend to decrease it. To appreciate how this occurred, one must look at the data base from which Crow's equation was derived. All his stands were from the Ridge and Valley region of eastern West Virginia and were essentially pure oak stands. Thus among the oaks, the trees in the white oak group were most vulnerable.

Table 1. Stand data and hazard rating for stands in Compartment 4, Western Block of the WVU Forest.

STAND	S.A.F. COVER TYPE		OAK S.I.	B.A. OF OAK.
1	55	(NRO)	78	67.2
2	44	(CO)	63	76.2
3	44	(CO)	68	65.1
4	28	(BC/M)	75	20.4
5	59	(YP/WO/RO)	80	25.8

SUSCEPTIBILITY RATINGS

STAND	HOUSTON/ VALENTINE DEFOLIATION	GANSNER, ET AL POTENTIAL DEFOLIATION	GANSNER, ET AL PROJECTED 1990 DEFOLIATION
1	resistant	24%	20% approx
2	"	24	"
3	"	24	"
4	"	9	"
5	"	9	"

VULNERABILITY RATINGS

STAND	REGRESSION GANSNER/HERRICK (# of trees)	A.I.D. GANSNER/HERRICK (# of trees)	CROW (B.A.)
1	3.54%	4.07%	29.2%
2	4.62	--	21.8
3	3.87	4.29	20.0
4	3.50	--	32.1
5	3.50	--	35.6

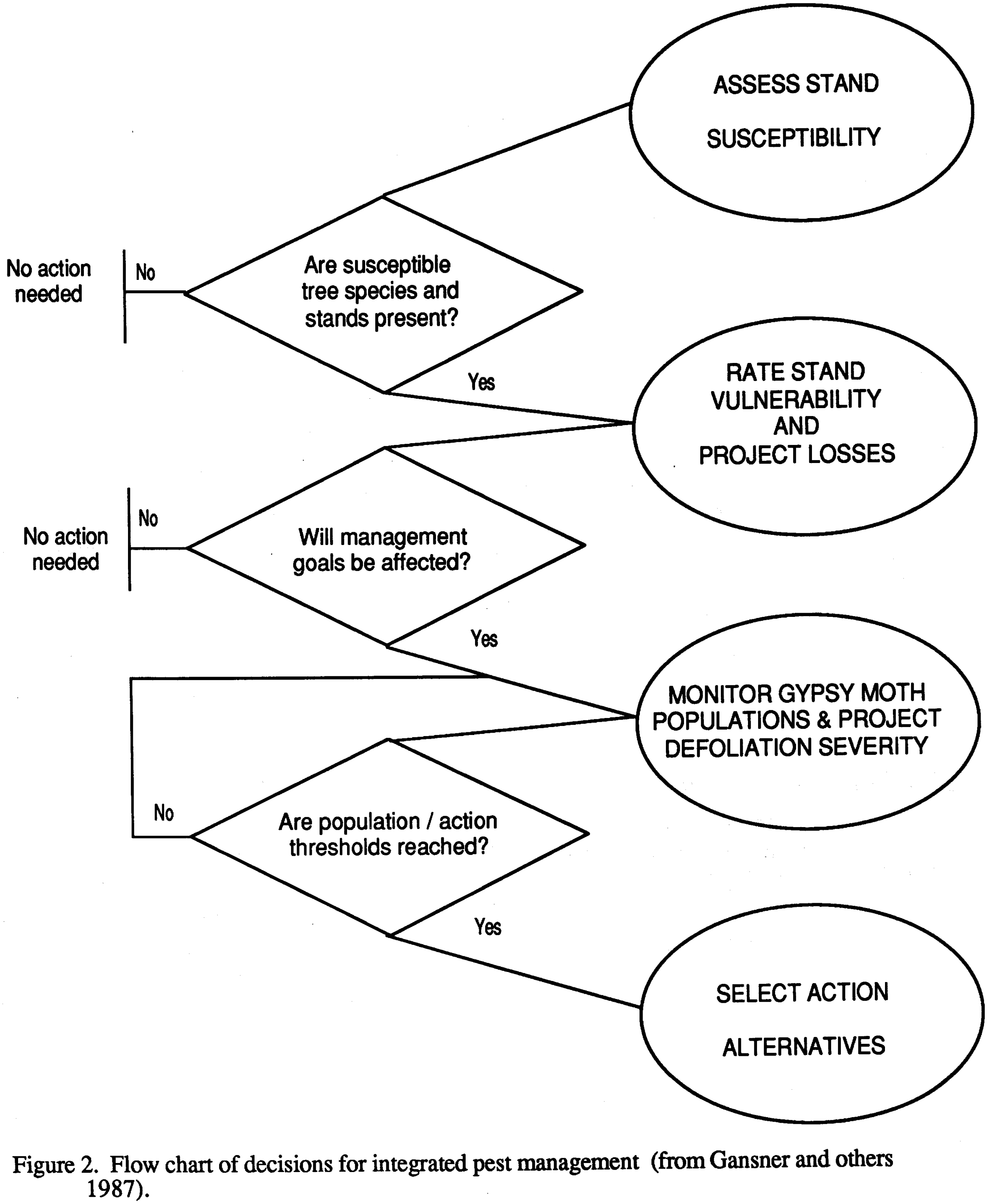

Figure 2. Flow chart of decisions for integrated pest management (from Gansner and others 1987).

