HISTORY OF RESEARCH ON MODELLING GYPSY MOTH POPULATION ECOLOGY

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ABSTRACT

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

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

INTRODUCTION

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

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

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

HISTORY OF MODELLING RESEARCH

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

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

Regression-based empirical models

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

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

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

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

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

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

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

Process simulation models

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

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

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

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

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

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

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

CURRENT POPULATION MODELING RESEARCH

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

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

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

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

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

GYPSY MOTH LIFE SYSTEM MODEL

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

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

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

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

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

Animal and Plant Health Inspection Service
Otis Methods Development Center

Institutions

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

Background

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

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

Model Design

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

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

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

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

Weather Subsystem

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

Stand Subsystem

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

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

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

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

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

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

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

Gypsy Moth Subsystem

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

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

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

Natural Enemies

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

PREDATORS:
- Insects
  - *+[1] *Calosoma sycophanta, C.* spp.
- * Birds
- Small mammals
  - * white footed mouse *Peromyscus leucopus*
  - shrews *Sorex* spp., *Blarina brevicauda*

PATHOGENS:
- Virus
  - * nucleopolyhedrosis virus
- Bacteria
  - *Streptococcus faecalis*
  - *Serratia marcesceus*
  - *+ *Bacillus thuringiensis*
- Fungi
  - *Beauvaria bassiana*
  - *Paecilomyces farinosus*
- + Microsporidia spp.

PARASITES:
- Diptera (flies)
  - *+ *Parasetigena silvestris*
  - *+ *Compsilura concinnata*
  - *+ *Blepharipa pratensis*
  - + *Exorista larvarum*
- Hymenoptera (wasps)
  - *+ *Cotesia melanoscelus*
  - + *Phobocampe dispar*
  - *+ *Brachymeria intermedia*
  - + *Monodontomerus aureus*
  - *+ *Ooencyrtus kuvanae*
  - + *Anastatus dispar*
  - *Itoplectes conquisitor*

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

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

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

Input Data Files and Output Tables and Files

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

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

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

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

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

Current Status and Future Plans

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

CONCLUSIONS

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

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

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

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