



United States
Department of
Agriculture

Forest Service

Pacific Southwest
Forest and Range
Experiment Station

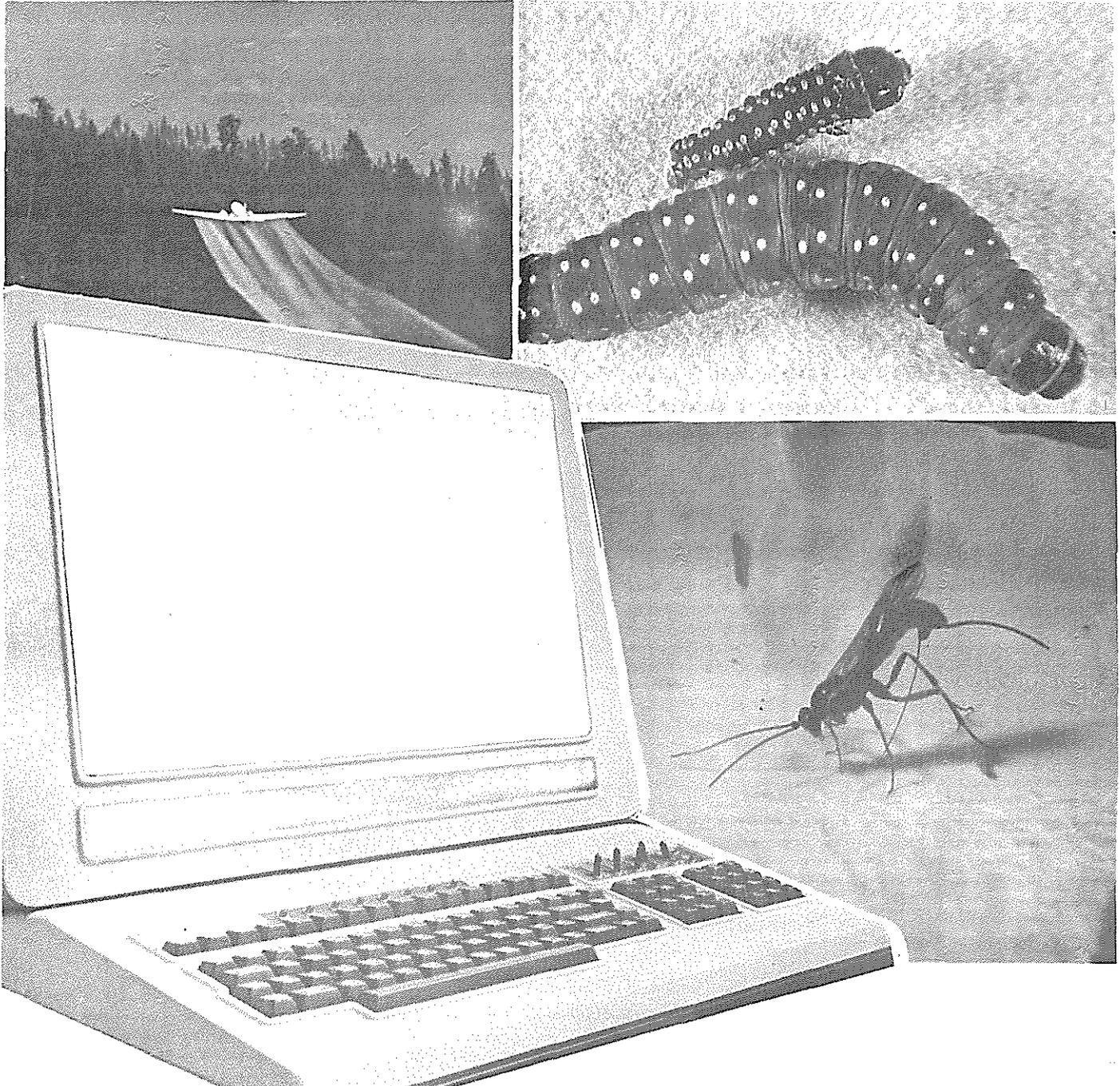
Research Paper
PSW-159



Computer Simulation for Integrated Pest Management of Spruce Budworms

Carroll B. Williams, Jr.