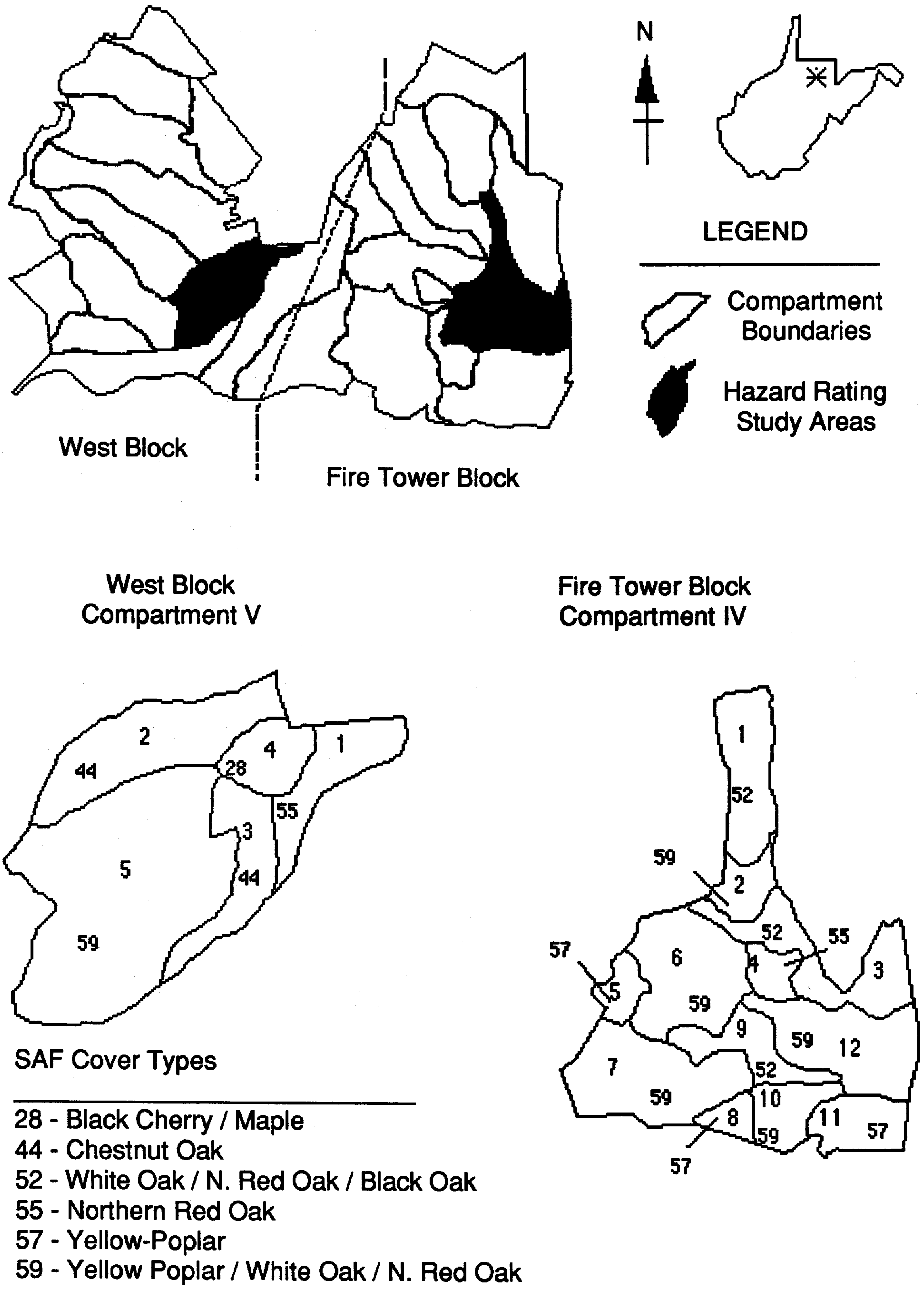

Figure 3. Study sites at the WVU Forest.

The point of all this is that one should be very careful to use hazard rating equations that were developed under conditions similar to those where they are being applied.

A final note concerning the application of IPM and hazard rating concerns the timing of these actions. IPM is not a good system to employ during "crisis management". That is to say, IPM should be an on-going component of resource management and should be implemented to give adequate time to use long-term preventative measures such as silvicultural control. The aim is to prevent the need for crisis management, a situation where forest management is subjugated to gypsy moth and not the landowners objectives.

CONCLUSIONS

Hazard rating is a component of integrated pest management, which in turn is a component of integrated resource management. This paper discusses the relationships of hazard rating to IPM and resource management. Methods of developing hazard rating systems are discussed and further discussions elaborate on the application of hazard rating within the context of resource management. Through the course of these discussions a number of needs have been identified or implied. These needs are as follows:

- Data incorporated in hazard rating systems should, to the extent possible, be standard forest inventory data so that special data collection is avoided.

- Hazard rating and IPM should be included as a normal component of forest management.

- Hazard rating should be applied at the stand level, but may also be applied at the landscape level. In both these applications, use of geographic information systems (GIS) will facilitate application and integration into management.

- Hazard rating equations must be applied only to appropriate areas with similar climatic, site and forest cover types to the conditions under which the models were developed.

- Hazard rating equations need to be validated by comparing predicted with actual susceptibility and vulnerability. This validation process should lead to updating and revision of equations to improve predictability.

Finally, several extensive reviews of insect hazard rating have been published recently. An overview of hazard rating was supplied by Hedden (1981) as a part of a conference devoted to the subject. Mason (1987) and Hicks and Fosbroke (1987) reviewed hazard rating in the proceedings of a conference dealing with gypsy moth. Hicks and others (1987) reviewed hazard rating and compared its application to gypsy moth and southern pine beetle. These and other references are useful in orienting managers to the subject of insect hazard rating.

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The Revelation
by Ray Hicks

Truth is seldom ever revealed
but a glimpse I got as north I wheeled,
from East Windsor on Tuesday eve,
a sign from heaven I perceived.
While heading up the Interstate
The vision came at exit 48
And slowly I began to smile
The sign said "Hazardville 1/2 mile".
I looked about the lonely scape
Expecting oaks, abundance great,
But all I saw was maple trees,
"There is no hazard here to see".
And so my thoughts began to gel,
If this is really Hazardville,
Then hazard ain't what I thought, why fight
For Once! perhaps the economists are right!
And so it is we must design
New terms that will define
Those most basic concepts
And parameterize our model steps.
I can think of quite a few
That express them to me, maybe you?
What about phytoentoprobabilistic
Or stochiometriceccentristic?

But you must have much better terms
That tell why trees are eat by worms
And so I leave this job to you
And wish you luck, you'll need it too!

WHAT CAUSES THE PATTERNS OF GYPSY MOTH DEFOLIATION?

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The New York Botanical Garden, Institute of Ecosystem Studies,
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ABSTRACT

Gypsy moth defoliation is typically observed to occur on xeric ridge tops before more mesic, lowland forest, in oak-dominated habitats in the Northeast. In subsequent years defoliation may also occur in mesic forests. What causes this pattern of defoliation? Differences in the degree of defoliation may be due to differences in the density of gypsy moth populations in these "defoliation-susceptible" and "defoliation-resistant" habitats, with higher densities on ridge tops -- the "focal area hypothesis." It is also possible that ridge tops have a lower foliage biomass than mesic forests, such that the same density of gypsy moth results in a proportionately greater removal of foliage -- the "foliage biomass hypothesis."

The results of a long-term study in Vermont, where these classic defoliation patterns were observed in the first year of defoliation (1989) are discussed with regard to these alternative, but non-exclusive "focal area" and "foliage biomass" hypotheses. Percent defoliation was 17 x greater on the ridge top than in the surrounding mesic forest. Egg mass densities in 1988 and 1989 were not significantly different between habitats and the number of eclosed female pupae did not differ in 1989. However, total pupal density and larval densities were significantly greater on ridge tops in 1989 (approx. 1.3 to 3-fold higher). Leaf area removed was greater on the ridge top supporting the "focal area hypothesis." However foliage biomass, as indicated by tree and canopy height, and leaf area index was also lower on the ridge top, supporting the "foliage biomass hypothesis." It would appear that the patterns of the first year of defoliation are explained by both higher larval densities and lower foliage biomass on ridge tops compared to mesic forests.

The implications of these findings to the potential for ridge tops to act as focal areas in subsequent years is discussed. The data suggest that this will be unlikely, even though densities and defoliation may be higher on ridge tops. From a management standpoint the data indicate that suppression of ridge top populations will have little impact on defoliation in the surrounding areas, but future monitoring is necessary to ascertain whether or not this is the case. The data suggest that inclusion of estimates of foliage biomass in different forest habitats will markedly improve the prediction of local defoliation based on egg mass densities, and may enhance regional-scale rating of stand susceptibility to defoliation.

