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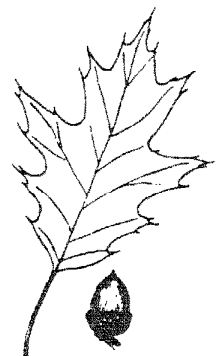
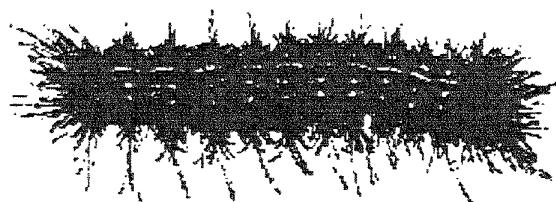
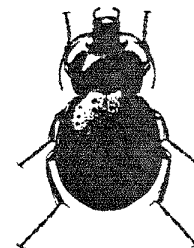
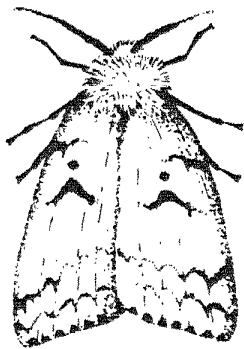
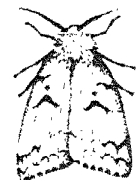
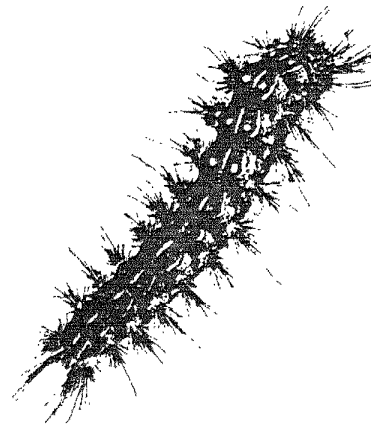
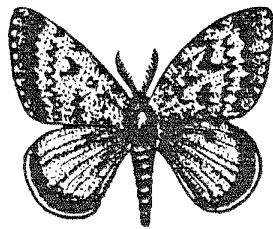
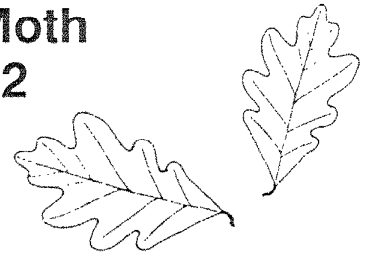
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Proceedings

U.S. Department of Agriculture Interagency Gypsy Moth Research Forum 1992



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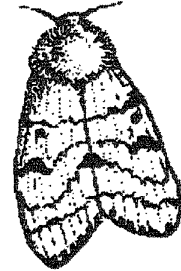
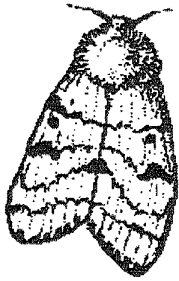
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1992



January 13-16, 1992
Loews Annapolis Hotel
Annapolis, Maryland

Edited by
Kurt W. Gottschalk and Mark J. Twery

Sponsored by:

Forest Service Research

Forest Service State and Private Forestry

Agricultural Research Service

Animal and Plant Health Inspection Service

Cooperative State Research Service



FOREWORD

This meeting was the third in a series of annual USDA Interagency Gypsy Moth Research Forums that are sponsored by the USDA Gypsy Moth Research and Development Coordinating Group. The Committee's original goal of fostering communication and an overview of ongoing research has been continued and accomplished in this meeting.

The 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, Agricultural Research Service (ARS)
C. Schwalbe, Animal and Plant Health Inspection Service (APHIS)
R. Riley, Cooperative State Research Service (CSRS)
T. Hofacker, Forest Service-State and Private Forestry (FS-S&PF)
M. McFadden, Forest Service-Research (FS-R), Chairperson

USDA Interagency Gypsy Moth Research Forum
January 13-16, 1992
Loews Annapolis Hotel
Annapolis, Maryland

AGENDA

Monday, January 13

REGISTRATION
POSTER DISPLAY SESSION I
WELCOME MIXER

Tuesday, January 14

PLENARY SESSION Moderator: Max McFadden, FS-R

Welcome
M. McManus, FS-R

Forest Health Monitoring and the Gypsy Moth
Gerard Hertel, FS-S&PF

The Potential for Biotechnology in Forest Pest Management
Lois Miller, Univ. Georgia

PLENARY SESSION, continued Moderator: W. Wallner, FS-R
Asian Gypsy Moth Problem
Presenters: P. Schaefer, ARS; S. Bogdanowicz, Cornell Univ.; W. Wallner, FS-R

CONCURRENT SESSION I Moderator: E. Dougherty, ARS
Recombinant DNA Technology
Presenters: J. Slavicek, FS-R; N. Dubois, FS-R

CONCURRENT SESSION II Moderator: L. Butler, WVU
Effect of *Bt* on Non-Target Organisms
Presenters: J. Peacock, FS-R; B. Sample, West Va. Univ.

POSTER DISPLAY SESSION II

Wednesday, January 16

CONCURRENT SESSION I Moderator: T. O'Dell, FS-R
Abnormal Performance Syndrome (APS)/Insect Rearing
Presenters: J. Tanner, APHIS; M. Keena, FS-R

CONCURRENT SESSION II Moderator: A. Liebhold, FS-R
 Phenological Modelling
 Presenters: D. Gray, VPI; J. Logan, VPI

POSTER DISPLAY SESSION III

CONCURRENT SESSION I Moderator: V. Mastro, APHIS
 Sterile Insect Technique, Pheromone Disruption
 Presenters: M. Montgomery, FS-R; D. Leonard, FS-S&PF

CONCURRENT SESSION II Moderator: K. Gottschalk, FS-R
 Forest Type Suitability in Newly-Invaded Areas
 Presenters: F. Sapio, MI DNR; W. Berisford, Univ. GA

GENERAL SESSION Moderator: G. Hertel, FS-S&PF
 The Knowledge Bases Behind GypsES
 Presenters: M. Saunders, Penn. State Univ.; M. Twery, FS-R; L. Schaub, VPI; M. Foster, Penn. State Univ.; J. Ghent, FS-S&PF

Thursday, January 17

CONCURRENT SESSION I Moderator: N. Leppla, APHIS
 Biological Control Revisited
 Presenters: R. Weseloh, Conn. Agric. Exp. Sta.; A. Hajek, BTI

CONCURRENT SESSION II Moderator: M. Montgomery, FS-R
 Insect Host Interactions
 Presenters: R. Lindroth, Univ. Wisc.

GENERAL SESSION Moderator: W. Ravlin, VPI
 Sampling for Decision Making
 Presenters: A. Liebhold, FS-R; K. Thorpe, ARS

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BIOLOGICAL CONTROL REVISITED

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Animal & Plant Health Inspection Service, Methods Development,
Federal Building, Hyattsville, MD 20782

WORKSHOP SUMMARY

Recent administrative and biological events have provided new opportunities to reconsider biological control of the gypsy moth. At the national level, the Animal and Plant Health Inspection Service (APHIS) has established the National Biological Control Institute to promote, facilitate and provide leadership for biological control regardless of institutional affiliation. An immediate and very important goal is to design and establish new procedures for issuing permits to release beneficial organisms. These procedures will expedite the process of foreign exploration, laboratory assessment, importation, release and evaluation of parasites, predators and pathogens for use in controlling the gypsy moth in specific situations. Equally special is the new Interagency Biological Control Coordinating Committee (IBCC) of the United States Department of Agriculture. It has just generated and sponsored the National Biological Control Program (NBCP) to accelerate research, development and implementation of biological control throughout the United States. Another notable event is the recently initiated study, "Pest and Pathogen Control Through Management of Biological Control Agents and Enhanced Natural Cycles and Processes," being conducted by the National Academy of Sciences, National Research Council, Board on Agriculture. This study is intended to scrutinize national research needs, regulatory constraints, and impediments to the implementation of biological control. Biological events that have provided the impetus to revisit gypsy moth biological control involve its geographic radiation and associated population dynamics. The gypsy moth has become well established in northeastern North America; however, it continues to spread, mainly to the south and west. This has led to a strategy of attempting to retard its movement in both directions. The boundary of this geographic radiation seems to have three zones: I. Invasion (scattered, discrete populations), II. Transition (continuous infestation), and III. Establishment (defoliation and population collapse). In addition to the European gypsy moth in eastern North America, the Asian gypsy moth has invaded the West. The latter is more mobile because the females fly and it has a wider host range. Clearly the pest status of the gypsy moth is increasing and greater emphasis is being placed on reducing the severity of its damage and restricting its geographic distribution.

The goal of this workshop was to increase awareness and stimulate creative thinking about new opportunities for using biological control to suppress gypsy moth populations. Tom ODell (Forest Service, FS) explained the context for gypsy moth biological control in the NBCP (classical, augmentation and conservation) and emphasized conservation biological

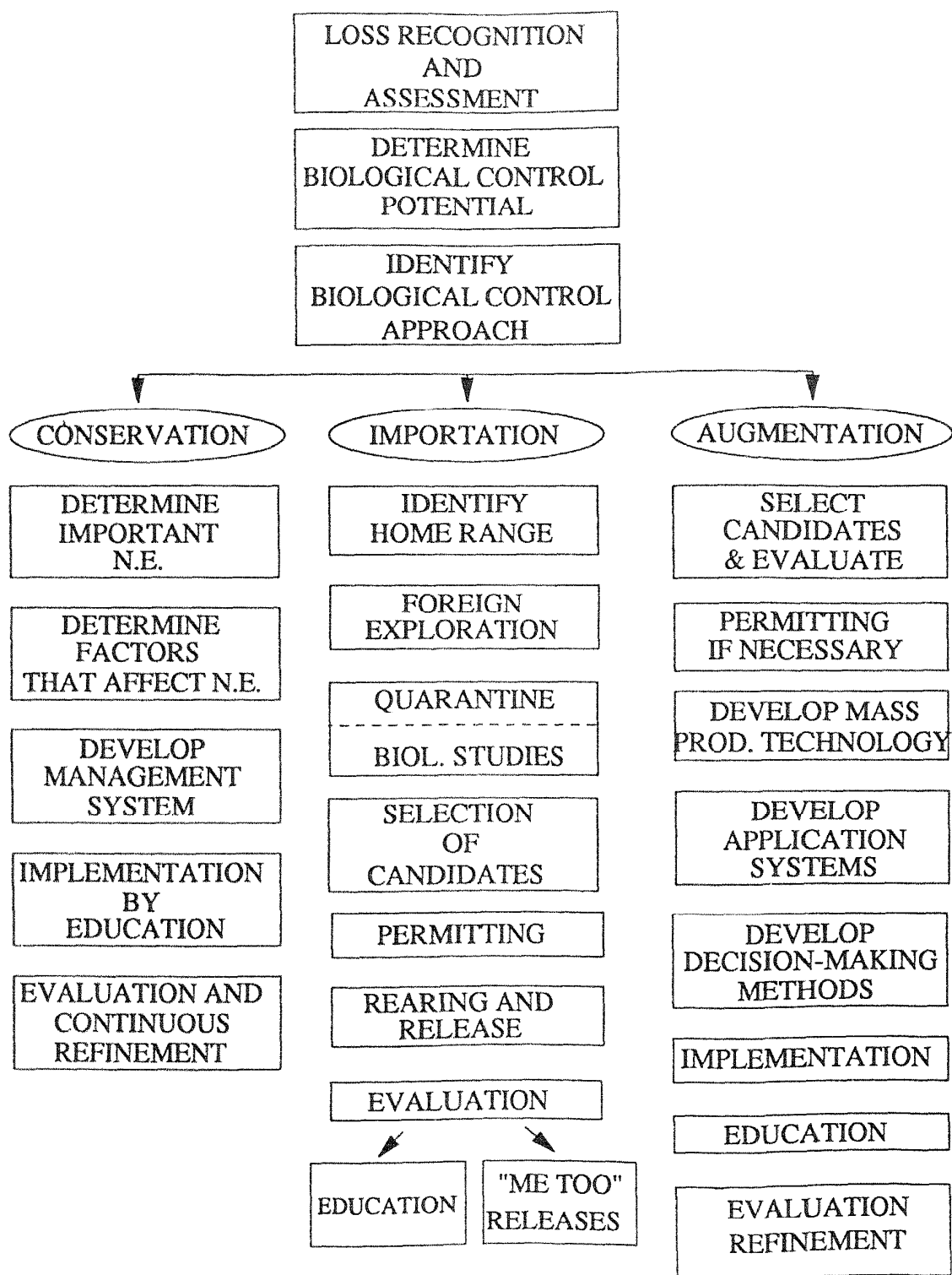


Figure 1. Major actions in the process of implementing classical (importation), augmentation, and conservation biological control (N.E. is natural enemy).

control (Figure 1). Roger Fuester (Agricultural Research Service, ARS) described classical biological control, the importation and release of natural enemies. Ron Weseloh (Connecticut Agricultural Experiment Station) presented augmentation biological control by using predator examples and Ann Hajek (Boyce Thompson Institute, Cornell University) interjected examples of all three approaches, with emphasis on microbial agents. The forum encouraged interaction by providing structured discussion enhanced with specific questions and answers. This dialogue will be emphasized, rather than the comprehensive information in individual presentations. Readers are encouraged to contact the speakers and other participants for more information and indepth discussion.