Patrick J. Shea



Authors:

CARROLL B. WILLIAMS, JR., is a pioneer scientist studying integrated management systems for forest insect pests and diseases, with headquarters in Berkeley, Calif. He is a University of Michigan graduate (B.S., 1955; M.S. 1957; and Ph.D., 1963, in forestry). He joined the Forest Service in 1957. **PATRICK J. SHEA** is in charge of the Station's field evaluation of chemical insecticides research unit, with headquarters at Davis, Calif. He joined the Forest Service and the Station staff in 1967. He earned degrees (B.S., 1962; M.S., 1972) in entomology at the University of California, Berkeley.

Acknowledgment:

We are grateful to D. Gordon Mott, Northeastern Forest Experiment Station, Forest Service, U.S. Department of Agriculture, for assistance in the development of the ideas expressed in this paper and for services in computer programming.

Publisher:

**Pacific Southwest Forest and Range Experiment Station
P.O. Box 245, Berkeley, California 94701**

July 1982

Computer Simulation for Integrated Pest Management of Spruce Budworms

Carroll B. Williams, Jr.

Patrick J. Shea

CONTENTS

Introduction	1
Components of the Pest Management System	2
Population Dynamics	2
Forest Stand Dynamics	3
Economic Impact	3
Control Systems	3
Structure of the Model	4
Simulations	7
Variation in Parasite Search Rate (a_p)	7
Variation in Insecticide Survival Rate (SC)	7
Optimizing Pest Management	8
References	11

IN BRIEF . . .

Williams, Carroll B., Jr.; Shea, Patrick J. **Computer simulation for integrated pest management of spruce budworms.** Res. Paper PSW-159. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 1982. 11 p.

Retrieval Terms: spruce budworms, insecticides, parasites, integrated pest management

System simulation can be used to develop a decision support system for scientists and forest managers in suppressing populations of forest insect pests. Information from the literature describing the effects of insecticides on the western budworm (*Choristoneura occidentalis* Freeman) and its major parasites, and models from population research on the spruce budworm (*C. fumiferana* Clem.) were used in a trial of the method. A simple model was developed to describe budworm-parasite systems which differed according to the hypothetical effectiveness of the parasites. Computer simulations described the survival of these systems when subjected to different levels of control by insecticides, and also described possible cost-benefits associated with different levels of control for the various budworm-parasite systems defined in the model. The primary components of the model for the simulations were

1. Mathematical models of the population dynamics of the pest insect and its parasites.
2. Mathematical functions for impact of different population levels of the pest insect on generalized forest product yields or values.
3. Estimates of the effectiveness of various "control" factors (parasites, insecticides) in suppressing and in preventing high populations of the pest insect.
4. The economic framework for cost-benefit analyses of the various control options.

Computer simulation of the model produces both stable and oscillating average population densities over time, depending on the parasite's searching efficiency or attack effectiveness. In general, as the parasite's effectiveness

increases, the budworm-parasite systems become more stable, and the average or steady density of the budworm decreases with increased parasite effectiveness.

In the simulations, when insecticide is applied to the oscillating system, the amplitude of the density oscillations increases at the lowest levels (control rates). However, at higher insecticide levels, amplitude decreases until a level of control is reached where the system becomes stable. The level of control at which the oscillations attain maximum amplitude increases with increasing parasite effectiveness. The level of control which produces a steady system decreases with increasing parasite effectiveness.

Similarly, in stable budworm-parasite systems, as insecticide control rates increase, the host density increases, then decreases at high insecticide rates. The control rate which produces the maximum density level increases as parasite effectiveness increases.

The simulations revealed that the level of budworm population suppression in stable or steady density budworm-parasite systems is not proportional to the amount of control applied in that insect generation. Only when very high control rates (insecticide dosages) are applied is much effect produced on the budworm population. Cost-benefit analyses showed that under these conditions, very high investments are worthwhile but moderate investments produce little effect.

A steady density budworm-parasite system (budworm density of 2150 without insecticides) was simulated to illustrate through cost-benefit comparisons the most economical pest population level achievable in control efforts. A variety of linear and curvilinear relationships between pest density and the value of damage were depicted for this system. If pest density was reduced from 2150 to some smaller value, a variety of costs were incurred and a number of gains were possible, depending upon the initial relation between pest or budworm density and the value of the damage.