DEVELOPMENT OF A SAMPLING SYSTEM FOR *ARMILLARIA* RHIZOMORPHS IN MIXED OAK STANDS: A PROGRESS REPORT

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ABSTRACT

The assessment of the problems caused by gypsy moth is dependent on a number of characteristics of a forest stand. One of the main impacts of defoliation is the mortality of standing trees. Mortality is seldom caused directly by defoliation, but is usually associated with a secondary agent which attacks the tree in its weakened condition. The shoestring root rot organism, *Armillaria* spp. (probably *A. gallica*), is one of the most important of the secondary agents after defoliation . *Armillaria* is present in large quantities after defoliation episodes. Its abundance is correlated with tree mortality in defoliated stands. Preliminary studies found differences in the presence and abundance of rhizomorphs in the soil between undisturbed stands and stands defoliated previously by insects. Rhizomorph distribution within the plots was uniform in the undisturbed stand, but was significantly greater near dead trees in the defoliated stands. Greater rhizomorph abundance near recently dead trees or stumps may have important implications for management decisions in the presence of gypsy moth infestations. Total rhizomorph abundance was greater on plots defoliated 5 years before sampling than on more recently defoliated plots, and least on undefoliated plots. Overall rhizomorph density was highly correlated to rhizomorph density near dead trees.

This study was designed to test a sampling procedure to estimate the abundance of *Armillaria* rhizomorphs in forest stands and predict the vulnerability of the stand to *Armillaria* root disease after defoliation. It was superimposed on a silvicultural treatment designed to test the effectiveness of partial cutting on reducing the impact of gypsy moth defoliation on forest stands.

Eight stands of approximately 50 acres (20 ha) each have been selected for the silvicultural treatments, four with moderate susceptibility to defoliation and four with high susceptibility. Half of each stand will be thinned during the winter of 1989-90 in a manner which will reduce the susceptibility or vulnerability of that portion of the stand, producing four replications of each of four treatments, including the unthinned control stands. No stands have yet received defoliation, but gypsy moth is present, and defoliation is anticipated within one to three years. In the current study we established a systematic grid with ropes over each plot. At each grid point a judgment of the likelihood of high or low rhizomorph abundance was recorded, random samples of soil were removed from each of the strata for extraction of rhizomorphs, and estimates of rhizomorph abundance and sampling variance are being computed for each stratum and the plot.

SHORT-TERM EFFECTS OF GYPSY MOTH DEFOLIATION ON NONGAME BIRDS

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ABSTRACT

The response of a nongame bird community to tree defoliation and mortality caused by gypsy moths was studied during the summers of 1984, 1985, 1987, and 1988 in deciduous forest habitat of eastern West Virginia. Birds and structural vegetation characteristics were sampled on 42 permanent stations. The 1984 and 1985 stations were considered undefoliated because whole tree defoliation did not occur until 1986. The 1987 and 1988 stations were categorized as defoliated or undefoliated based on canopy coverage and snag density values when compared to the pooled 1984 and 1985 station values. Some bird species showed higher frequencies of presence at defoliated compared to undefoliated stations, but no species showed lower frequencies of presence at defoliated stations.

For each of 32 bird species, two-group discriminant analyses were used to construct a bird presence gradient and a defoliation gradient based on vegetation characteristics at each station. Regression analyses were used to examine the dependency of canonical variable scores along the presence gradient and canonical variable scores along the defoliation gradient. Results showed that 17 species responded positively, 4 species responded negatively, and 11 species displayed no response to gypsy moth induced defoliation and tree mortality.

We suggest the short-term pattern of generally positive effects of gypsy moth defoliation on nongame birds is related to the increased amount of suitable habitat, increased habitat diversity, and increased food supply. However, a potential exists for the future reduction in reproductive success of many species because of increased nest predation and brood parasitism. Therefore, we caution that the long term responses of bird species to heavy defoliation and subsequent tree mortality remain unknown.

THE EFFECTS OF GYPSY MOTH INFESTATION ON GRAY SQUIRREL HABITAT AND POPULATIONS

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ABSTRACT

The overall objective of this project was to determine the effects of defoliation on gray squirrel habitat. We will evaluate the existing Habitat Suitability Index (HSI) Model for gray squirrels on the University Forest and determine the effects of thinning on HSI values computed for thinned and unthinned stands. Habitat variables used in the U. S. Fish and Wildlife Service gray squirrel model were measured on 8 10-12 ha treatment (to be thinned in spring 1990) and 8 unthinned stands on the University Forest, Morgantown, WV, and 3 other nearby hardwood tracts. Six different habitat variables were measured on 112 0.04-ha plots using standard forest measurement techniques. Squirrel abundance was measured on these same stands from 6:00-9:00 AM from June-October 1989 using time-area counts.

Habitat Suitability Indices for each stand varied from 0.13 to 0.54. Pearson's correlation was used to test the association between habitat variables and HSI values to determine what variables were needed in the regression model. Four of six habitat variables were significant, but all six variables were put into the model. Multiple regression analysis was used to determine if HSI values were dependent on the habitat variables. The analysis showed that HSI values were dependent on hard mast copy, total canopy closure, mean dbh of overstory trees, and hard mast species diversity ($R^2 = 0.97$, $n = 19$, $P<0.0001$).

Fifty-nine squirrels were counted during 154 morning counts. No relationship was found between squirrel counts and HSI values ($R^2 = 0.15$, $P = 0.235$). Causes might be too few squirrel counts, low numbers of squirrels, too few den trees, too few mature mast producing trees, or poor mast production in previous year. In general, good squirrel habitat was clumped within the stands. It was in these areas that higher HSI values were obtained and squirrels were seen. Thus, we had higher squirrel counts, while the overall HSI values were low and few squirrels were counted there.

EFFECTS OF GYPSY MOTH INFESTATION ON AESTHETIC PREFERENCES AND BEHAVIOR INTENTIONS

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Using the Scenic Beauty Estimator (SBE) approach, within-stand color photographs were taken of 27 forested sites representative of the Central Appalachian Plateau. These sites had been repeatedly infested by gypsy moth (*Lymantria dispar*) (GM) to varying degrees since 1985, with resulting tree mortality from 6% - 97%. Eighty-one slides (3 slides/site) were randomly arranged and presented to 415 subjects. Subjects were composed of professional foresters, forestry students, recreation students, members of the Izaak Walton League, and a pool of general students. Within each group, half of the respondents were told the damage was caused by GM and the other half were not told. In order to evaluate the effect of GM on recreation visitation, half the subjects rated the slides for scenic beauty (SBE) and the other half for likelihood of visiting (LOV).

Analysis of the ratings revealed no differences in the ratings according to group membership, knowledge of the presence of GM, or which questionnaire (SBE or LOV) respondents received. All respondents were therefore pooled in order to develop a single predictive model. Potential predictor variables included % basal area dead, mean tree height, mean DBH, % oak basal area, stand age, and total basal area. Since mountain laurel (*Kalmia latifolia*) flowers tend to be more abundant in sites with high mortality, additional potential predictor variables included the number of slides/site with visible mountain laurel flowers and the % of mountain laurel regrowth above 1 foot.

A quadratic function of tree mortality by preference rating best described the variablity in ratings ($R^2 = .60$). The effect of flowering Mountain Laurel was also significant with the covariate "slides/site with visible flowers" increasing the R^2 to .74. Scenic preferences and appeal for visitation increased initially as mortality approaches 20-30%. Up to this point, increased sunlight, visual penetration, and undergrowth may have mitigated the negative effects of mortality. As mortality exceeded 20-30%, however, ratings dropped sharply.