NATIONAL BIOLOGICAL CONTROL PROGRAM

The USDA, NBCP is an interagency biological control program to be funded and administered by the Cooperative State Research Service (CSRS), ARS, APHIS, and FS. This initiative will focus long overdue attention on biological control, a vital and essential pest management strategy. The NBCP is a highly targeted program directed at solving pest problems and providing the basic knowledge necessary to deliver biological control technology to the producer and the public. This initiative will provide for dynamic interaction among basic science, developmental science, education, and implementation for the purposes of discovering new biological control agents, understanding biological relationships necessary to improve the use of these agents, and implementing practical systems for biological control of pests.

Biological control makes maximum use of natural cycles and interactions of pests and their natural enemies that already are operating in agricultural, forest and urban areas. In cases where natural interactions do not provide economic control, three approaches are used to enhance biological control. Efforts to conserve and enhance the effects of these organisms are commonly referred to as "conservation". Naturalized pests can be controlled by one-time or occasional introductions of biological control agents, typically obtained from the geographic origin of the pest. This method is "classical" biological control. Other pests can be controlled only by repeated introductions of one or more agents, "augmentation", sometimes with each planting or several times during a growing season.

CLASSICAL BIOLOGICAL CONTROL OF GYPSY MOTH

Roger Fuester explained that foreign exploration for natural enemies has occurred throughout most of the home range of the gypsy moth: Europe, Japan, Taiwan, Algeria, Morocco, Tunisia, Soviet Far East, China and others. Parasites have typically shown more promise than predators and pathogens. However, many potential biological control agents remain to be evaluated by studying host acceptance, specificity, and preferred stage; diapause induction and termination; and mating and oviposition enhancement. Selection of candidates focuses on species that are: 1. Univoltine, 2. New or untried, and 3. Found to attack female gypsy moths

preferentially. After selection, permits are obtained from APHIS, one for importation and another for release. Better methods are needed for optimal host and parasite rearing and for release of correct stages and sex ratios of parasites. It is essential to identify habitats suitable for release and to involve appropriate cooperators. Pre-release and post-release biological and economic evaluation is recommended with 3-year follow-up. Successful cases of biological control must be documented and publicized.

David Onstad (Illinois Natural History Survey) expressed concern that parasites be examined for pathogens, particularly microsporidia that can have a negative effect on development.

Ann Hajek described recent studies on a fungus imported in 1910 to control the brown-tail moth. The fungus, *Entomophaga maimaiga*, reappeared in the Northeast in 1989 on gypsy moth, having been obscure during the intervening years. Also, a microsporidian was imported from Europe to control the gypsy moth but, due to federal regulations, it has only been released in 10-acre plots.

Paul Schaefer (ARS) asked if the fungus was the same as the one released in 1910. Ann Hajek responded that it is assumed to be the same. She also cautioned that there are public and scientific concerns about the introduction of exotic insect pathogens.

Sandy Liebhold (Forest Service) asked if it is worthwhile to explore for more strains of *E. maimaiga* and, if so, where? Ann Hajek recommended exploration in places with different climates.

Vicente Sanchez (Forest Service) noted that microsporidia have a wide host range in both vertebrates and invertebrates, and this could be a concern for future introductions. Joe Maddox (Illinois Natural History Survey) responded that there is no evidence of cross infectivity between these taxa for specific microsporidia.

Tom ODell suggested that *Compsilura concinnata*, a parasite initially imported from Europe in 1906, probably would not be released because of its wide host range and potential for impacting rare and endangered Lepidoptera. He also has been unable to release the polyphagous braconid, *Glyptapanteles liparidis*, which was imported from China, because he can not provide a complete host list.

Bill Kauffman (APHIS) questioned the currently accepted host range of the tachinid, *Ceranthia samarensis*, since testing has been conducted only in Canada and not during all seasons. Roger Fuester commented that very little is known about this species and that it is difficult to study because it has about 80% incidence of diapause.

Mark Ticehurst (Gypsy Moth Management Group) asked who would be responsible for this critical pre-release and post-release evaluation in the absence of support from the State Departments of Agriculture. Roger Fuester thought APHIS could help.

AUGMENTATIVE BIOLOGICAL CONTROL OF GYPSY MOTH

Ron Weseloh explained that *Calosoma sycophanta* was imported into Massachusetts from Europe in 1905-1910 to aid in biological control of the gypsy moth. It became established easily, and as of 1929, was present throughout many of the gypsy moth-infested areas of North America (Burgess and Crossman 1929). Today, it is common throughout most of New England and extends into New York, New Jersey, central Pennsylvania, and northeast Maryland.

C. sycophanta is a specific natural enemy of the gypsy moth that is well adapted and synchronized to its prey. Beetles remain inactive during years when gypsy moths are scarce, only feeding and reproducing when the pests become abundant. Consequently, the beetle is very closely attuned to the gypsy moth outbreak cycle. The beetle cannot disperse rapidly, but a relatively low number of adults is able to produce enough larvae to cause the destruction of many gypsy moth pupae. It is only necessary to have about 400 beetles per hectare in order for them to have an impact on gypsy moth populations. Having *C. sycophanta* established throughout the entire gypsy moth infested region would be advantageous.

Ron Weseloh recommended increased emphasis on biological and economic evaluation of natural enemies to quantify benefits, rather than expect funding on the basis of "faith". This kind of evaluation requires experimentation (i.e., Campbell's work on the importance of small mammals). Ants should be evaluated because they seem to be important predators of early instar gypsy moth larvae in forest litter. Perhaps their activity could be increased by spraying small trees with sugar solution. In other situations, ant traps could be used to decrease the number of ants and thereby determine their influence on gypsy moth abundance.

Bill Kauffman (APHIS) contributed information on his efforts to establish an evaluation system for natural enemies of the Russian wheat aphid. This work was divided into at least three categories: 1. Techniques for natural enemy establishment, 2. Evaluation of "check plots" to determine their presence or absence, and 3. Economic evaluation emphasizing relationships between natural enemy establishment, pest densities and plant health. He further commented that this kind of work may be possible with *C. samarensis*, an effective parasite of low density gypsy moth populations. Forestry Canada has a rearing facility at Saint Foy, Quebec, where they can produce enough of these parasites to conduct field studies in Ontario. Moreover, they have made great progress in rearing this parasite and anticipate additional improvements in the near future. *C. samarensis* has demonstrated an exceptional searching ability and appears to have a narrow host range. It is only known from the gypsy moth and one other lymantriid.

Joe Elkinton (University of Massachusetts) asked why the potential importance of *C. samarensis* was not discovered earlier. Roger Fuester answered that a few specimens have been found in Austria but it is more abundant in Eastern France and Western Germany, particularly in areas near Switzerland. It is also found 300 miles on either side of the Rhine

River. None of these areas have been adequately explored. Forestry Canada has a contract with the International Institute of Biological Control at Delemont, Switzerland for collection and shipment of a population of *C. samarensis* adults each year. It is necessary to obtain more parasites annually because they are host specific and difficult to rear. Paul Schaefer thinks that *Ceranthia* may be synonymous with *Siphona* and this taxonomic confusion may explain why so little is known about *C. samarensis*.

Ron Weseloh asked if Forestry Canada has considered field release of *C. samarensis*. Bill Kauffman responded that it has been released but has not become established, probably because it needs an alternate host for over wintering. Jim Vaughn (ARS) reminded that release permits in the U.S. require analysis of potential native targets. Norm Leppla agreed and described an effort within APHIS to renew their permitting system. This effort is being lead by Ernest "Del" Delfosse, Director of the National Biological Control Institute. He also plans to conduct a national workshop emphasizing host specificity testing. He is eminently qualified due to his experience in defending the Australian Biological Control Act.

Ann Hajek returned to the subject of cost effective rearing and discussed the need for *in vitro* production of viruses. Gypchek® can be produced *in vitro* but not operationally at this time. Quality control is an important consideration. The cost of using Gypchek® may be competitive with other suppression technologies in the near future.

CONSERVATION BIOLOGICAL CONTROL OF GYPSY MOTH

Tom Odell discussed the topic by using the tachinid, *C. concinnata*, as an example. It has a wide host range and reasonably high base populations that could be maintained by establishing and conserving plants that are utilized by alternate hosts. The Chinese incorporate these "parasite food plants" in their forest management plans. However, very little is actually known about the food resources required by adult parasites and how food availability affects their viability. He also noted work in the Pacific Northwest that has enhanced ant populations by maintaining logs in the forest litter. He announced that the Forest Service is likely to increase "conservation" research in the near future.

Ann Hajek reinforced the importance of studying all aspects of environmental manipulation to enhance biological control. Use of the fungal pathogen, *E. maimaiga*, provides an example of the major methods for this manipulation. *E. maimaiga* was introduced from Japan in 1910 and 1911 to the Boston area, but by 1912 the introductions had been considered a failure. *E. maimaiga* was not reported from North America again until 1989, when epizootics due to *E. maimaiga* were found in seven northeastern states. The simplest explanation for this mysterious chain of events is that *E. maimaiga* actually became established 80 years ago and, at some time, began spreading from its introduction sites. Regardless of the uncertainty about the history of this fungus, it provides an example of very successful biological control.

Since *E. maimaiga* does not occur throughout much of the gypsy moth distribution, and is not

well-established in some areas where it exists. during 1990-1991 it was introduced into small plots in five states. In central New York, *E. maimaiga* was used to innoculatively augment existing low level populations and infection levels of 95% resulted in several plots. Using similar methodology, in 1991, *E. maimaiga* infections were recovered at 82.4% of introduction sites in Virginia, West Virginia, Maryland, and Pennsylvania. Although May and June, 1991, were extremely dry, epizootics occurred at several of these sites.

A solid understanding of ecological community dynamics is required to develop conservation of natural enemies. For example, a virus and fungus that affect the gypsy moth can occur in the same insect. However, the fungus is less effective at temperatures above 30° C but operates at a wider range of host densities. Epizootics occur at similar host densities for both pathogens but the virus is more effective at higher densities.

Kathy Shields (FS) asked which pathogen kills the insect when there is a mixed infection. Ann Hajek said that both are present when the insect is dissected and some individuals die from each. Joe Maddox commented that it is also important to know which organism arrived first and recommended increased research on this aspect of infection. Mark Ticehurst emphasized the role of soil moisture in determining the number of spores.

Ann Hajek described her work on resting spores relative to soil moisture. Conservation has been practiced with *E. maimaiga* by enhancing establishment during introduction. *E. maimaiga* spores are introduced at the bases of trees and watered at variable intervals to yield increased levels of infection. Joe Elkinton expressed the enormous potential for causing high mortality of gypsy moths in low populations by understanding and manipulating fungal reproduction.

Unfortunately, pathogens have not been exploited extensively for classical biological control. The primary reason for this circumstance is that exotic microorganisms are grouped with genetically engineered organisms for regulatory purposes, making the introduction process for pathogens much more difficult than for parasites and predators.

ACKNOWLEDGMENT

I thank Tom ODell for organizing this workshop and accepting responsibility for assuring its success. His enthusiasm and indefatigable efforts sustained and coordinated the program. I also thank the speakers and other participants who freely contributed their considerable expertise, experience, and precious ideas. I appreciate the special effort of Kathy McManus to record the proceedings and facilitate this documentation. Mike McManus graciously provided the opportunity for all of us to revisit biological control of the gypsy moth.

DEPOSITION OF AERIALY APPLIED *BT* IN AN OAK FOREST AND ITS
PREDICTION WITH THE FSCBG MODEL

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ABSTRACT

Seventeen single-swath aerial spray trials which were conducted over a fully leafed, 16 m tall, mixed oak forest. The distribution of cross-swath spray deposits were sampled at the top of the canopy and below the canopy. Micrometeorological conditions were measured above and within the canopy during the spray trials. The U.S. Forest Service FSCBG model was run to predict the target sampler catch for each trial using forest stand, airplane application equipment configuration, and micrometeorological conditions as inputs. Observations showed an average cross swath deposition of 100 IU/cm² (237.6 mg/m²) with large run to run variability in deposition patterns, magnitudes, and drift. Eleven percent of the spray material which reached the top of the canopy penetrated through the tree canopy to the forest floor.

FSCBG predictions of the ensemble average deposition was within 17% of the measured deposition at the canopy top and within 8% on the ground beneath the canopy. Run to run deposit predictions by FSCBG were considerably less variable than the measured deposits. Individual run predictions were much less accurate than the ensemble average predictions as demonstrated by an average Root-Mean-Square-Error (RMSE) of 30 IU/cm² (70.9 mg/m²) at the top of the canopy. Comparisons of the differences between predicted and observed deposits indicated that the model accuracy was sensitive to atmospheric stability conditions.

SEQUENCE ANALYSIS OF THE GYPSY MOTH VIRUS VIRULENCE GENE, p77

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ABSTRACT

DNA sequencing of the *Bg*/II-P fragment of LdNPV-g (19.9 to 22.3 map units) revealed the presence of a 2,016 nt ORF that could encode a polypeptide of 672 amino acid residues (76,944 Mr), and was designated p77. The predicted amino acid sequence of the LdNPV-g p77 gene has a 65.5% similarity and 46.1% identity with the AcNPV OB virulence protein gene, p74. Computer aided analysis of the predicted amino acid sequence of p77 revealed the presence of three very hydrophobic regions near the carboxy terminus, indicative of transmembrane domains, suggesting that this polypeptide may be a viral membrane protein. We have mapped two transcripts from this gene by primer extension analysis and S1 nuclease protection assays. The most abundant of the two transcripts mapped to a sequence 20 nt upstream of a consensus late baculovirus gene promoter (ATAAG), located at -213 to -209 relative to the p77 start codon (ATG). The minor transcript mapped to the 3rd nucleotide of a second consensus late baculovirus gene promoter (ATAAG), located at position -133. Also, two putative TATAA and one CCAAT boxes were identified. In vitro translation of hybrid selected mRNAs from *Bg*/II-P yielded a 77 KDa product, as determined by SDS-PAGE. Analysis of sequences surrounding the start codon of p77 has led us to propose a possible mechanism for translational regulation of this gene.