Consistent with past studies, college students appear to provide a good representation of the general public in regard to reaction to forest insect damage. The potential for bias resulting from a group's views of proper forest management does not seem to be a factor in regard to preference ratings. In addition, basic awareness of the presence of insect damage did not significantly influence ratings, suggesting the limited usefulness of information or education efforts aimed at shaping public responses to GM damage. Finally, scenic beauty preferences appear to be closely linked to recreation behavior intentions, thus providing managers with a relatively simple and inexpensive surrogate measure of visitor behavioral responses to insect damage.

USING SILVICULTURE TO MINIMIZE GYPSY MOTH IMPACTS

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ABSTRACT

Several studies are underway to test and evaluate the use of silvicultural treatments to minimize gypsy moth impacts. Treatment objectives are to change stand susceptibility to gypsy moth defoliation or stand vulnerability to damage after defoliation. Decision charts have been developed to help forest and land managers to select the appropriate treatment for their forest and insect conditions. Extensive plots to test silvicultural manipulations have been and are being established by several state organizations including the West Virginia Division of Forestry, Ohio Division of Forestry, Pennsylvania Bureau of Forestry, and several private companies and consulting foresters. Other states (Michigan, Indiana, Virginia) are close to establishing plots. These extensive plots will be monitored for gypsy moth defoliation and mortality which will be used to compare with control stands in the same areas.

Intensive plots are established on the West Virginia University Forest in cooperation with the WVU Division of Forestry. Two treatments, presalvage thinning and sanitation thinning, are being tested against paired control stands. In addition to measures of defoliation and mortality, regeneration, seed production, gypsy moth life stages and mortality sources, predators, and secondary organisms are being measured in the plots. A research and demonstration area has been established in the Arnold's Valley Opportunity Area, Glenwood Ranger District, Jefferson National Forest as part of the AIPM Project. Silvicultural treatments will be established and followed in conjunction with control stands and stands treated with low- and high-level insect control tactics.

The use of both intensive and extensive plots to evaluate silvicultural treatments maximizes the amount of information that can be obtained from a limited funding base. As the installed treatments are defoliated and mortality is documented, the effectiveness of using silvicultural treatments can be determined.

EFFECTS OF GYPSY MOTH-ORIENTED SILVICULTURAL TREATMENTS ON VERTEBRATE PREDATOR COMMUNITIES

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ABSTRACT

The impact of forest thinning, as an alternative gypsy moth management technique, on insectivorous birds and small mammals is being investigated in the West Virginia University Forest. The effects of thinning on predation of gypsy moth larvae and pupae by vertebrates are also being examined. Pre-thinning studies were conducted during the spring, summer, and fall of 1989 in 8 control stands and in 8 stands scheduled to be thinned during the winter of 1989-1990. Insectivorous birds were spot-mapped, and small mammals were pitfall and snap trapped to estimate abundance per stand. Mast traps were erected to estimate seed production per stand.

Cage exclosures of gypsy moth larvae and pupae were distributed to determine sources and magnitudes of predation. The three exclosure types were a control allowing all sources of predation, 1 inch screen excluding predation by birds, and 1/2 inch screen excluding predation by birds and small mammals. Exclosures were located at ground, trunk, and foliage levels. Results for the larvae trial showed that small mammals and invertebrates were important ground predators, invertebrates were important trunk predators, and predation was low from all sources in the foliage. For the pupae trial, small mammals were the dominant predators on the ground, and predation was low at trunk and foliage locations.

A tracking technique was developed to examine differential predation of larvae and pupae by small mammals. The circumferences of styrofoam plates were painted with a mixture of fluorescent powder and petroleum jelly. The plates were baited with either a larva or pupa and collected after 1 week exposure periods. The tracks on plates with a preyed larva or pupa are currently being examined under ultraviolet light to discriminate predation by mice and shrews.

DEMONSTRATION OF THE GYPSY MOTH ENERGY BUDGET MICROCLIMATE MODEL

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ABSTRACT

The use of a "User friendly" version of "GMMICRO" model to quantify the local environment and resulting core temperature of GM larvae under different conditions of canopy defoliation, different forest sites, and different weather conditions was demonstrated.

The model is a steady-state, one dimensional, numerical simulation of hardwood forest canopy and sub-canopy microclimate which was developed to examine some insect-host-environment interactions. The microclimate sub-model calculates radiation, leaf and air temperatures, and vapor pressure profiles. Soil and litter temperatures are calculated by the force-restore method. Caterpillar temperatures at each layer and for two contrasting resting positions are calculated with a four term energy budget equation. As the canopy undergoes defoliation by the insect, the model calculates the projected changes in microclimate.

In the PC version demonstrated here, the user can easily input various sites (slope, aspect, latitude), forest canopies, weather conditions, insect instars and time of the day. Therefore, comparisons of various conditions can be made and the effects of changes in these variables on the microclimate and larvae temperature at various locations in the forest from the top of the canopy to beneath the litter can be quantified.

The model can similarly be used to examine the physical environment of predators and parasites. Researchers in these areas are encouraged to try using the model.

The authors will give it, with instructions and help, to anyone interested in using it. It currently requires an IBM 286 PC or compatible to run the user friendly menu version. It can be made available as uncompiled Fortran77 code for use on the DG system or other mainframes.

MICROMETEOROLOGICAL MEASUREMENTS DURING THE BLACKMO 88 SPRAY TRIALS

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ABSTRACT

Instrumentation was arrayed on a 120 foot tower to detail the local atmospheric conditions during the Blackmo 88 spray experiment. Measurements were continuous for 30 minute periods encompassing each spray pass. Vertical profiles of wind, temperature, humidity, heat and momentum flux, radiation and three component turbulence intensity were measured during each run. In addition, simultaneous upper air wind temperature were measured from the nearby mid-state airport with an acoustic radar operated by the Meteorology department of PSU. In all, 9 hours (18 runs) of data were taken over a period of 3 days, and a very high quality, complete data set was obtained for use in analyzing the deposition patterns.

The mean 30 minute profiles of temperature and wind from the various times of day show completely different thermal stability regimes during various times of day. The turbulence measurements during each run demonstrate that minute-to-minute changes in turbulence, solar heating, leaf wetness and local atmospheric stability are severe enough to cause wide disparities in the patterns of spray drift and deposition. The upper air measurements show that the most preferred times for aerial spraying, early morning and late evening, are periods of rapid stability transitions in the lower atmosphere and, therefore, uncertainty in drift patterns in spite of the low wind speeds at these times.

The data is now being used to correlate spray deposition patterns to local atmospheric conditions and to test the FSCBG model.

DETECTION OF LATENT NUCLEAR POLYHEDROSIS VIRUS IN THE GYPSY MOTH

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ABSTRACT

It is unclear if and precisely at what level the nuclear polyhedrosis virus (NPV) of the gypsy moth persists in its' insect host. DNA hybridization, the method currently used for the detection of persistent viral infections, can only detect 100 to 1,000 copies of the viral genome per cell. It is likely that viral genomes persist in insects at levels far below this. Using polymerase chain reaction (PCR), we have developed a method for the detection of viral DNA at a level of one copy of the viral genome per 100 cells. This assay holds considerable promise for determining if the gypsy moth virus persists in insects since it is very sensitive, highly specific for gypsy moth viral DNA and can be used for DNA samples extracted from a single embryo.

GYPSY MOTH LIFE SYSTEM MODEL

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ABSTRACT

The model is composed of four major subsystems that are driven by weather. The stand subsystem incorporates the effects of damage by the gypsy moth into annual tree diameter and height growth as well as tree mortality. These calculations are driven by ambient temperature accumulated for a year. The gypsy moth, predator/parasite, and pathogen subsystems are driven by the difference between daily minimum and maximum temperatures that are accumulated into 30 degree-day steps (step size can be altered by the user). Rain can also decrease gypsy moth development rates. Weather data can be introduced or stochastic weather generation requested. The gypsy moth subsystem follows the growth of the nominal insect in each cohort, density of insects, and larval movement between strata. The predator and parasite subsystem follows several natural enemy guilds and species that have been determined to be significant mortality agents of the gypsy moth; feedback is provided for some of these populations as gypsy moth is their food source. The pathogen subsystem follows naturally occurring nucleopoly-hedrosis virus (NPV), and introductions of both NPV and *Bacillus thuringiensis* (Bt) as insecticides. This subsystem models distribution of NPV in the environment and in infected gypsy moth.

The spatial scope of the model is a single forest stand. No spatial coordinates of trees are needed but the model does use vertical stratification of the tree canopies. The stand is partitioned by tree species and diameter class for calculation of tree growth and mortality and for calculations of foliage biomass for use in the gypsy moth portion of the model. Stand variables are updated once each year; these updates include stand management prescriptions imposed by the user.

Foliage, gypsy moth, and natural enemies are followed on a finer time scale within each year. After sufficient degree-day accumulation, foliage begins to grow and gypsy moth eggs begin to hatch. As long as the current generation of gypsy moth exists, each accumulated 30 degree-days produces another simulation step. Following the completion of an insect-generation cycle, annual summary accounts and links to the stand model are completed for a year, and another year produces another generation. These routines operate on a spatial scale that aggregates among the diameter classes for each tree species present. Four strata are distinguished: (1) overstory trees, (2) understory trees, (3) boles of overstory trees, and (4) a shrub and ground layer.

Four input data files are required and three others are optional. These provide the users with maximum flexibility in controlling the model. There are a number of table and plain ASCII text files that can be generated; the latter are designed for use as input to graphic packages or for use in statistical analyses.

MODIFIED LIGNIN SULFONATE FORMULATION FOR THE PHOTO PROTECTION OF GMNPV

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ABSTRACT

Many potentially useful insecticides and herbicides undergo relatively rapid degradation on exposure to sunlight. This research studied the formulation and behavior of a novel water-soluble carrier which was designed to form thin surface layers over leaves and stalks. This formulation contained a modified lignin sulfonate, photoreactive cross-linking agents and GMNPV. The research demonstrated that this formulation is converted by sunlight into a crosslinked film which is both water-insoluble and protects GMNPV from UV light. Bioassay studies demonstrated that this approach is as effective as the Forest Service formulation used for GYPCHEK. However, the modified lignin sulfonate formulation contain approximately one-fifth as many PIBs to achieve the same LD_{50}. Future tests will be performed in bogs to evaluate efficacy under damp conditions.

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STATISTICAL COMPARISONS OF AGDISP PREDICTION WITH MISSION III DATA

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ABSTRACT

Statistical comparison of AGDISP prediction were made against data obtained during aerial spray field trials ("Mission III") conducted in March 1987 at the APHIS Facility, Moore Air Base, Edinburg, Texas, by the NEFAAT group (Northeast Forest Aerial Application Technology). Seven out of twenty one runs were observed and predicted means (O and P), mean bias error (d) standard deviation of the difference (σ_d), root mean square error of the difference (RMSE), and average absolute gross error of the difference (|d|), index of agreement (r), variance comparison (Var), fraction of positive residuals (f_p) and average relative error (RE=RMSE/O) of prediction.

Also, the test of the sensitivity of AGDISP to its input parameters was done in this study. AGDISP was first run by using parameters that were designated as the "typical condition". The meteorological parameters were obtained by averaging each variable over twenty one runs, those for aircraft, such as aircraft weight, flight height and speed, were average values in the field trials, and nozzle configuration and a droplet spectrum were the same as used during field trials.

Then, AGDISP was run for several test cases and the same statistical parameters as mentioned above were calculated using predictions for these cases and the "typical condition".

The results of our studies indicate the following:

1. Without applying the catch efficiency to measure data, the average relative errors of AGDISP prediction over the seven runs was 70% and 80% for number and volume deposition, respectively. The ranges of errors for the individual runs were from 32% to 158% for droplet number density and from 43% to 208% for volume density. For the measurement data corrected for collection efficiency of 0.7, these mean errors were 83% and 81% for droplet number and volume density, respectively.
2. When a sensitivity study was conducted with AGDISP, with variations in flight height within 30% of the normal height of 15.5 m, predictions by AGDISP varied by 61% and 27% for droplet number and volume density, respectively.
3. For application under wet or dry spray conditions, AGDISP predicted variations in volume deposition within 82% of that for typical condition. With light winds (<1 m/s), differences in deposition predicted by AGDISP were within 42% of "typical condition" for droplet number density and zero for volume. While with strong wind (about 7 m/s), these values are 20% and 36%.
4. When half the number of nozzles fitted to the aircraft were modelled, or no vertical offset was included in the input parameters, AGDISP outputs varied by up to 10% in volume deposition and up to 5% in droplet number density when compared to runs made under the actual configuration. With 10 nozzles or uniform distribution along the spray boom, variations in deposition were within 38% of typical values.
5. Variations in AGDISP output with a four size droplet spectrum as input parameters were within 6% and 18% of that obtained with an eight size spectrum for droplet volume and number density, respectively. With a single size spectrum, predicted variations in droplet volume and number density were 73% and 104% of that with the eight spectrum.

A MULTIPLE REGRESSION MODEL FOR PARASITIZATION OF GYPSY MOTHS BY THE INTRODUCED LARVAL PARASITE *COTESIA MELANOSCELUS* (HYMENOPTERA: BRACONIDAE)

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ABSTRACT

Cotesia melanoscelus (Ratzeburg) is a bivoltine, solitary, endoparasite of larvae of the gypsy moth, *Lymantria dispar* (L.). Imported from Europe after the turn of the century, it readily became established and now occurs throughout the generally infested area. Rates of parasitization are highly variable, particularly during the second (overwintering) parasite generation when females attack third and fourth instars of the gypsy moth. Detailed observations on parasitization of gypsy moths by this species were made in yellow pine-hardwood stands at Belleplain State Forest on the coastal plain of southern New Jersey during 1982-1989. Each year of the study, *C. melanoscelus* was the dominant larval parasite of *L. dispar*.