USE OF UV IRRADIATION TO INACTIVATE GYPSY MOTH VIRAL DNA ON THE EGG SURFACE

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ABSTRACT

In an attempt to answer the question of baculovirus persistence in insects, polymerase chain reaction (PCR) technology is being employed to examine DNA from embryos for the presence of viral sequences. Using gypsy moth eggs and the *Autographa californica* nuclear polyhedrosis virus (AcNPV) we determined that viral DNA from occlusion bodies OBs contaminating the surface of eggs is often amplified yielding false positive samples and confusing the interpretation of results from PCR experiments. This contaminating viral DNA was still PCR amplified after treatment of eggs with carbonate, proteinase and DNAase. Treatment of eggs with short wave UV light for 30 minutes completely inactivated all viral DNA from OBs contaminating the surface of the egg. This treatment did not alter egg viability and is currently being used as a routine procedure in the PCR analysis of gypsy moth embryos for persistent viral sequences.

EFFECT OF GYPSY MOTH VIRUS REPLICATION ON LARVAL DEVELOPMENT

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ABSTRACT

The effects of *Lymantria dispar* nuclear polyhedrosis virus (LdNPV) infection on gypsy moth larval development with respect to size, molting and pupation were examined. In later instars, virus infection was found to slow weight gain, delay the onset of apolysis, inhibit molting and block pupation. The magnitude of these effects increased with an increase in virus dose. Ecdysteroid UDP-glucosyl transferase activity (EGT) was observed in gypsy moth tissue culture cells infected with LdNPV. Differences in ecdysteroid titers in hemolymph from control and LdNPV infected larvae were also found. These observed consequences of virus replication may be the result of nutritional or hormonal interactions between virus and host and may have an effect on epidemiological studies on virus infected insects in the field.

EFFECTS OF *BACILLUS THURINGIENSIS* ON NON-TARGET INSECTS

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ABSTRACT

With increasing concern in recent years about environmental effects of Dimilin, state and federal agencies have increased the use of *Bacillus thuringiensis* var. *kurstaki* (*B.t.*) in gypsy moth (*Lymantria dispar* (L.)) suppression projects. *B.t.* is not without its own problems. The primary concern is for non-target Lepidoptera.

Miller (1990) found that *B.t.* significantly reduced total abundance and species diversity of non-target caterpillars. Venable (1990) estimated that of 223 baseline moth species in the Washington, DC? area, 48% are susceptible to *B.t.* and 34% are marginally susceptible. In our ongoing studies in WV, we are finding significant impact on non-target Macrolepidoptera larvae.

Sampling methods currently in use for non-target studies include light traps, malaise traps, tree banding, foliage pruning, and aquatic sampling. Samples are returned to the laboratory, sorted, and insects are identified. Two notable problems with non-target studies are the natural fluctuations of insect populations in the absence of treatment effects and the difficulty of identifying non-target Lepidoptera larvae to species. In our laboratories at West Virginia University, we use photography to document larval appearance and rearing to obtain easily identifiable adults. In this way, we have photographic documentation of about 170 species of forest canopy Macrolepidoptera larvae. We need to be as precise in our species identification as possible. Use of "feeding guilds" or "operational taxonomic units" may obscure patterns of treatment effects.

Issues which need consideration in on-going and future studies of *B.t.* non-target effects include (a) treatment parameters: application rates, formulations, and engineered strains, and (b) study parameters: appropriate sampling methods, appropriate plot size, adequate baseline data, adequate replications, appropriate statistical methods, consideration of use of indicator species, and a broad ecosystem approach involving indirect as well as direct *B.t.* effects.

INTRA-SPECIFIC VARIATION IN RESPONSE TO GYPSY MOTH HERBIVORY ON
RED OAK (*QUERCUS RUBRA* L.) SEEDLINGS

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ABSTRACT

Variation in response to gypsy moth defoliation within a host species may be a function of the host genotype. Acorns collected from nine maternal families of red oak (*Quercus rubra* L.) were germinated and grown in a greenhouse during the summer of 1991. Half of the members of each family were individually subjected to third-instar gypsy moth larval feeding for three days in July, and determinations of leaf area consumed, resistance to defoliation, larval weight change, and larval growth efficiency were made. Following a month of recovery by the seedlings, all were harvested so that biomass for stem, leaf, and root components could be determined.

Defoliated seedlings had lower survival, reduced leaf growth rates, and a different proportional allocation of biomass than their non-defoliated counterparts. Survival among defoliated individuals was positively correlated with pre-defoliation leaf area. Different families had high, not significantly different survival rates in the control group, but responded quite differently in the defoliated group. These differences appear to be a function of pre-defoliation leaf area, which differed among families and was due to significantly different leaf area growth rates. Family biomass allocation patterns differed among surviving, defoliated seedlings. There was no difference in larval growth efficiency on trees of different maternal families. However, larval absolute growth rate did differ among families, varying as a function of pre-defoliation leaf area. Resistance to defoliation was not significantly different among families. Seedlings with higher allocation to resistance had lower dry weights, though there was no difference in resistance between surviving and non-surviving individuals.

Assuming maternal effects were small, the results suggest a significant genetic component of individual variation in response to defoliation, which may be subject to differential selection in the event of herbivory.

SEQUENTIAL EGG MASS SAMPLE PLANS FOR URBAN HABITAT

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ABSTRACT

Sequential sample plans for gypsy moth egg masses have been developed for continuously forested areas in the Eastern United States. However they are not appropriate for areas influenced by the presence of man-made objects. The objectives of this study were to 1) develop sequential sample plans for gypsy moth egg masses in urban habitats and 2) develop a comprehensive sampling approach for gypsy moth egg masses in urban and forested habitats.

Data were acquired from Fairfax and Arlington Counties, Virginia. Fifty plots were used to develop the plans. Egg mass sample data were described using a negative binomial distribution. We calculated an index of aggregation value (K) of 0.44. The average sample number and operating characteristic curve were developed to determine the acceptability of the sample plans by gypsy moth managers. Three sequential sample plans based on the commonly used treatment thresholds were developed (Table 1). The upper and lower stoplines can be determined with the slope and intercept (negative intercept for lower stopline).

Use of the sample plans involves the gypsy moth manager laying an one mile grid over a county. In each plot, a minimum number of samples are taken. After the minimum number of samples have been taken the cumulative number of egg masses are compared to the stoplines. If the cumulative egg masses are above or below the stoplines sampling would cease. If the cumulative egg masses are between the stoplines sampling would continue until the cumulative number fell outside the stoplines or the maximum sample number was reached.

The comprehensive sample plan we would like to propose is a sample plan within a sample plan. It includes the use of binomial and sequential egg mass sample plans. A comprehensive sample plan would be developed for urban and forested habitats. Sampling would begin using a binomial sample plan. If a treatment decision could not be made after a predetermined number of samples, managers would begin using a sequential sample plan.

Table 1. Sequential sample plans for treatment thresholds of 250, 500, and 1,000 egg masses per acre.

Treatment Threshold (egg masses/acre)	Plan 1 250	Plan 2 500	Plan 3 1,000
Min Sample Number	7	8	8
Max Sample Number	18	23	24
Intercept	40.19	90.68	193.5
Slope	6.08	11.78	24.57

A SIMPLIFIED MODEL FOR THE PREDICTION OF THE EVAPORATION RATE OF PESTICIDE DROPLETS AERIALY SPRAYED FROM AIRCRAFT

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ABSTRACT

A simplified model was developed to predict the evaporation rate of pesticides aerially sprayed. Deposit data collected from field trials and analyzed by washoff and image analysis methods were used to test the model. Results showed that the model with a mode based on the theoretical evaporation formula of a droplet of pure water tended to overpredict the evaporation rate of *Bt* as much as 11% on average.

RECOMBINANT DNA TECHNOLOGY IN *BACILLUS THURINGIENSIS*

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ABSTRACT

The realization in the late 1970's that genes that encoded for insecticidal crystal proteins (ICP) of *Bacillus thuringiensis* (*Bt*) in susceptible insects were located on plasmids, precipitated a flurry of research activity in Recombinant DNA Technology. Susceptibility to *Bt* is associated with the affinity of these ICPs for receptors on the brush border membranes of midgut epithelial cells; larvicidal specificity appears to be related to specific binding characteristics including the affinity to and or the concentration of the receptor sites present in different insect species.

Our studies conducted in collaboration with D.H. Dean (Ohio State Univ.) and M. G. Wolfersberger (Temple Univ.) show that against second instar gypsy moth (*Lymantria dispar*), cryIA(a) ICP is approximately six times more toxic than the cryIA(c) ICP. Larval development was completely arrested by the cryIA(a) ICP at sublethal doses of 10 and 5 nanograms of protein per cm² of diet surface, and only partially arrested by the cryIA(c) ICP. At concentrations of 40 to 120 ng/cm², cryIA(a) ICP was dose-limiting where mortality leveled at around 78%. This effect was not observed with the cryIA(c) ICP. The addition of as little as 25 spores/cm² of a HD73cry⁻ mutant increased mortality 3 to 4- fold at all doses tested for each ICP; percent mortality increased when the spore concentration was increased to 250,000 spores/cm². Spores alone had no effect on larval mortality or development. Homolog-scanning mutagenesis was used to generate double reciprocal recombinants of the two cryIA genes. Bioassay of the chimeric proteins encoded by the recombinants resulted in the following: 1) exchange of either the conserved region (affecting AA residues 90-332 on the ICP) or the amino portion of the hypervariable region (AA residues 333-450) resulted in complete loss of all activity by the chimeric proteins generated from the altered cryIA(a) genes. The exchange on the altered cryIA(c) genes also resulted in total loss of activity by the chimeric proteins. 2) The exchange of the carboxy terminal portion of the hypervariable region of the cryIA(a) gene, generated a cryIA(a) chimeric ICP (AA residues 451-612) that was no longer dose-limiting compared with the original cryIA(a) ICP. This exchange also failed to result in the transfer of any insecticidal activity to the chimeric protein generated from the altered cryIA(c) gene. 3) Enhanced insecticidal activity as a result of spore addition was observed only when the chimeric proteins were insecticidal. It appears that the toxin specificity-determining region for the gypsy moth may be located partly in the carboxy terminal portion of the conserved region and partly in the amino terminal portion of the hypervariable region. This portion

corresponds to a previously uncontested variable 8 amino acids located between AA residues 282 to 333 on the ICP. Similar studies with other insect species have not implicated these amino acids and results with similar exchanges using homolog- scanning mutagenesis differed from the results obtained with the gypsy moth.

PREDICTING THE WITHIN-SEASON DYNAMICS OF GYPSY MOTH NPV EPIZOOTICS

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ABSTRACT

Biologists have made little use of recent advances in the mathematical theory of the dynamics of insect pathogens, because of difficulties with parameter estimation and misgivings about the simplicity of the models in question. We use an existing simple model for the dynamics of insect pathogens, slightly modified both to provide greater accuracy and to allow for more straightforward parameter estimation. We estimated each of the model parameters independently for the nuclear polyhedrosis virus (NPV) of gypsy moth (*Lymantria dispar* (L.)), estimating three of the four model parameters from the literature. To estimate the rate of transmission, we present an experimental protocol which involves fitting a reduced version of the model to data from a small-scale transmission experiment. Without circularity or curve-fitting, we tested the model with literature data giving initial densities and weekly NPV mortality for epizootics in eight gypsy moth populations on 4-9 hectare plots in Massachusetts, USA. The model predictions are reasonably accurate for five of the eight populations, suggesting that gypsy moth NPV dynamics within a season are driven by a small number of biological processes. The three populations for which the model did poorly began the season with low host densities, indicating that standard assumptions about disease transmission may not hold for gypsy moth NPV dynamics at low densities. These results suggest that future models of the dynamics of gypsy moth NPV should take into account changes in virus transmission with density.

PREDICTING THE SPREAD OF ENGINEERED VIRUS

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ABSTRACT

We performed two field experiments, one to quantify larval dispersal, and one to quantify virus spread. For both experiments, we used eggs that were collected from outbreak gypsy moth populations in and around Amherst. These eggs were surface-sterilized in 5% formalin to remove any pre-existing virus, and then deployed in the field in fiberglass screen packets (about 5,000 eggs per packet). Both experiments took place in Cadwell Forest, which has had an extremely low density of gypsy moths since 1982. To measure larval dispersal, we released 230,000 uninfected larvae (46 packets) on a central tree, and recaptured uninfected them using sticky traps placed in the canopy. Not surprisingly, most of the larvae dispersed in a downwind direction, and larval dispersal dropped off strongly with distance. To measure virus spread, we released 900,000 uninfected larvae (180 packets) uniformly over two 1 hectare areas, with 500,000 virus-infected larvae released at the center of each of the two plots. We began this experiment at the same time as the larval dispersal experiment, and began sampling at the end of that experiment, after larvae had dispersed. Surprisingly, initial larval dispersal was a very poor predictor of subsequent virus spread. Virus spread was downwind only in the third week after the virus was released (the first week of sampling). Similarly, virus incidence declined with distance only in the third week. Even though all the virus infected larvae started at the center of the plot, by the fifth week the fraction of larvae that were infected with the virus was virtually uniform over a six hectare area centered around each plot. No infections appeared in either of two control plots in which we released only uninfected larvae, and restriction analysis of a few samples from each plot confirmed that the virus that we collected was the virus that we released.

SPATIAL AND TEMPORAL ANALYSIS OF GYPSY MOTH DETECTION RECORDS IN FLORIDA

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ABSTRACT

Annual catches of male gypsy moths (GM) in Florida over the last 12 years have ranged from 29 in 1980 to 469 in 1990. The up and down pattern of moth catch generally corresponds with the acreage defoliated in the Northeast and Midwest. Most moths have been caught at campgrounds or recreational vehicle (RV) parks in the northern and central portions of peninsular Florida. Few males have been caught in the Florida panhandle even though this is the region with the greatest amount of suitable host material. Delimitation surveys have never shown any evidence of an established GM population.

In January 1991 we visited several RV parks which had high GM counts in 1990. Users of these parks tended to be retired persons spending the winter months in Florida. Hometown ZIP codes of 829 persons in 4 parks showed that well over half of them came from Michigan (25%), New York (13%), Pennsylvania (8.2%) and other northeastern states where GM is well established. We suspect that high percentages of short-term tourists and new residents also come from these areas.

The standard detection practice during the 1980s was to check GM pheromone traps at the middle and end of the May - August trapping period. Despite the low temporal resolution of these data, it is clear that many males were trapped well before the flight period of northern populations. Using the phenological model of Casagrande et al. (Environ. Entomol. 16: 556-562; 1988), we calculated that May-flying males likely come from eggs that hatch between March 1 and April 15. Late February to early April was also the period of greatest hatch for Massachusetts egg masses shipped to Florida from 29 August 1982 to 29 April 1983 (Mastro, Dixon & Toles, OMDC 1983 Ann Rpt). Many trees flush during March and at least a few neonates apparently locate acceptable and suitable hosts. In the absence of an established population, the early season males must come from human-vectored egg masses.

Specimens and identification reports in the Florida State Collection of Arthropods show that four hardwood defoliators (*Hyphantria cunea* (Drury), *Orgyia leucostigma* (J. E. Smith), *Malacosoma americanum* (Fab.), and *M. disstria* Hübner) of the northern U.S. occur

throughout much of Florida. Populations of these species fluctuate, but outbreaks occur only sporadically on small acreages. The host tree factors, meteorological factors, and natural enemies that regulate these species could well exert similar control on GM populations.

In summary, numerous GM egg masses are brought into Florida each year by new residents, winter residents, and tourists. The few traps with multiple males and the low annual counts indicate the GM survival rate is extremely low. We speculate that host-tree factors, natural enemies, and climate (long humid summer and mild winter) have so far combined to prevent gypsy moth population establishment.

DIFFERENTIAL MORTALITY IN MALE AND FEMALE GYPSY MOTH PUPAE ATTACKED BY INVERTEBRATE NATURAL ENEMIES

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ABSTRACT

Within the generally infested area, survivorship of females is of primary importance in the population dynamics of the gypsy moth, *Lymantria dispar* (L.), because there are sufficient males to ensure that females reaching the adult stage are fertilized. Therefore, we wished to determine the possibility of bias in attacks by invertebrate natural enemies on male and female pupae of the gypsy moth. Observations were made from 1983 to 1991 in mixed oak stands at Belleplain State Forest in southern New Jersey. Apparent causes of mortality in pupae were determined after completion of moth emergence. Where possible, 100 pupae were obtained from each site for a sample.

The introduced chalcid, *Brachymeria intermedia* (Nees), exhibited the strongest bias. Parasitization of male pupae was 2-6 times higher than female pupae in most years. Ovipositing females apparently are often dislodged by the vigorous movement of the relatively large female pupae. Parasitization by ichneumonids was generally low and exhibited no bias with relation to host sex. Ichneumonids are relatively large and might be better than *Brachymeria* at coping with large female gypsy moth pupae.

Mortality by tachinids and sarcophagids could not be distinguished and was grouped for analysis. There was a strong interaction between year and host sex, parasitization of male pupae being higher than female pupae in 1985, 1986, and 1988; lower in 1987; and similar

the other years. *Parasetigena silvestris* (R.-D.) was the dominant species recovered. *Blepharipa pratensis* (Meigen), a species reported to kill mostly female hosts, was very scarce.

Larvae of the introduced carabid, *Calosoma sycophanta* (L.), destroyed more gypsy moth pupae than other invertebrates. No bias was exhibited toward prey of either sex. Predation was highest when gypsy moth populations were relatively high. Other mortality, consisting mostly of disease and dehydration, varied from year to year, but not between sexes.

The bias of *Brachymeria* and tachinids in attacking male pupae contributed to the overall higher total mortality due to invertebrates in male gypsy moth pupae. There was an interaction between year and pupal sex, but mortality caused by invertebrates was clearly higher in male pupae than female pupae for 4 years in a row (1984-87). Because of the sex-based bias in mortality by invertebrate predators, sex ratios (% females) of adults were sometimes much higher than pupae, e.g., 58% vs. 41% in 1984 and 63% vs. 50 % in 1986.

EVALUATION OF SILVICULTURAL TREATMENTS TO MINIMIZE GYPSY MOTH IMPACTS

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ABSTRACT

An evaluation of the effectiveness of silvicultural treatments to minimize gypsy moth effects on forests is ongoing at the West Virginia University Forest. Two treatments, sanitation thinning and presalvage thinning, are being tested. Following defoliation in 1990 and 1991, preliminary estimates of defoliation, growth and mortality were measured on permanent plots. Defoliation patterns were similar in thinned and unthinned stands with susceptible species > resistant species > immune species. Tree vigor changed following defoliation with thinned stands having a higher proportion of healthy trees than unthinned stands. Net growth decreased following defoliation and mortality. Net growth of survivors increased for non-oaks, but decreased for oaks. Mortality in thinned stands was lower than for unthinned stands.

MODELLING GYPSY MOTH EGG PHENOLOGY THROUGH A PHYSIOLOGICAL INVESTIGATION

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ABSTRACT

Gypsy moth egg phenology is generally considered to comprise phases of prediapause, diapause, and postdiapause. Models of egg phenology have attempted to predict egg hatch without regard to the prediapause and diapause phases by assuming commencement of postdiapause on an arbitrary date. This has been necessitated by an inability to distinguish transition between any of the phases. The ability of these models to accurately predict egg hatch in areas geographically disparate from those of the models' origins has been disappointing.

A model of gypsy moth diapause has been proposed by Tauber *et al.* where individuals express an ever changing response to temperature, resulting in a gradual transition between diapause and postdiapause phases. However, data used to support this hypothesis can also be interpreted within the framework of a three phase model with discrete transitions between phases.

Thus an ability to distinguish the phases of gypsy moth egg phenology should improve our understanding of the process of gypsy moth diapause by permitting direct tests of the hypotheses of gradual versus discrete phase transition. It should also improve our estimates of the temperature-time requirements of egg hatch.

A technique to measure respiration rate of individual gypsy moth eggs (Gray *et al.* this volume) has been used to distinguish the prediapause and diapause phases and thereby to estimate a non-linear temperature-dependent prediapause developmental rate function. The technique is being utilized in ongoing experiments designed to estimate developmental rate functions of diapause and postdiapause, and to test hypotheses of phase transition. The technique has also been utilized in experiments designed to estimate the rates of depletion of stored triglycerides in an attempt to quantify the effects of non-lethal temperatures on egg survival.

A comparison of published single phase egg hatch models and the three phase model was conducted using hatch and hourly temperature records from Shenandoah National Park. Predictions of first egg hatch by the single phase models ranged from 20 days earlier

(model of Johnson *et al.*) to 15 days later (model of Lyons and Lysyk) than observed. The model of Johnson *et al.* overestimated variability of egg hatch in the population. Predicted 90% emergence was 5 days later than observed. The model of Lyons and Lysyk failed to capture the variability of egg hatch. Predicted 90% emergence was 5 days earlier than observed. Considering the absence of empirically derived estimates of developmental rates for the diapause and postdiapause phases, the three phase model did a good job of estimating egg hatch. Predicted first emergence was 12 days earlier than observed. However, by 10% emergence prediction trailed observation by 5 days and the remainder of predicted egg hatch was only slightly more variable than observed.

The three phase model was almost completely insensitive to oviposition date. Simulated oviposition dates ranging from June 15 to July 30 had no effect on simulated egg hatch. Thus it mimics certain biological functions of the diapause process. It produces seasonality and serves to synchronize the population.

A TECHNIQUE TO MEASURE RESPIRATION RATES OF INDIVIDUAL GYPSY MOTH EGGS

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ABSTRACT

Respiration rate is a physiological variable that is positively correlated with metabolic activity. As such it can be a valuable tool for distinguishing ontogenetic stages or for measuring physiological response(s) to a variety of environmental conditions. Unlike many biochemical assays, its non destructive nature permits repeated sampling during the course of an experiment.

Respiration rate has been shown to be a useful indicator of the diapause state. However, until recently techniques of respiration rate measurement required that investigators use several hundred individuals per sample when dealing with very small individuals such as gypsy moth eggs. This precluded the separation of diapausing from nondiapausing individuals within the sample and eliminated the ability to estimate the variability present in the population in its developmental response to the environmental variable under investigation.

We used an infrared gas analyzer (Licor 6251) to measure the respiration rate of individual gypsy moth eggs. Eggs reared under a variety of constant temperatures experienced a dramatic decline in respiration rate, indicative of the transition between the prediapause and diapause states. Observation of the transition permits measurement of the temperature-time requirement of the prediapause phase of ontogeny and estimation of the variability of this requirement in the population. Similar measurements can be made to determine the temperature-time requirements of diapause and postdiapause, and to investigate the manner in which the transition between these two phase is made. Such information can then be used in constructing a model of egg phenology.

INTRODUCTION AND SPREAD OF *ENTOMOPHAGA MAIMAIGA* ALONG THE GYPSY MOTH LEADING EDGE

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ABSTRACT

In April, 1991, we collected soil containing resting spores of *E. maimaiga* from a site in Massachusetts that had experienced high levels of mortality from the fungus the previous year. Approximately 0.7 kg of soil was placed around the base of five oak trees at each of 34 sites in Virginia, West Virginia, Maryland, and Pennsylvania. Some of the sites received 1 liter of water at the base of each tree. Fifteen additional sites received sterilized potting soil as controls. Cadavers of gypsy moth containing *E. maimaiga* were recovered from 27 of 34 release sites, despite the fact that rainfall in May and June was below normal throughout the region and temperature was higher than normal, conditions that are not optimal for *E. maimaiga*. Percentages of larvae that were positive for *E. maimaiga* at release sites varied from 0% to 81.21%, and averaged 23.98% (SE=4.87). Infection levels in plots where spores received water were greater (mean = 15.76% SE=7.04) than infection levels at comparable plots that did not receive water (mean = 3.54% SE=2.18). *E. maimaiga* was recovered from sites up to 350 m from the point of release. Percentage of cadavers infected with *E. maimaiga* declined with distance from the site. *E. maimaiga* was also recovered from a few cadavers from 3 of 15 control sites. This raises the possibility that the occurrence of *E. maimaiga* at both release and control sites was caused by the natural spread of the agent from areas further north. The far higher levels of infection in most release sites, and the decline of infection with distance from the central release point indicates that the main source of infection was the infected soil placed at the center.

SPECIFIC ATTACHMENT OF GYPSY MOTH VIRUS TO INSECT CELLS

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ABSTRACT

Among baculoviruses, the nuclear polyhedrosis viruses (NPV) consist of two distinct phenotypes, the polyhedra-derived virus (PDV) and the budded virus (BV). PDV initiates the primary infection in the insect midgut, while BV is responsible for establishment of secondary infections in other tissues. While previous studies suggest that BV exhibits specific receptor binding to insect cells, the present research represents the first evidence for specific binding of PDV. Fluorescence-activated cell sorting (FACS) analysis revealed saturable binding of FITC-labeled PDV (PDV/FITC) from *Lymantria dispar* NPV to the gypsy moth cell line, IPLB-Elta. Competition for limited receptors was found when PDV/FITC was incubated with excess levels of unlabeled PDV. In addition, excess levels of unlabeled BV effectively competed with PDV/FITC suggesting that both viral phenotypes may be able to use the same receptor. While it is known that BV enters host cells by the pathway of adsorptive endocytosis, PDV does not use this pathway and the exact mechanism of entry of this phenotype is unclear. The present work will provide initial information necessary for an understanding of the mechanism by which PDV establishes the primary infection in the insect midgut.