Multiple regression analysis of 10 variables monitored over the 8-year period indicated that temperature, host density, abundance of overwintering cocoons (formed the previous year), and basal area of oaks within the stand were the most important factors affecting rates of parasitization by this braconid during its second generation. When rates of parasitization were plotted against mean temperatures during the period from May 1 to June 15 (includes the attack period of adults emerging from overwintered cocoons, development of the first parasite generation, and the attack period of adults emerging from first generation cocoons), a second-order regression gave a rather good fit ($r = 0.568$), suggesting that the gypsy moth is favored at moderate temperatures, but that the parasite is favored at low or high temperatures. Second generation parasitism was positively correlated ($r = 0.408$) with the parasite to host ratio, that is, the previous year's parasite cocoon counts divided by the present year's gypsy moth larval counts. Parasitization was negatively correlated ($r = -0.267$) with the basal area of oaks in the stand, a variable considered to serve as an index of the area to be searched by the parasites. The multiple regression model obtained by using these three variables as predictors accounted for 51% of the variation in rates of parasitization by second brood *C. melanoscelus*.

DOES PREVIOUS STAND MANAGEMENT INFLUENCE GYPSY MOTH-RELATED MORTALITY?

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ABSTRACT

Oak-hickory forest stands were sampled for tree mortality using a series of temporary plots. Stands were classified by gypsy moth defoliation and by thinning treatment timing. Uncut, undefoliated stands had a 12.1 percent mortality (sq. ft. basal area/acre), while thinned, undefoliated stands had mortality rates of 3.6 to 7.2 percent. Defoliated, uncut stands ranged from 17.6 to 55.7 percent mortality depending on defoliation intensity and frequency, while thinned, defoliated stands had mortality rates ranging from 10.2 to 51.7 percent. Significant differences in mortality occurred between thinning treatments in undefoliated stands. Defoliated stands, due to high variability, showed few significant differences due to thinning. Thinning of forest stands does accomplish its goal of reducing mortality in undefoliated stands, however, the effect is not present when stands are defoliated. Defoliation causes increased mortality in larger size stems while maintaining mortality rates of small stems.

GYPSY MOTH IMPACTS ON OAK ACORN PRODUCTION

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ABSTRACT

Gypsy moth outbreaks can have drastic effects on many forest resources and uses. Because gypsy moth prefers oak foliage, oak stands are the most susceptible to defoliation and resultant damage. The value of oak mast for many wildlife species is high. The high carbohydrate content of acorns provides the energy necessary for winter survival. Loss of mast crops due to direct and indirect effects of gypsy moth defoliation may result in large-scale reductions in wildlife habitat and food sources.

Direct defoliation effects during years of moderate and heavy defoliation can come from three sources: direct consumption of flowers, abortion of immature acorns due to low carbohydrate supply, and lack of flower bud initiation. These effects are generally short-lived, having residual effects for only 1 or 2 years after defoliation ends. Information available to date suggests that abortion of immature acorns is the most significant of these three effects. It is possible to go for 2 to 5 years in succession with complete failures of acorn production.

Longer term indirect effects of outbreaks result from: crown dieback and poor vigor, mortality of oaks and hickories, and shifts in species composition of current and regenerated stands. These effects can reduce viable seed for regeneration and wildlife food. Crown dieback can turn productive acorn producers into nonproducers. Trees may take as long as 10 years to recover their full vigor. Mortality of mast producers in stands is distributed across a wide range from low to moderate to heavy. Estimates of the impact of mortality on stand-level acorn production show that considerable mortality (>60 percent of the basal area) must occur before significant reductions in acorn production occur. This result is due to mortality occurring primarily in intermediate and suppressed trees that are not heavy producers. This thinning from below may even stimulate production by residual trees. Many stands that were predominantly oak before defoliation and mortality occurred have regenerated to red maple and black birch. This shift in composition results in a long-term reduction in mast production in these areas.

THE WEST VIRGINIA UNIVERSITY FOREST HAZARD RATING STUDY: THE HAZARDS OF HAZARD RATING

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ABSTRACT

The West Virginia University (WVU) Forest is a 7,600-acre tract located along the leading edge of gypsy moth infestation. The hazard rating study at the WVU Forest serves three objectives. First, hazard rating is being used to determine the extent and distribution of damage that can be expected when gypsy moth defoliation occurs. Second, susceptibility and vulnerability equations currently available in the literature are being tested. Finally, through the use of computer technologies such as geographic information systems (GIS), the project demonstrates how to streamline the hazard rating process by applying surrogate variables (e.g. aspect and slope position) for prediction variables that are expensive to measure (e.g. species composition and site index).

Two of the 23 compartments at the WVU Forest were chosen for an in-depth stand analysis. Data were collected on a 1-chain grid to delineate stands. More complete data (including variables used in published hazard rating systems) were collected on a subsample of plots and analyzed using the Silviculture of Allegheny Hardwoods (SILVAH) software. Stand maps were developed and these were compared to stand maps made in the 1950's. The data from the SILVAH plots were used to compute gypsy moth hazard using several susceptibility and vulnerability equations.

The display shows the result of applying these hazard rating equations to six stands in the Fire Tower Block at the WVU Forest. We expect that the high proportion of oak (>75% of the basal area) makes stands 1-3 highly susceptible and vulnerable to gypsy moth. We also expect stands 5 & 6 to be relatively immune to defoliation because of their low proportion of oak (<25%). The three susceptibility equations that we used classified all 6 stands as probably resistant to defoliation. The two vulnerability rating systems developed by Gansner and Herrick predict 5% stem loss in all six stands. The vulnerability equation developed by Crow predicts higher mortality in stands 1, 5, & 6 (>29% basal area loss) than in stand 2 & 3 (20%). Though defoliation has not occurred, we still expect the highest damage to occur in stands 1-3.

Differences in the conditions of stands used to develop these models and those at the WVU Forest seem to account for the unexpected predictions. We are currently building new equations using data from the Appalachian Plateau and are expanding the testing of published models at the WVU Forest. For more information on gypsy moth hazard rating see the paper by Hicks in this proceedings.

INTERACTIVE EFFECTS OF DEFOLIATION AND LOW RESOURCE LEVELS ON PHOTOSYNTHESIS, GROWTH, AND GYPSY MOTH LARVAL RESPONSE TO RED OAK SEEDLINGS

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ABSTRACT

The potential for defoliation of oak seedlings by gypsy moth is quite high. We were interested in examining the interactions between various natural stresses and resulting gypsy moth feeding preferences and the results of defoliation stress on the growth and photosynthetic responses of the oak seedlings. A factorial greenhouse experiment was carried out with northern red oak (*Quercus rubra* L.) seedlings. The seedlings were grown under one of eight conditions: high or low light, high or low nutrients, and high or low water in a split-block design with shade cloth over half of the blocks. After two months of growth under these conditions, one-half of the seedlings were completely defoliated manually. This foliage was fed to fourth instar gypsy moth larvae in a preference test with leaf discs from each of the eight treatments in a petri dish. At the end of three months, photosynthetic parameters were measured on a subsample of the seedlings. After four months, trees were harvested, separated into stems, roots, and leaves, leaf area measured, and dry weights obtained. Seedling mortality was also compared for the defoliation treatments.

Photosynthetic quantum yields were similar for plants in all treatments. Light compensation point was significantly higher and dark respiration rate significantly greater for plants grown in high light than for plants grown in low light, an expected acclimation pattern. there were no significant interactions with defoliation. However, there was a significant defoliation x water interaction for maximum net photosynthesis, such that defoliation increased photosynthetic rate when drought stress was present (compensatory photosynthesis), but not when water was plentiful.