ABNORMAL PERFORMANCE SYNDROME IN THE GYPSY MOTH:
DIET AND PARENTAL EFFECTS

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ABSTRACT

Abnormal performance syndrome (APS) in the gypsy moth is characterized by poor hatch, reduced survival, and slow asynchronous development. Several comparison tests have been conducted to define specific factors involved in the induction and expression of APS. Expression of APS is mediated, primarily, by dietary ingredients. Rearing environment and diet processing can accentuate the expression of APS by further slowing development. The following conclusions can be made about the role of various dietary ingredients in the expression of APS: (1) methylparaben and sorbic acid are not involved in the expression, and (2) interactions between wheat germ, casein, and vitamins, in part, cause the expression. APS must be induced in the parental generation if the progeny are to express it. The specific factors involved in the induction process must still be determined. However, dietary factors (something lacking or contained in the diet) and/or environmental factors are known to be involved in the process. The incidence of APS varies between families and within strains and between strains indicating a genetic component. In addition, APS is present in wild strains in the first laboratory generation indicating that APS can be induced in nature. Thus, in addition to improving laboratory production of gypsy moth, an understanding of the cause and effects of APS may improve our knowledge of population dynamics of wild populations and open new possibilities for the development of biotechnology control strategies.

NEW APPROACHES TO SAMPLING FOR DECISION MAKING

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ABSTRACT

Every year, over a million acres of forest are sprayed, as part of the USDA Forest Service Co-operative Suppression Program and other programs that are designed to reduce or prevent the impacts of defoliation by the gypsy moth. Specific procedures vary among the various states and agencies that participate in these programs, but nearly all of the programs within the generally infested area rely on pre-season counts of egg masses in order to evaluate the necessity of treating stands.

A variety of procedures exist for counting egg masses. The most commonly used method is the use of multiple fixed radius plots (typically 1/40th acre). This method is time consuming. The "five-minute walk" was a technique developed to estimate egg mass density using less labor. Under this method, observers simply walked through the stand and kept count of all visible egg masses. Eggen and Abrahamson presented an algorithm for converting these counts into the more conventional expression of density as egg masses per acre. Recently, Liebhold et al. and Fleischer et al. found that this technique was subject to bias and did not provide estimates with an adequate level of precision.

Using this system, do managers generally make good predictions about defoliation and consequently make good management decisions? Unfortunately, we presently don't have an exact answer to these questions but considerable evidence suggests that decision errors are in fact quite common. Many stands where pre-season counts indicate no defoliation will occur and treatment is therefore unnecessary, end up getting defoliated. Conversely, many stands where pre-season counts indicated defoliation will occur, would not become defoliated even if they were not treated. There are probably two reasons for these errors: 1) measurement error that occurs from taking relatively few egg mass samples from a heterogeneously distributed population and 2) intrinsic error about the relationship between the true pre-season egg mass density and subsequent defoliation. Mitigating this problem will entail dealing with both of these problems.

Twenty-five years ago, Campbell recognized that the dynamics of gypsy moth populations are affected by population conditions in nearby areas; there is often considerable synchronicity in yearly fluctuations in the development of gypsy moth outbreaks. Typically populations seem to rise and fall in synchrony over large regions, probably as a result of similar weather effects on population processes. Though astute managers take advantage of information on regional conditions and population trends, this procedure is rarely formalized

in the decision-making process. In the future, information from regional monitoring systems will be used, along with stand-level information as a method for improving our defoliation predictions.

GEOSTATISTICAL MODELS FOR FORECASTING GYPSY MOTH OUTBREAKS

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ABSTRACT

Outbreaks of the gypsy moth, *Lymantria dispar*, often occur over very large areas but are notoriously difficult to predict. Previous models developed for predicting outbreaks have relied on data collected at a single point and have largely ignored spatial processes. We have adapted a geostatistical modeling approach, originally developed for geological applications, to the problem of forecasting gypsy moth defoliation distribution.

We digitized historical aerial sketch maps from all of the northeastern U.S. states and compiled these in a geographical information system where detectable defoliation is coded as either 1 or 0 in 2 by 2 km rasters. In Massachusetts, defoliation maps were collected from a 30 year time-series, thus, the data represent a 30 year time-series of binary map data.

Geostatistical methods are designed for quantifying spatial dependence and interpolation among spatially stratified samples; these procedures were developed by mining engineers for mineral and petroleum prospecting but have numerous application in applied ecological problems. We used the geostatistical tool, "semi-variogram", to quantify spatial dependence in purely spatial, temporal and space-time dimensions. Semi-variograms are plots of 1/2 the mean squared difference of values for points separated by a continuum of distance classes. Spherical (non-linear) models were fit to these semi-variograms. These semi-variogram models were then used to parameterize a 3-dimensional "kriging" procedure to extrapolate future maps. Kriging is a geostatistical technique that provides best unbiased weighted-average estimates from nearby samples. Kriging is usually used for interpolating among spatially stratified samples in two dimensions. We have used a 3-dimensional analog of this procedure to extrapolate future defoliation maps. This technique is a statistically-based approach to modeling space-time processes.

There are many different Kriging techniques; we adopted "simple Kriging" which assumes some *a priori* value before performing the weighted mean estimation. In this example, we used the over-all defoliation frequency for these *a priori* values. In areas where a long defoliation history does not exist, landscape data may be used to predict these frequencies.

We have experienced mixed results with this technique. The kriging appears to do a reasonably good job of delineating *where* (within the spatial domain) defoliation will occur but it does only a "so-so" job of predicting *when* defoliation will occur. We are presently experimenting with the incorporation of gypsy moth census data to refine the defoliation forecasts. Egg mass counts and male moth captures will greatly increase our ability to refine forecasts in both temporal and spatial dimensions.

QUANTITATIVE ANALYSIS OF GYPSY MOTH INVASION OF NORTH AMERICA

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ABSTRACT

The gypsy moth, *Lymantria dispar* (L.), was accidentally introduced to North America in 1868 or 1869 at the Medford, Massachusetts home of E. Leopold Trouvelot, a French naturalist. Since that time, the range of this insect has spread to include most of the northeastern states in the US and eastern provinces of Canada. We compiled the chronology of gypsy moth invasion in North America from historical quarantine records and assembled these data in a geographical information system (GIS). Individual US counties and Canadian census districts were used as the smallest spatial unit in this database.

These data indicated that three distinct periods occurred during which diffusion rates differed: a high rate (9.45 km/year) from 1900 to 1915, a low rate (2.82 km/year) from 1916 to 1965, and a very high rate (20.78 km/year) from 1966 to 1990. Furthermore, expansion was slower (7.61 km/year) during the period of 1966-1990 in counties where the mean minimum January temperature was less than 7° (C). Surprisingly, gypsy moth spread did not appear to be related to the abundance of suitable forest cover.

The rate of gypsy moth spread was estimated independently by modeling the process as a combination of exponential growth and natural dispersal as a diffusion process:

$$N_{x,t} = \frac{N_{0,0} e^{rt - x^2/4Dt}}{4\pi Dt}$$

where $N_{x,t}$ is the gypsy moth density at distance, x , from the point of release and time, t , from the time of release of $N_{0,0}$ organisms at time 0. D is the diffusion coefficient, a measure of the capacity for dispersal, and r is the intrinsic rate of reproduction. The assumption of random movement in this model implies that the population will spread radially, at an equal rate in all directions. Skellam (1951) showed that for any detection threshold, T , such that the infested area at any time t is restricted to points where $N_{x,t} > T$, the expansion velocity of the infested front, V , is constant and can be described:

$$V = 2\sqrt{rD}$$

We estimated r from empirical observations of gypsy moth increase under ideal conditions and D was parameterized using field data collected by Mason & McManus (1981). Using these independent estimates, we calculated that V , the rate of radial expansion, should be 2.5 km/yr. This estimate was substantially less than the empirically derived expansion rates. The higher observed rates of expansion are probably due to human-caused movement of gypsy moth life stages which was not incorporated in our estimates of D .

LANDSCAPE CHARACTERIZATION OF FOREST SUSCEPTIBILITY TO GYPSY MOTH DEFOLIATION IN PENNSYLVANIA

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ABSTRACT

Although there has been considerable work on the association of forest characteristics with gypsy moth defoliation, these studies have focussed entirely on the stand level (i.e. woodlots of 10-1000 ha). There remains a lack of understanding of the relationship between various landscape-scale features and gypsy moth defoliation in the regional context. In this study,

we examined historical gypsy moth data from the state of Pennsylvania to determine how various landscape features are related to susceptibility to gypsy moth defoliation on a meso-scale level. Broadening of our understanding of the relations among landscape processes to different spatial scales is important in the development of a more meaningful ecological models of those relationships. Furthermore, increasing emphasis is being placed on region-wide planning, in nearly all other aspects of natural resource management, including gypsy moth management. Development of an ability to forecast gypsy moth defoliation on a meso-scale level will be valuable in these region-wide systems.

Aerial sketch maps of gypsy moth-caused defoliation in Pennsylvania from 1969-89 were assembled in a raster-based geographical information system (GIS). These images were manipulated using Boolean algebra to determine the total defoliation frequency for each 2 by 2 km grid cell over the twenty-one year study period. The probability of defoliation for each cell was calculated by dividing the frequency of defoliation by the total number of years at risk to defoliation. The number of years at risk to defoliation was calculated as the number of years each area was considered within the generally infested area minus a constant lag term, to correct for the period in years between first designation of quarantine until first defoliation. For Pennsylvania the lag was estimated as 5 years.

Average defoliation probabilities were calculated for each of 6 major forest-types occurring in Pennsylvania. Pitch pine, oak-pine and oak-hickory types were the most susceptible to defoliation; maple-birch-beech, aspen-birch and non-forest types were the least susceptible. Forest type areas were further cross-tabulated by elevation classes. The three most susceptible forest types exhibited decreased susceptibility at elevations lower than 200 m.

NUTRITIONAL ECOLOGY OF GYPSY MOTH - HOST INTERACTIONS

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ABSTRACT

As the gypsy moth becomes established in the Great Lakes states concern has grown over its potential impact on aspen forests, as aspen is a major forest product of the region. Our research has focused on phytochemical and biochemical mechanisms mediating interactions between aspen and the gypsy moth.

The primary chemical defense of aspen (*Populus tremuloides*) is phenolic glycosides, particularly salicortin and tremulacin. The putative mode of action of these compounds in nonadapted insects is to cause midgut lesions. Insects adapted to aspen detoxify phenolic glycosides via midgut esterases. Our research has shown that the gypsy moth is moderately adapted to phenolic glycosides; intermediate to high levels of the compounds (> ~3% wet weight) reduce insect performance (decrease larval growth rates and pupal weights, prolong development times).

In the field, aspen clones exhibit substantial variation in both phenolic glycoside concentrations and resistance to defoliation by gypsy moths. Our current research is testing the hypothesis that differential defoliation is a consequence of variation in aspen defensive chemistry. Initial results support the hypothesis. Gypsy moths exhibit 3-fold variation in pupal weight on different aspen trees, which exhibit 14-fold variation in phenolic glycoside concentrations. Larval growth rates and pupal weights are strongly and inversely correlated with phenolic glycoside concentrations.

Related research has shown that aspen phytochemistry is influenced by resource (nitrate, carbon dioxide, light) availability. Gypsy moth consumption rates increase on foliage with low N levels; concomitant ingestion of phenolic glycosides reduces larval performance. Other research has shown that gypsy moth larvae exhibit compensatory feeding on protein-deficient diets, but not on mineral- or vitamin-deficient diets. Vitamin deficiency predisposes larvae to infection by NPV.

Potential interaction of phenolics with ascorbic acid was investigated with larvae fed red oak or aspen leaf diets supplemented with oak or aspen phenolics, with and without ascorbic acid. Aspen phenolics decreased larval growth rates and increased consumption rates. Oak phenolics did not alter growth but increased consumption rates. Main effects of ascorbic acid and interactive effects of ascorbic acid x phenolics were not significant.

Potential interaction between phenolic glycosides and the insecticide *Bt* was addressed by feeding larvae artificial diets containing either or both of the toxins. Effects of *Bt* were greater in the presence of phenolic glycosides. These results suggest that the efficacy of gypsy moth management via *Bt* application may be affected by the chemical composition of aspen hosts.

SPRAY DEPOSIT ASSESSMENT SYSTEM

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ABSTRACT

The main method of controlling gypsy moth populations is through the use of control materials. The efficacy of these materials is often governed by how well they are distributed within the forest canopy. This is especially true with microbial insecticides, which have to be ingested in order to exert their activity. The nature of the distribution of a material within a forest canopy can only be determined if the deposit is either assayed by chemical techniques, or visualized and measured.

Image analysis techniques which had been used until recently to analyze deposits on natural or artificial targets were often inaccurate, labor-intensive and slow. The system developed at Penn State represents a refinement of these techniques, and uses some novel methods not yet published. It represents a standardization of method, and offers a quicker and more accurate means of assessing deposits on natural and artificial targets.

The principal technique used in this system is image analysis, which uses the visual contrast between the material measured and the target material. An automated XY table is used to scan as many fields on the target as required to obtain a valid sample. The diameters of all the droplets scanned are recorded.

To obtain accurate calculations of droplet sizes from stain sizes, a spread factor must be used. An accurate spread factor must be measured under field conditions. For this purpose, a twenty foot spray tower is used under ambient temperature conditions which have been selected to match those of the spray day.

FIELD SAMPLING OF PESTICIDE SPRAY DISTRIBUTIONS USING TEFLON SPHERES AND FLAT CARDS

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ABSTRACT

A still air, controlled experiment showed that the aerodynamic boundary layer around spherical samplers caused a 7% reduction in impaction efficiency of spray droplets (mean diameter $\approx 180 \mu$) over that of flat cards. Comparison of sphere and flat card catch data from a USDA APHIS open field, aerial spray trial indicated that the impaction on the cards decreases as the wind speed increases. This decrease in effective card catch can be estimated by determining the droplet fall angle from mean settling velocities and the horizontal wind speed, and projecting the card surface area into the direction of the falling droplets.

A RECOMBINANT PROBE REPRESENTING GYPSY MOTH
VITELLOGENIN MESSENGER RNA

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ABSTRACT

In the gypsy moth, vitellogenin (Vg), is synthesized in the female larvae during the last larval stadium. Recent studies have indicated that the expression of Vg genes in gypsy moth larvae is regulated by the juvenile hormone [Hiremath & Jones (1992) *J. Insect Physiol.* (in press)]. The juvenile hormone, as in other insects, plays an important role in the normal growth and development of the gypsy moth. Treatment of gypsy moth larvae with JH analogs results in the decrease of the translatable Vg mRNA in the fat body. Thus, Vg gene could serve as a good candidate for analyzing the mechanism of action of JH in the gypsy moth. Knowledge of the mechanism of action of JH has great potential in designing biological control agents.

In order to understand JH regulation of Vg gene expression, it is necessary to isolate and characterize gene(s) coding for Vg. Towards this end, we attempted to isolate a recombinant probe containing Vg-related sequences. An oligonucleotide probe coding for the N-terminal sequence of the large subunit of Vg was used as a probe to identify the Vg mRNA [Hiremath & Eshita, (1992) *Insect Biochem.* (in press)]. The 5.4 kb Vg mRNA was purified by agarose gel electrophoresis and used to construct a cDNA library. A putative cDNA clone (pVL-80) selected using cDNA λ , prepared using Vg mRNA as template, was subjected to further analysis. The clone had a 900 bp insert. In northern analysis the clone hybridized specifically to the 5.4 kb Vg mRNA. No hybridization was observed with poly(A) RNA from female larvae treated with a juvenile hormone analog, consistent with the earlier findings indicating that the 5.4 kb RNA is not detectable under these conditions [Hiremath & Jones (1992)]. The recombinant probe could detect the Vg-related RNA even in total RNA preparations. The recombinant probe will be used to isolate and characterize Vg gene(s).

TOXICITY OF *Bt* TO LARVAE OF NON-TARGET LEPIDOPTERA
IN LABORATORY BIOASSAY

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ABSTRACT

The susceptibility of larvae of 14 species of native, non-target Lepidoptera to *Bacillus thuringiensis* Berliner var. *kurstaki* (*Bt*) was determined in a laboratory bioassay. The species evaluated were: *Phigalia titea* (Cram.) and *Prochoerodes transversata* (Drury) (Geometridae), *Actias luna* (L.) and *Antheraea polyphemus* (Cram.) (Saturniidae), and the following 10 Noctuidae: *Amphyipyra pyramidoides* Gn., *Eupsilia vinulenta* (Grt.), *Chaetagnaea sericea* (Morr.), *Eutolype rolandi* Grt., *Psaphida resumens* Wlk., *Orthosia hibisci* (Gn.), *Catocala obscura* Stkr., *C. sordida* Grt., *C. coccinata* Grt., and *C. praeclara* G. & R..

Appropriate host foliage was treated with a neat (undiluted) application of Foray 48B at a rate that approximated the field application of 36 BIU's per acre using a Mini-Becomist nozzle in a cylindrical spray tower. Larvae of each species were treated at the instar in which they occur when *Bt* is applied aerially in southern New Jersey. Larval mortality was monitored daily for 5 days; survival to the pupal stage was also recorded.

Generally, larvae of those species treated in the first or second instar were very susceptible to *Bt* infection following consumption of *Bt*-treated foliage. However, first/second instar larvae of *P. transversata* were not very susceptible to *Bt*; only about 12% of the larvae succumbed by day five and very few died before pupation. Larvae of those species treated in the third to fifth instar were generally less susceptible, although three species assayed in the fourth instar, *A. pyramidoides*, *E. rolandi* and *C. coccinata*, suffered about 60%, 47% and 90% mortality, respectively, by day 5; most of the survivors died before pupation.

We conclude from these data that one should not generalize about the effect of *Bt* on non-target Lepidoptera, especially in terms of predicting susceptibility based on larval instar at the time of *Bt* application. Our data showing the interspecies differences within the genus *Catocala* further support our contention that we must deal with the *Bt* susceptibility of non-target Lepidoptera on a species to species basis.

EVALUATION OF GYPCHEK® APPLIED AT LOW DOSAGE AND VOLUME

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ABSTRACT

Gypchek, the gypsy moth baculovirus product, is environmentally safe and efficacious at high dosage but remains costly to produce (\$56 per ha treatment, exclusive of formulation and application costs) and difficult to apply. Thus, integration of Gypchek into gypsy moth management strategies has been delayed. Major savings in treatment costs could be achieved through reductions in dosage and applied volume.

We tested the standard Gypchek treatment (two aerial applications of 1.25×10^{12} occlusion bodies per ha) and two variations: two applications at 40% of the standard dosage and 25% of the standard volume, and a single application of 2.5×10^{12} occlusion bodies per ha. Applications were on replicate 12-ha plots harboring dense gypsy moth populations on the U.S. Marine Reservation, Quantico, Virginia.

Gypsy moth egg mass populations were reduced in all plots of all Gypchek treatments while populations in all control (non-sprayed) plots rose. After-treatment population differences between controls and each Gypchek treatment were significant but differences between Gypchek treatments were not. Similarly, average defoliation in control plots (80%) was significantly higher than in either the standard (10%), the low dosage/low volume (31%), or the single application (31%) Gypchek treatment.

Population reduction and foliage protection achieved with both the low dosage/low volume and single applications of Gypchek indicate that these prescriptions may satisfy certain management needs. The low dosage/low volume prescription would be most cost-effective and will be pilot tested in the 1992 field season.

MEASUREMENT OF DIMILIN RESIDUES USING ETHANOL

EXTRACTION AND HPLC ANALYSIS

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ABSTRACT

A new method for measurement of Dimilin residues on oak leaves has been developed. This method differs from other methods because it uses ethanol as a solvent. Ethanol has the advantage of extracting Dimilin more selectively than other commonly used solvents, including acetone and methylene chloride, making it possible to differentiate Dimilin from coextracted plant compounds on high pressure liquid chromatography (HPLC) traces. Extraction efficiency was tested by measuring the concentration of Dimilin extracted from fortified leaves. Sixty sets of leaves were fortified with a range of concentrations encompassing deposition rates expected when Dimilin is sprayed at a rate of 1/2 ounce AI per acre. Leaves were washed with ethanol and Dimilin concentrations were measured with HPLC. The average recovery was 87.44 percent with a standard deviation of 5.6 percent.

This method was used to measure Dimilin concentrations on a subset of oak foliage sampled during an accountability and persistence study. Dimilin residues were measurable in all cases.

MATING FITNESS OF GYPSY MOTHS WITH INHERITED
STERILITY: SPERM TRANSFER

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ABSTRACT

Inherited sterility is being developed as a tactic to control incipient populations of gypsy moths. Eggs from females crossed with males irradiated with 8 or 10 krad are distributed in infested areas. F_1 insects from these eggs are sterile. Thus, control depends upon the fitness of the F_1 insect, ultimately, mating fitness. When caged in single pairs, fewer than one half of the females mated with F_1 males contained normal quantities of eupyrene (functional) sperm. Further, egg masses from females crossed with F_1 males were similar in size to those of virgin females and only about 1/3 as heavy as females crossed with normal males. Females mated with feral males contained sperm slightly more frequently than those mated with laboratory-reared males. When males were given up to four females sequentially, only about 20% of the F_1 males were able to fully fertilize two females as compared with about 50 and 70% of NJSS and feral males, respectively.

When normal males were held in constant light during the pupal stage, nearly 75% were either aspermic or transferred only apyrene (nonfunctional) sperm. Females crossed with such males, would readily mate again, receiving a normal compliment of eupyrene sperm.

Thus, we conclude the following:

- (1) F_1 males with inherited sterility are deficient in sperm transfer capability.
- (2) Gypsy moth females mated with aspermic males will mate again and receive sperm from the second male.
- (3) The number of insects released will need to be greatly increased in control programs utilizing inherited sterility to compensate for the lack of sperm transfer by F_1 males.

CURRENT STATUS OF THE STAND DAMAGE PORTION OF THE GYPSY MOTH LIFE SYSTEM MODEL

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ABSTRACT

The Stand-Damage Model, part of the Gypsy Moth Life-System Model System, simulates interactions between a forest stand, gypsy moth defoliation, and stand management actions over time. The model has been implemented on DOS microcomputers. Full documentation is in review. This includes a user's guide, description of the formulation and biological basis, as well as all of the computer code, including both the model proper, and the user interface. Ecological processes are considered for each tree species and for each canopy stratum (overstory and understory trees) and tree growth is driven by annual total accumulated heat, measured in day-degrees. As a stand-alone model, it can be used to investigate the consequences of various user-supplied levels and sequences of defoliation, and how defoliation interacts with silvicultural prescriptions. The user is able, through a series of menus and edit screens, to describe initial conditions and history of the forest stand and to manipulate all the parameters of the stand, species specific tree growth and mortality functions, as well as the mechanisms and intensity of defoliation effects. This also permits the user to calibrate the model to specific local conditions. Full default values are provided for all stand parameters and for each of the 20 tree species that may be considered during a simulation. Range validation is checked for all parameters and initial conditions.

Model output has been considerably enhance by the addition of direct graphic displays of the results of simulations. There are four graphic formats and a full tabular description of each simulation provided. The user has the option to select any of these output options. The user is provided with the means to fully document the input and output files that the model creates. The user can direct output to files or to a printer.

Installation of the software is done through software that permits the user to select the drive and directory to house the model and associated data files. The user has the option at all times to reconsider selected options. Special options are also available for support of non-graphic monitors, monochrome graphic or VGA monitors, as well as the full range of color graphic monitors. Testing of the model has been initiated and the model has demonstrated reasonable behavior in comparison to available field data. Testing will be continued in the coming year. The user interface will be updated to provide full mouse and graphic screen window-management support.

EFFECTS OF *Bt* ON NON-TARGET ORGANISMS: FIELD STUDIES

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ABSTRACT

Little is known about the non-target impacts of forest applications of *Bacillus thuringiensis* (*Bt*). In a recent study in Oregon, both Lepidoptera species richness and abundance were reduced at sites that were sprayed with *Bt*. In New Hampshire, following *Bt* application, Lepidoptera biomass was reduced and birds in the treated areas made fewer nesting attempts than birds in untreated areas.

The purpose of this study is evaluate impacts of *Bt* application on non-target Lepidoptera and food of the endangered Virginia big-eared bat, a Lepidoptera specialist. Twenty-four 20 ha plots (12 treated with *Bt*, 12 untreated) were located in Grant and Pendleton Counties, WV. Pretreatment data were collected in 1990. Post-treatment data were collected in 1991 and will continue in 1992. One application of *Bt* (Foray 48b, undiluted, 96 oz/acre, 36 BIU/acre) was applied by helicopter in May 1991. Residue and deposition samples were collected at intervals from 3 to 96 hours post-spray.

Pole-pruning, light trapping, malaise trapping, and aquatic sampling were used to evaluate impacts to non-targets. Preliminary analyses have been performed on the 1990 and 1991 pole-pruning and light-trap data. Within one year of *Bt* application, both richness and abundance of Lepidoptera larvae were reduced at sprayed sites. Noctuidae and Geometridae experienced the greatest impacts. Other arthropods (tenthredinid larvae, Homoptera, Neuroptera, and Araneae) were not reduced in abundance. Among moths collected in light traps, species richness was significantly reduced at treated sites. Additionally, approximately 30% of the genera collected were found to be reduced in abundance at *Bt* treated sites.

These preliminary results suggest that *Bt* application may reduce available food and adversely affect Virginia big-eared bats. Additionally, because reproduction in birds may be limited by availability of food, these reductions in Lepidoptera abundance may also adversely affect avian populations.

ENZYME PROFILES AND GENETIC VARIATION IN *COMPSILURA CONCINNATA*
(DIPTERA: TACHINIDAE)

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ABSTRACT

A critical task in evolutionary biology is the determination of the genetic and ecological mechanisms of change in populations. Classical biological control or biocontrol attempts to regulate populations of target organisms through the intentional introduction of natural enemies. These introductions are a fundamental strategy of integrated pest management and provide experimental material in natural ecosystems for studying the genetic mechanisms leading to variability among populations. These differences can be used to detect host-adapted strains or biotypes of natural enemies. This study begins research to identify genetic variation in putative enzyme loci visualized with enzyme electrophoresis for the parasitic fly *Compsilura concinnata* Meigen which was introduced from Europe as a biocontrol agent of the gypsy moth.

Individuals from a laboratory population of the tachinid *C. concinnata* were analyzed utilizing the method of horizontal starch gel electrophoresis to determine which enzyme and buffer systems would provide adequate resolution for a population genetic study. Forty-nine enzymes and 4 different buffer systems were used to run homogenates of flies drawn from the 8th generation of a laboratory population. For the enzyme systems studied, 75% were found to provide sufficient resolution to make them useful in establishing population profiles. Different forms of an enzyme or isozymes were found in 9 of the systems analyzed. Putative polymorphic loci were found in 4 of the enzymes examined and for the 39 enzymes resolved the estimated proportion of polymorphic loci ($\hat{P} = 0.19 \pm 0.06$) was moderately low. Values for wild populations of other insects are typically higher ($\hat{P} \approx 0.2-0.5$). The average heterozygosity ($\hat{H} = 0.063 \pm 0.03$) estimated was lower than for other diptera (*Drosophila spp.*, $H = 0.150$), suggesting that there has been some reduction in the diversity of this laboratory population. Comparing the variation in proteins relative to their substructure revealed an unexpected absence of differences in single subunit enzymes ($\hat{H} = 0.0$). There was an expected decrease in variability as protein complexity increased from the dimeric ($\hat{H} = 0.105$) to the tetrameric ($\hat{H} = 0.059$) enzymes. This latter trend is recognized to be reflective of the functional constraints limiting variation in multimeric proteins.