Defoliated plants had a 32.6 percent mortality rate; significantly higher than that of undefoliated plants (1.3 percent). Dry weights and leaf areas ere significantly reduced by most of the factors. Two-way interactions of stresses with defoliation were significant and in most cases positive, in the sense that defoliation had a lesser effect in depressing growth in the presence of stress than when resources were abundant. There were no significant effects on root:shoot ratio. There were differences in gypsy moth larval leaf consumption/preference due to stress factors. Foliage grown under high light was preferred over foliage produced under shade stress.

The number and magnitude of interactions among stresses imposed in this study were unexpectedly high. Stresses interacted to affect photosynthetic properties, leaf characteristics, and growth. Defoliation x stress interactions on tree responses to defoliation were pronounced.

PREDICTING DEFOLIATION BY THE GYPSY MOTH USING EGG MASS COUNTS AND A *HELPER* VARIABLE

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ABSTRACT

Traditionally, counts of egg masses have been used to predict defoliation by the gypsy moth. Regardless of the method and precision used to obtain the counts, estimates of egg mass density alone often do not provide satisfactory predictions of defoliation. Although defoliation levels greater than 50% are seldom observed if egg mass densities are less than 600 per hectare (250/acre), data from Melrose Highlands and the Intensive Plot System (IPS), as well as recent data from New Jersey and Pennsylvania, reveal that egg mass densities above this "threshold" result in damaging defoliation in less than 50% of the observations.

The accuracy of defoliation predictions can be greatly helped by including measures of the habitat and quality of the population in the predictive function. Using data from the IPS, several measures of habitat, i.e., site index, stand basal area, % oak in the site, and soil moisture class, improved predictions. An index of soil moisture (scores of 1-4) obtained from SCS maps was most helpful. Measures of population quality that were helpful included fecundity, vertical location of the egg mass, and incidence of viral infection in larvae emerged from an egg mass.

Instead of providing complex models that need to be solved to obtain a prediction of defoliation level, the models were used to construct an isogram of 60% predicted defoliation for each soil class across a range of egg mass densities and population quality. The example given shows that >60% defoliation occurred in only 9 of the 38 cases where egg mass density was above 250 EM/acre (dashed line). The isogram shows how using egg mass location in conjunction with density can greatly increase accuracy of defoliation predictions; it correctly classified 34 of the 38 cases where density was above 250 egg masses/acre. This illustrates how the accuracy of gypsy moth defoliation predictions can be improved when information on habitat and population quality is used along with estimates of population density.

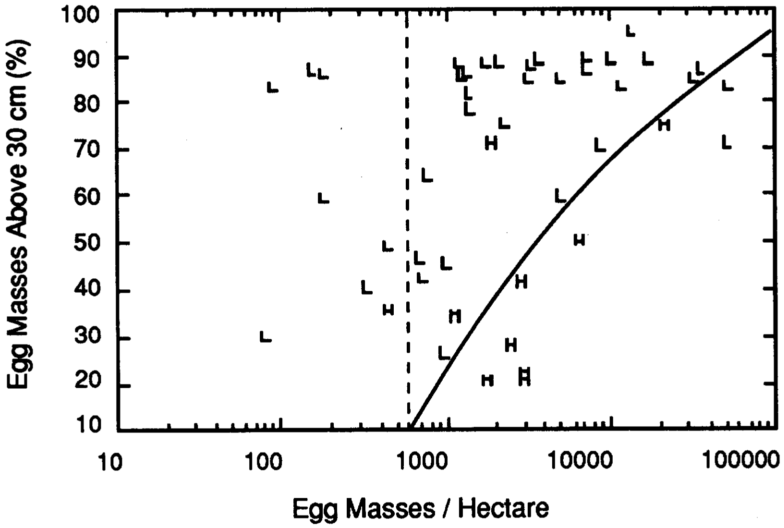

Figure 1. Actual observations of < 60% (L) and > 60% (H) defoliation on a dry site. The dashed line is a typical suppression-action threshold and the solid line is the prediction of 60% defoliation for dry sites.

IDENTIFICATION, CLONING, AND EXPRESSION ANALYSIS OF THREE PUTATIVE *LYMANTRIA DISPAR* NUCLEAR POLYHEDROSIS VIRUS IMMEDIATE EARLY GENES

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ABSTRACT

Viral immediate early gene products are usually regulatory proteins that control expression of other viral genes at the transcriptional level or are proteins that are part of the viral DNA replication complex. The identification and functional characterization of the immediate early gene products of *Lymantria dispar* nuclear polyhedrosis virus (LdNPV) will further our understanding of viral pathogenesis at the molecular level and may yield insights into a molecular means of enhancing viral potency. In addition, the transcriptional promoters of these genes can be used to drive the expression of foreign genes inserted into the viral genome.

Lymantria dispar nuclear polyhedrosis virus (LdNPV) early transcripts were identified through northern analysis. RNAs isolated from 652Y cells, infected with clonal isolate 5-6 (CI 5-6), 2 and 7 hours postinfection were probed with LdNPV genomic fragments from a cosmid library. Fifteen viral transcripts were detected: three were chosen for further study. A cDNA library was constructed (in lambda gt11) from poly A+ RNA isolated from 652Y cells 7 hours after infection with CI 5-6, and probed with LdNPV genomic fragments containing the coding sequences for the three genes of interest. Several positive plaques for each gene were identified and used for further study.

The clone lambda LdIE-I contains a cDNA of 880 bp and is derived from a transcript of approximately 950 bases in length. This gene, designated IE-I, is initially expressed 4 hours postinfection (p.i.), and is synthesized throughout infection at near steady state levels. At least three other distinct viral transcripts were identified that contain IE-I sequences. The approximate genomic location of the IE-I gene is from 6.0 to 6.7 map units. In addition, IE-I contains sequences with limited homology to the *Autographa californica* NPV gene IE-N. The clone lambda LdIE-G1 contains a cDNA of 750 bp that is derived from a gene (termed IE-G1) that codes for a transcript of approximately 750 bases in length. IE-G1 is expressed primarily from 2 to 10 hours p.i. (the transcript is detectable after a 1 hour adsorption period), and maps to the genomic area between 9.3 and 13.7 map units. The clone lambda LdIE-G2 contains a cDNA of 1950 bp that is derived from a gene (termed IE-G2) that codes for a transcript of approximately 2050 bases in length that maps to the genomic region between 9.3 and 13.7 map units. IE-G2 is expressed primarily from 4 to 10 hours p.i., and is first detected 2 hours p.i. In addition, at least 4 other viral transcripts overlap the IE-G2 gene.

UNDERSTANDING PREDATION: IMPLICATIONS TOWARD FOREST MANAGEMENT

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ABSTRACT

It is generally accepted that when gypsy moths rest in the litter survival is low due to predation by ground-foraging generalist predators and that predation can maintain these populations indefinitely. Forest Service research on predators of gypsy moth continues to focus on population dynamics, the mechanisms of predation and forest management implications.

It has been shown that abundance and diversity of small mammals differed considerably among forest stands that varied in potential susceptibility to defoliation by gypsy moth. In particular, stands most susceptible to defoliation had fewer small mammals and, hence, it is hypothesized that predators at these sites had a reduced effect on gypsy moth populations. At Bryant Mountain in Vermont, year to year differences in survivorship of gypsy moth pupae were strongly influenced by predator density particularly *Peromyscus leucopus*. It was also shown that within year differences in survivorship of pupae (when comparative *Peromyscus* densities in both the susceptible and resistant stands were similar) resulted from differences in the vertical stratification of cover which affects the foraging behavior of small mammals and the increased availability of more palatable alternative foods, especially low bush blueberry (*Vaccinium* spp.), which significantly reduces the consumption of arthropods in the diets of small mammals. The interrelationships between predator density, type and spatial distribution of cover and availability of alternative foods offer a number of forest management implications. Forest and wildlife managers should focus more attention on the habitat requirements of small mammals, particularly those that are ground foraging generalists, to insure their impact in maintaining innocuous gypsy moth populations.

Recent visits to the Soviet Union to study gypsy moth predator-prey interrelationships have provided (1) important information regarding the convergent evolution of ecological equivalents to vertebrate predators of the gypsy moth in the U.S., and (2) a better understanding of the role of predators in Soviet forest protection. Species studied included *Apodemus sylvaticus*, *A. flavicollis*, *Clethrionomys glareolus*, and *Dryomys nitedula*.

The objectives in researching the relationship between predator impact potential and forest management implications are twofold. First, to ascertain the possibility and feasibility of habitat manipulation which could enhance the magnitude of predation and, second, to provide sufficient information which would enable forest managers to avoid inadvertent detrimental consequences that would reduce or possibly eliminate predator community impact as a result of applied selected forest management practices thereby encouraging management practices that are compatible with maintaining natural predator communities. Long-term studies, which are designed to access abundance and habitat relationships of small mammal communities on a localized scale, are still needed to give additional insight into the importance of small mammals to the population dynamics of gypsy moth and also to determine their role in future management scenarios which would reduce the susceptibility of northeastern deciduous forests to defoliation by gypsy moth. Specific management implications derived from these and subsequent studies focusing on predator-prey relationships will allow: (1) more accurate classification of forest stand susceptibility; (2) more reliable gypsy moth population forecasting; (3) the development of useful life system models; (4)

more effective integrated pest management; and (5) the evaluation of silvicultural practices on predator-prey interactions and stand susceptibility to defoliation.

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CHANGES IN VERTICAL DISTRIBUTION OF XYLEM PRODUCTION IN HARDWOODS DEFOLIATED BY GYPSY MOTH

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ABSTRACT

Trees distribute the production of xylem through the bole in an unequal manner. Defoliating insects such as the gypsy moth (*Lymantria dispar*) affect the balance of that distribution. Historical defoliation data were combined with detailed stem analysis of 49 mixed oaks (*Quercus rubra, Q. alba, Q. prinus, Q. coccinea, Q. velutina*) and associated species, including red maple (*Acer rubrum*), in southern New England. The cross-sectional area of an annual ring within the branch-free bole was normally greater toward the base despite a greater ring width at the base of the crown. In years of very poor growth due to defoliation or other causes, the cross-sectional area approached uniformity through the branch-free bole. Partial rings and missing rings were evident in the understory red maple, but never in the oaks, despite growth rings as small as 0.1 mm.

In some oak species growth was reduced overall by as much as 50% in years of defoliation, and a continued effect was observed for three years after a defoliation. Assuming one two-year defoliation episode each decade, volume growth of surviving trees was reduced 9.7% overall. Increased growth in neighboring, non-defoliated trees was significant in the year of defoliation and again three years afterward. Compensatory growth in the year following defoliation was found only in red maple. A redistribution upward was detectable in all defoliated trees, but did not affect the overall form of the bole, due to the cumulative nature of stem taper.

USING RIBOSOMAL RNA TECHNOLOGY FOR CLASSIFYING MICROSPORIDIA

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ABSTRACT

The microsporidia are an obligately parasitic group of protists with a number of unusual cytological and molecular characteristics. They have no mitochondria, their nuclear division is primitive, their ribosomes and ribosomal RNA's are reportedly of prokaryotic size, and their large ribosomal subunit contains no 5.8S rRNA. There are about 87 microsporidian genera that are based primarily on spore shape, numbers of nuclei in the spore, nature of the sporophorous vesicle, and several ultrastructural characteristics of the spores and vegetative stages. Because they have few other morphological characters it is difficult to develop phylogenetic relationships and identify specific isolates of microsporidia.

Molecular sequencing methods have been useful in establishing the phylogenetic relationships of higher taxa, including Microsporida. These same sequencing methods are currently being used to develop a phylogeny of microsporidian genera and to identify specific microsporidian species. Portions of the 23S and 16S rRNA have been sequenced for all five species of microsporidia isolated from the gypsy moth.

The sequences of the gypsy moth microsporidia were compared and a phylogenic tree developed by the use of parsimony analysis. Based on these results, we can distinguish all of the five species of gypsy moth microsporidia and we believe that rRNA sequences can be used for identifying most other species of microsporidia. The use of rRNA has great promise in the development of probes for species specific identifications because of the high copy number of ribosomes in cells.

We currently need relatively large quantities of pure microsporidian spores in order to obtain rRNA sequences, but the use of newly developed techniques (PCR) to amplify specific rRNA genes or pieces of DNA should greatly reduce the quantify of spores needed for restriction enzyme analysis.

ARCHITECTURE OF THE BLACK MOSHANNON FOREST CANOPY MEASURED BY HEMISPHERICAL PHOTOGRAPHS AND A LI-COR LAI-2000 SENSOR

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ABSTRACT

Non-destructive measurements of light penetration were made at 10 heights in the canopy on twelve different sites in the PA oak forest where the Blackmo 88 spray-micrometeorological experiment was conducted. Vertical profiles of Leaf Area Index, LAI, were calculated from these measurements, and the data were used to define the spatial variability of the forest canopy density.

Two different sensors were used for the light measurements, a remotely controlled camera with a 180 degree hemispherical lens (polar projection) and a LI-COR LAI-2000 radiation sensor. The paper presented the physics and mathematical theoretical background for these measurements. The two sensors generally performed similarly with some differences near the top of the canopy.

The average leaf area index in this stand during the spray experiment was 3.72 square meters of leaf area per square meter of ground. This was reduced to 3.02, a 19% reduction, during partial defoliation in 1989. Spatially, the canopy was quite variable. The standard deviation of the leaf area density over the 12 measurement locations was approximately 70% of the mean (3.02).

This experiment demonstrated a relatively simple non-destructive sampling technique to measure leaf area distributions in mature forest stands. The realistic use of model simulations for spray operations or insect-host interactions will require the documentation of the leaf area distribution characteristics of a large range of forest types and stand densities. The sensors and techniques used here are dependable, accurate and inexpensive ways to accomplish this.

AERIAL APPLICATION OF *BACILLUS THURINGIENSIS* TO AN OAK FOREST: DEPOSIT ANALYSIS AND PREDICTIONS WITH FSCBG

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ABSTRACT NOT RECEIVED

USDA Interagency Gypsy Moth Review
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East Windsor, Connecticut

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Eight invited papers and 68 abstracts of volunteer presentations on gypsy moth biology, ecology, impacts, and management presented at the U. S. Department of Agriculture Interagency Gypsy Moth Research Review.

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