Past natural enemy introductions for biological control of the gypsy moth, with few exceptions, have not considered molecular variation within the organisms released. Electrophoretic methods have been used to study genetic variation and have provided a rapid and cost effective scheme for characterizing biotypes in various organisms. The enzyme systems identified in this study will be useful in future research to understand how genetic changes influence natural enemy populations. This molecular approach to the population genetics of biocontrol can be applied in the detection of more efficacious strains of natural enemies useful in the regulation of host populations. Research into the evolutionary biology of these populations may provide new information that improves and refines the quality of ecologically acceptable biocontrol strategies developed by applied entomology.

ASIAN GYPSY MOTH (AGM) BIOECOLOGY: COMPARISONS WITH NORTH AMERICAN GYPSY MOTH AND OTHER SPECIES OF *LYMANTRIA*.

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ABSTRACT

The Genus *Lymantria* tentatively contains 158 species worldwide. Among these, the most notorious is gypsy moth, *L. dispar*. Comparisons of variation among *dispar* forms and among some species within this genus reveals that in many cases there are greater differences among forms of *dispar* than there is between the closely related congeners. Illustrations of these variations among adults revealed greatest differences among Japanese populations, where southern Honshu and Kyushu form are exceedingly dark in males and unusually large (up to 50% larger in size (pupal weight; male wing length) when compared to North American Gypsy Moth (NAGM). Korean forms are also darker but less pronounced. In China, females appeared an unusual pure white and this appears to be common on continental Asia. In northern Japan, some forms were more similar to NAGM but appearance of dark females occurs uncommonly. Adult female moths often show interesting variation in "banding" patterns, some illustrated examples included presence of a median fascia or band in forewings in females from Korean and central Honshu, Japan. Similarly a post-median fascia or band appears in the hindwing in females from Beijing

area of China. Larval variation is also pronounced, often with greater yellow coloration, particularly in NE China. Throughout the Asian area, expression of black-backed larval mutants are known but their frequency of expression is usually less than 1%.

Most significant of behavioral differences (AGM vs. NAGM) is the ability of AGM females to fly a sustained level or ascending flight. This occurs in eastern Asia (designating these AGMf, f for female flight). In Europe and western Russia, females can not fly (designated AGMnf for non-flight). An apparent transition zone thus occurs in central Russia at the base of the Ural Mountains, where the two functional forms intermix. Among the AGMf, all flights appear to occur after mating, therefore females are gravid and fertile. Two types of flights are possible: (1) Diurnal ovipositional flights that precede oviposition. These are usually intra-forest, sub-canopy flights. In Hokkaido, Japan, females performing this type of flight show a strong attraction for white birch, *Betula plataphylla*. This behavior leads to a concentration of egg masses on this host and a mini-alternate host cycle since on hatching, larvae disperse (i.e. balloon) off the *Betula* and settle and feed in nearby *Larix leptolepis* trees. Later in the season, defoliation is often evident only on the *Larix*. (2a) Nocturnal flights where females appear at artificial lighting sources and eventually deposit egg masses (greater than 500 eggs) in unnatural sites e.g. light posts, building walls, signs, ship superstructures (resulting in potential for intercontinental dispersal), signs, etc. Another subtype (2b) appears to occur in the Lake Baikal area of Siberia where nocturnal flights, of longer distance (max. ca. 15 - 30 km), carry females to prominent rock bluffs where egg masses are deposited on protected rock surfaces, far removed from any suitable host trees.

Concern arises over the consequences of genetic mixing of AGMf with NAGMnf that will likely occur in the Pacific Northwest. Previous cross-mating study indicates that at least some genetic crosses (e.g. NAGM females X Japanese Honshu males) show evidence of genetic incompatibility since female progeny of such crosses are genetic intersexes (i.e. sterile females with male-like coloration to wings and male antennae). Male progeny are perfectly normal (i.e. fertile) and these males will permit the Japanese genome to mix with that of NAGM. It remains unknown if similar results occur when Korean, Chinese or Siberian AGM intermix with NAGM.

Aside from the functional polymorphism (female flight), phenotypic expression of genetic variation is abundant, especially in the range of larval coloration. Subtle differences occur in many different geographical populations of *dispar* and levels of genetic incompatibility occur among some populations. Overall, this variation raises questions as to species limits and points to a need for intensive genetic investigations.

PHENOLOGY PREDICTION IN GypsES

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ABSTRACT

Knowledge of the timing of phenological events is an important component of most pest management programs. For example, application of insecticides requires precise timing to coincide with the most susceptible gypsy moth life stage and suitable tree growth. Our goal is to predict phenology over the landscape and to make this technology readily available to managers.

The most important landscape features influencing temperature are elevation and slope position. Currently, we calculate temperature at a given elevation by decreasing the temperature at a base elevation by 0.6°C for every 100m of ascent. Our approach is based on combining information from local weather data (e.g. from NOAA) and the USGS Digital Elevation Model.

Simulations of date of emergence for 50% of second instars at various elevations reveal that the phenology-elevation relationship is linear. The convenient feature of linearity allows an efficient approach of describing phenology in a complex landscape: The phenology at the location with measured temperature data is simulated. With the temperature-elevation relationship the temperature of a location with higher elevation is projected. The simulation is then run for this higher elevation. The two points simulated define the line that describes the phenology-elevation relationship. This phenology-elevation relationship can now be used in the GIS to calculate a new layer based on the elevation layer. This new phenology layer is constituted of the date of the phenological event for each cell. This map of phenology is the base for planning spray applications in time and space.

The goal of the GypsES project is to provide gypsy moth managers with computer-aided tools that facilitate designing monitoring programs, and making control decisions. Phenology layers are required by GypsES to delineate treatment blocks and to time treatment applications.

CURRENT STATUS OF THE GYPSY MOTH LIFE-SYSTEM MODEL

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ABSTRACT

The Gypsy Moth Life-System Model simulates interactions between a forest stand, gypsy moth and its natural enemies. Ecological processes are considered for each tree species and for each stratum (overstory, understory, ground, and boles). A new version of the model (without the Stand submodel) has been written using the C-language which may be compiled both in the DOS operating systems. Data structuring, available in the C-language, make the code more readable, and saves memory used by the model due to dynamic memory allocation. Majority of the code for the natural enemies was completely rewritten; for the gypsy moth submodel, it was substantially restructured; several subroutines were translated to C automatically using the FOR-C software.

Significant changes in the logic of the Gypsy Moth Submodel have been made: 1) cohort creation was synchronized with the creation of time intervals, 2) the concept of physiological time was applied to make cohorts compatible with each other when migration between hosts occur, 3) the migration algorithm was improved to avoid a mixture of different larval instars in one cohort, 4) the feeding algorithm was improved by taking into account uneven spatial distribution of gypsy moth larvae, 5) gypsy moth larvae are allocated to resting sites according to the number of resting sites within a strata, strata preference and availability of resting strata from a given feeding stratum, 6) all processes, including migration and starvation, were calibrated to time intervals.

Predator and Parasite submodels were completely rewritten. All parasitoid species were modelled by individual subroutines. Generic functions have been developed for simulation of processes common to all parasitoids. They are called from species specific functions. Age specific mortality and fecundity are used in the simulation of adult female parasitoid dynamics. A generalized functional response is used: predators and parasitoids search for different instars of gypsy moth simultaneously with different search rates. The parasitoids' cohort structure was modelled using linked lists.

Model output was considerably improved and extended. Sixty-six output tables provide information about different parts of a simulation. A graphic interface was developed to

follow model during a simulation. Sixty-one graphics are available which characterize foliage, gypsy moth and natural enemies both within one season and across years. It is possible to place two graphs on the screen for comparison. A graphic editor allows one to make various lines visible or invisible, to change colors, width or style of lines, and to rescale graphics if it is truncated or too close to X-axis. Majority of graphics may be converted into a fill-area charts. Outputs may also be saved for later review of graphics or to compare to other simulation results. A separate program permits viewing of previously produced results.

NEPHROCYTES OF THE GYPSY MOTH, *LYMANTRIA DISPAR*

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ABSTRACT

Nephrocytes are distinctive cells that exist in discrete groups at fixed sites within the body cavity of arthropods. They can be identified by their uptake of the dye, Trypan blue. Nephrocytes are capable of taking up selected molecules from the hemolymph by endocytosis; some substances are digested in the lysosomal system, and other resulting products may be released into the hemolymph. The role that these cells play in arthropod physiology is unclear.

Gypsy moth, *Lymantria dispar*, larvae were infected with lethal doses of either *L. dispar* nuclear polyhedrosis virus (NPV), or *Autographa californica* NPV. At intervals until pupation or death, they were injected with either a 1% solution of Trypan blue in saline, or with saline alone, and were dissected. Nephrocytes were identified, removed, and were prepared for examination by transmission and scanning electron microscopy using standard histological methods.

Two distinct groups of nephrocytes exist in gypsy moth larvae. The pericardial cells lie along both sides of the heart, and are restricted to the abdomen. They are attached to the heart, and to the alary muscles and underlying fat body by connective fibers. The cells are generally spindle-shaped, although occasionally irregular in contour, and have smooth surfaces. Another group of nephrocytes, approximately 17-26 in number, is located in the ventral body cavity. The cells are tightly attached to the ventral surface of a layer of fat body that encircles the gut at the junction of the foregut with the midgut. These ventral nephrocytes somewhat overlap each other, and are arranged in an irregular row which

extends across the sheet of fat body. The cells are connected to each other and to the fat body by ligament-like fibers and tracheolar attachments. They are large, smooth-surfaced cells, with single, branching nuclei.

The two types of nephrocytes have similar ultrastructure. They are surrounded by a basement membrane, and the peripheral cytoplasm is characterized by infoldings of the plasma membrane, forming an extensive network of labyrinthine channels. The channel openings are guarded by single or multiple diaphragm-like structures, which are 30-50 nm wide. Within the channels, many examples of membrane invagination can be seen, resulting in numerous coated pits and vesicles. Large, electron-lucent alpha vacuoles are situated among the channels at the periphery, and smaller, dense beta vacuoles are located toward the central region of the cell.

When gypsy moth larvae are infected with *L. dispar* NPV, nephrocytes do not become virus-infected. They remain translucent and appear normal, but contain many oddly-shaped dense vacuoles. When larvae are infected with *A. californica* NPV, both types of nephrocytes become distinctly reddish-brown, although the cells show no signs of virus. Infection with this virus results in an accumulation of dense granules throughout the nephrocyte cytoplasm, which presumably accounts for the change in coloration. The granules are irregular in shape and membrane bound. They exhibit a crystalline-type lattice that appears to have a tubular structure, and there often are bits of extremely electron-dense material within the granules. It is not known whether the changes observed in gypsy moth nephrocytes as a result of virus infection are merely a form of necrosis, or whether nephrocytes might play some role in insect defense.

POPULATION FLUCTUATIONS AND POTENTIAL IMPACT OF
SMALL MAMMAL PREDATORS OF GYPSY MOTH

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ABSTRACT

Small mammal predators may be the forest's first line of defense against gypsy moth defoliation. As the insect expands its range into the Southeast, small mammal populations may play a critical role in determining rate of spread and/or likelihood of gypsy moth establishment. Ideally, gypsy moth populations should be maintained at innocuous levels. However, small mammal populations do fluctuate and, at times, densities are extremely low. During periods of small mammal scarcity, gypsy moth populations may increase significantly and can be released from a relatively stable innocuous state. The objective of this study is to demonstrate that small mammal populations do exhibit substantial fluctuations, that their fluctuation is reflected in the magnitude of predation of gypsy moth, and that the small mammal fluctuations are driven by the availability of alternative food sources.

Small mammal surveys were conducted at several locations in Virginia and North Carolina; Bryant Mountain, Vermont; Chuguevo, Ukraine; and Black Lake, Siberia. Live traps, baited with a peanut butter-oatmeal mixture, were used. Freeze-dried or living gypsy moth pupae were placed at each trap station to determine predator impact except at the North Carolina and Virginia sites. At Bryant Mountain, the surveys were conducted in typical resistant and susceptible stands. Surveys of alternative food sources for small mammals were conducted at Bryant Mountain, and at Groton Plantation in South Carolina.

Small mammal survey results for Virginia and North Carolina in 1991, and the results of an earlier survey done in 1978-80 at Yates Pond, Wake County, North Carolina, revealed low density small mammal populations. However, the 1991 population was extremely sparse. The low small mammal population was a region-wide phenomenon that did not appear to build up during the year. The dominant species captured in this study and the Vermont study was the white-footed mouse (*Peromyscus leucopus*).

In a mast survey done in the Groton Swamp, South Carolina, wide fluctuations in mast production were demonstrated. Mast production may account for fluctuations in small mammal populations. Future small mammal surveys in the Southeast will include mast surveys.

The small mammal survey at Bryant Mountain, taken since 1979, has shown significant yearly fluctuations in density of white-footed mice at all elevations. Since 1985, when mouse populations were very high, the survey has included an evaluation of pupal predation in resistant and susceptible stands. The mouse population has sharply declined in both types of stands since 1985; on the other hand, survival of living pupae has dramatically increased. The summer diet of mice between resistant and susceptible stands consisted of a larger proportion of mast and smaller proportion of berries in the resistant stand. But arthropods were a major component in both stand types. An analysis of the stomach content in July of 1983 and 1985 verified this conclusion.

Survivorship of freeze-dried pupae in Ukraine and Siberia was even more dramatic than in the Bryant Mountain study. In the Ukraine study, pupal survival was minimal by the third day even for pupae placed in bark crevices 2 meters up the tree bole. High densities of ground foraging generalist predators, small mammals, resulted in low pupal survival. Conversely, low small mammal densities in Siberia resulted in practically complete pupal survival.

Fluctuation of small mammal populations are naturally occurring events that have an important impact on the dynamics of gypsy moth. Sparse small mammal populations are critical to gypsy moth population change. It is reasonable to hypothesize that low small mammal populations also play an important role in the rate of spread of new infestations such as in the Southeast. It is also reasonable to hypothesize that fluctuations in small mammal populations are driven by the availability of alternative food sources.

GypsES:

A DECISION SUPPORT SYSTEM FOR GYPSY MOTH MANAGEMENT¹

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ABSTRACT

Forest pest managers must face many complex decisions when attempting to deal with the gypsy moth. Resources are always scarce, forcing priorities to be set and allocation decisions made on short notice. 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 according to relative risk from gypsy moth and how to improve the efficiency of their gypsy moth control efforts.

GypsES is a decision support system for the management of gypsy moth using a knowledge-based geographic information system and multiple knowledge-based modules or 'advisors'. The advisors provide decision information on: Forest Hazard Rating and Risk Assessment; Insect Monitoring and Prediction; and Intervention Decision and Implementation. Key elements in the system include the ability to store and recall information about the user and the areas under management. This function, known as the Administrative Profile, incorporates budgeting constraints, treatment priorities and preferences, and other individual characteristics, all of which are customized for or by each user.

The hazard rating module is designed to incorporate all the elements of the forest conditions and management considerations that are necessary as a precursor to any gypsy moth-related

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activities. This includes primarily information on the types of trees in the areas of concern, so that the system can determine the susceptibility to gypsy moth defoliation. Vulnerability to damage is then calculated based on the stocking, vigor, and prior disturbance history as described by the user. Management objectives are then incorporated to produce a hazard rating. This hazard rating can then be used by the monitoring module to help determine sampling needs. In return, information from the defoliation prediction module is used within the hazard rating module to predict current risk of a gypsy moth infestation significant enough to need management intervention.

Techniques and methodology for sampling gypsy moth and its associated natural enemies have been developed and in some instances tested and validated. Knowledge in the egg mass sampling designer (EMSD) is a combination of egg mass sampling procedures developed in the Appalachian Integrated Pest Management (AIPM) Project and information available from other components in GypsES. The EMSD adapts sequential sampling procedures to estimate egg mass densities of management units. The parameters of sequential sampling are treatment (egg mass) threshold and acceptable error. The pheromone trapping system designer (PTSD) helps decide where pheromone traps should be placed and what type of pheromone traps should be chosen. These decisions are based on information about gypsy moth population, forest use and forest condition. Gypsy moth density estimates from pheromone traps have two purposes: 1) to provide the latest estimate of population densities in order to design egg mass sampling and 2) to provide a low cost general overview of the population over a large area. The PTSD currently deals only with leading edge situations of gypsy moth populations. The purpose of the phenology descriptor (PD) is to give the user a landscape-wide view of phenology and to provide information about phenology to the Treatment Component. The following questions are answered: At what date should spraying be started in a certain area? What areas can be sprayed at the same time? Should a Treatment Units (Treatment Component of GypsES) be split because one portion of the Treatment Unit should be sprayed much earlier than the other? Should Treatment Units be joined because they have a similar phenology? To answer those questions the PD has to have a measure of central tendency and variability of the phenology of the cells covered by a treatment unit.

Decisions regarding management of gypsy moth are always heavily influenced by political factors. The insect and the trees it attacks are highly visible to the public and draw much attention from the press. The treatment module focuses on two functions in the treatment process: decision and implementation. Treatment decision assists a user in configuring potential treatment areas as suggested by the risk rating accomplished in the hazard rating module, assigning treatment priorities based on the risk assessment, and determining the final set of affordable treatment units. Treatment implementation advises on scheduling of aerial application activities, evaluation of aerial applicators' bids, and calibration of spray nozzles.

Geographic information systems (GIS) enable gypsy moth management decisions to include store, manipulate and analyze geographical data in a spatial frame of reference. Although

maps are the most commonly used product of GIS, the most important contribution is their ability to handle and analyze multiple layers of spatially-referenced data. Map themes related to the determination of risk and hazard, the location of insect populations and other data for example may be overlaid to produce measures of areal association. One of the most significant uses of GIS in GypsES is the creation of new data layers through reclassification and/or map overlay operations. In addition the strength of influence of variables over distance may be calculated to provide otherwise unavailable information about a management unit from adjacent and surrounding areas.

The full GypsES system is being developed under the Unix operating system. This system was chosen to use the Macintosh hardware already available to the developers and to enable the end product to avoid being obsolete before its release, which is currently planned for late 1993. The Unix system allows use of the GIS program GRASS, which is a full-featured GIS in the public domain, a factor which helps minimize the cost to users. Hardware currently running GypsES includes Macintosh computers, Intel 80486 computers, Sun SPARCstations, and a DEC 5000 workstation, illustrating the portability of software developed in the X-Windows environment.

The Graphical User Interface (GUI), is the part of the program seen by the user. It includes a system of windows, icons, menus, and pointers (WIMPs) which are designed to be easy to understand. The design of the GUI was complete by July, 1990, and its basic programming has been accomplished in the months since. The individual modules within the GypsES system all use a set of four work windows in which different information can be displayed. Each opens with a simple flow chart to provide visual clues to the user about how the program's logic works and to simplify navigation through the program's many parts. Interactive use is guided by internal functions that simplify use and avoid excessive complexity to the user. An integrated help facility provides ready access both to information on how to use the system and on the knowledge bases behind it. Output to paper maps can be produced for any image that is visible on any screen in GypsES.

UNDERSTORY DEVELOPMENT FOLLOWING THINNING AND DEFOLIATION IN WEST VIRGINIA

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ABSTRACT

Understory composition was measured on 660 10.5-m² plots in 11 stands on the West Virginia University Forest in north central West Virginia. The overstory composition was dominated by oaks (*Quercus* spp.) on six stands and by a mixture of oaks and yellow poplar (*Liriodendron tulipifera*) on five. The only recent disturbances were a thinning during the winter of 1989-90 on eight of the stands or gypsy moth defoliation during the spring of 1990 and 1991 or both. In oak stands tree species dominated the understory on 41% of the plots and ferns dominated on 32%. In mixed yellow-poplar/oak stands fern dominated on 36% of the plots and trees dominated on 23%. Dominance by ferns was correlated with more mature stands in both types. Herbaceous ground cover increased in dominance in 1990, especially in the disturbed stands. The number of species on the 10.5-m² plots ranged from 1 to 25 in 1989. An increase in the numbers of species per plot in both 1990 and 1991 suggests that a cutting disturbance tends to increase diversity. Four commercial tree species comprised 75% of the total stems in 1989: yellow-poplar, red maple (*Acer rubrum*), black cherry (*Prunus serotina*), and oaks (predominantly *Q. rubra*). These four species represent only 60% of all trees species by 1991 reflecting the high seedling mortality rate. Black cherry showed the highest persistence through the understory classes, dominating all the stages from 30 cm tall through 1.5 cm dbh. The dominance of cherry among the understory stems more than 30 cm tall implies the possibility that it may well dominate the next stand. All areas are well stocked with advance regeneration of commercial tree species and should respond well to current and future disturbances.

APPLICATION OF A LAGRANGIAN STOCHASTIC MODEL TO AERIAL SPRAY
TRANSPORT IN AN OAK FOREST

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ABSTRACT

An aerial spray experiment was conducted during the spring of 1988 in the Penn Black Monshannon state forest. The trials of spray material concentration were collected on the lines perpendicular to the aircraft fly path at both canopy and ground levels, while the turbulent wind, temperature, and humidity profiles within and above the oak forest were measured simultaneously by an array of fast response sensors. Experimental data was collected during both neutral and unstable atmospheric stability conditions.

Aerial spray dispersion and deposition was simulated by a Lagrangian stochastic model. The in-situ measured profiles of turbulent wind, temperature, and moisture were used in the parameterization of the model. The gravity settlement and the form drag of the different drop sizes were treated by tracking particles with different spherical diameters. The interception and the evaporation of the spray drops was also considered in the model. The simulated concentrations and the measured concentrations at different atmospheric stability conditions were compared. The applicability of the Lagrangian stochastic model was evaluated for dispersion and drifting of aerial spray.

GYPSY MOTH NATURAL ENEMIES: HOW GOOD ARE THEY?

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ABSTRACT

The importance of rigorous evaluation of gypsy moth natural enemies is discussed. The experimental approach is advocated. Two examples are presented. Ants are predators of low density gypsy moth populations. They seldom attack caterpillars in trees, but can be induced to climb trees and attack gypsy moth larvae there. A field experiment designed to evaluate their effectiveness will be carried out in 1992 and 1993. Results should indicate whether or not it will be worthwhile to attempt to manipulate this predator. The second example, the beetle *Calosoma sycophanta*, is a specialist on high density gypsy moth populations. Only about 400 beetles per hectare are necessary for the larvae to have a conspicuous impact on gypsy moth pupae. However, adults disperse slowly, and are not present at the leading edges of gypsy moth infestations. Field releases in established areas have been successful, but releases where the beetle is not yet present would be advantageous both to establish them and evaluate their effectiveness. A program is outlined for rearing, releasing and evaluating *C. sycophanta* along the leading edge. Development of an efficient rearing procedure for larvae is discussed.

IMPACT OF GYPSY MOTH ON OAK IN PENNSYLVANIA DISTRICT 7

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ABSTRACT

In response to concern about the effect of gypsy moth on oak (*Quercus* spp.) timber supplies in Pennsylvania, the Forest Inventory and Analysis Unit of the USDA Forest Service did an analysis of 62 remeasured plots in District 7 (central PA). Defoliation, drought, and cutting during the 1980's put a severe strain on the resource in the study area. Plot measurements taken in 1978 were compared to those taken in 1989.

Cumulative mortality and cut averaged 345 cubic feet per acre between 1978 and 1989 across all plots. Most of it was in oak, amounting to 35% of the 1978 oak inventory. This rate is much greater than the average for Central Appalachian oaks. The volume of oak in poletimber and small sawtimber-sized trees (less than 16.0 inches DBH) declined sharply between inventories. But the volume in bigger sawtimber trees increased by 35%. Oak growing-stock volume decreased by 7%. The oak component on the plots was reduced from 54% of the total inventory in 1978 to 44% in 1989. However, gains by red maple (*Acer rubrum* L.), pine (*Pinus* spp.), hemlock (*Tsuga canadensis* (L.) carr), birch (*Betula* spp.), blackgum (*Nyssa sylvatica* Marsh.), ash (*Fraxinus* spp.), and other species offset the oak loss. So the volume of all growing stock increased by 15%; sawtimber volume gained 32%. Oak sawtimber volume increased only an average of 86 board feet per acre (+5%) between inventories. Noteworthy losses were recorded for white, black, and chestnut oak (*Q. alba* L., *Q. velutina* Lam., and *Q. prinus* L.). But northern red oak (*Q. rubra* L.) sawtimber volume netted a 30% gain. Oak sawtimber volume on the plots still averages more than 1,700 board feet per acre. Moreover, two-fifths of the oak timber is in trees 16.0 inches DBH and larger, and half of this big oak volume is in trees with II or better butt log grades.

A DIFFERENTIAL EQUATION MODEL FOR GYPSY MOTH
POPULATION DYNAMICS

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ABSTRACT

This work considers a three variable ordinary differential equation model for gypsy moth population dynamics. The variables are the gypsy moth biomass density, foliage biomass density and natural enemy biomass density. It also consists of twelve parameters which involve such things as the search rates, consumption rates, conversion rates, immigration rates and emigration rates of the species involved.

This system of differential equations is "stiff" in nature, making the use of an implicit method necessary. The method which was chosen is a second order backward Euler method. It is interesting to note that more standard methods such as a Runge Kutta or predictor corrector methods either failed totally, or gave incorrect results. This points out the importance of a thorough analysis of a model and the numerical method used to solve it since it is possible that a method may give an answer without that being the correct answer.

It has been found that this model evidences behavior similar to the results of field studies. For example, with the appropriate choice of parameters, the model predicts periodic outbreaks of gypsy moths with a period of approximately ten years of a four to five year duration with a one to two year period of intense outbreak, resulting in approximately eighty to ninety percent defoliation of the stand.

We should also note that this model also shows the complex nonlinear behavior found in similar ordinary differential equation models. Under suitable conditions it evidences the phenomena of period doubling. This may lead to another route to chaos involving biological systems.

**USDA Interagency Gypsy Moth Research Forum
January 13-16, 1992
Annapolis, Maryland**

List of Attendees

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