Broadly, this study showed that the process of constructing a mathematical systems model serves to define the kinds of information required for understanding the biological structure and dynamics of the system. The study also demonstrated the usefulness of computer simulation experiments with these models to predict system behavior under different conditions and the consequences of various management decisions.

The development of ecologically acceptable management methods for forest insect pest populations is a complex problem. It requires for its solution data from many investigations of the insect populations and the crops they affect, the efficacies of various control methods, and the economic and social systems in which all of the activities take place. The currently popular terms "integrated control" and "systems approach" indicate an increased awareness by biologists and resource managers of the complexities of pest-crop systems and the need to understand them in order to develop viable management techniques.

Many of these systems for forest pest management have been presented as generalized diagrams and flow charts (fig. 1), in which the forests (crops), the pests and other system components, and their hypothetical relationships are illustrated (Campbell 1972, 1973; Waters 1976; Waters and Ewing 1976). Less commonly, systems analysis and computer simulation have been used to illustrate the structure and dynamics of the system, the linkages between system components and the consequences of various management decisions on the dynamics of the system (Watt 1959, 1961, 1964, 1968; Miller 1959; Holling 1963, 1964, 1966; Berryman and Pienaar 1974; Mott 1973). A

thorough historical account of the development of the concepts and realities in forest pest management was provided by Waters and Stark (1980).

A great advantage of computer simulation is that it permits experimentation with mathematical representations of real-world systems which would be risky, difficult, and expensive with actual systems. For example, a prime requirement in the development of most management systems for forest defoliating insect pests is the evaluation of the effects of insecticide applications on these pest populations and their parasites, and of the amount of protection such applications may offer to various forest product yields and values. Field experimental programs designed to examine these interests are difficult and expensive to run, but they provide quantitative estimates for various system parameters that allow us to evaluate the effects of insecticide treatments on the actual pest-forest system.

Field studies of the effects of pesticides on the spruce budworms (*Choristoneura* sp.) and their parasites have shown severe suppression of host (budworm) populations and increased parasitism after treatment (Eaton and others 1949, MacDonald 1959, Williams and others 1969, Carolin and Coulter 1971). Parasite survival was enhanced by moderate reduction (50-70 percent) of the host population;

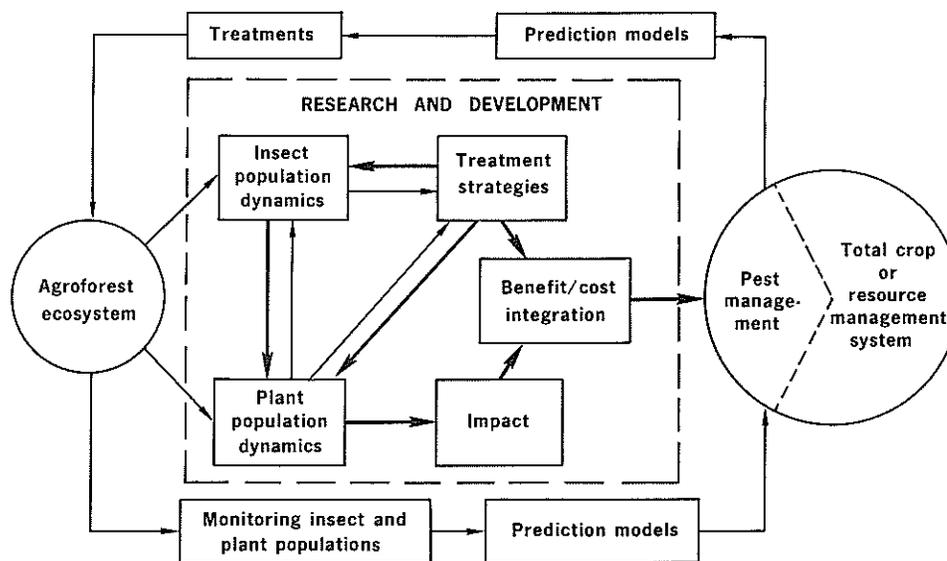


Figure 1—Model structure of an insect pest management system, with research and development components and action sequence (Waters and Ewing 1976).

increased parasitism under these conditions lasted for several years (Williams and others 1979).

In contrast, reports of spray programs to control agricultural insect pests have frequently described the initial severe suppression of the pest, but the virtual elimination of the natural enemies of the pests, followed by a resurgence of the pest populations; subsequent damage to crops is often higher than before pesticide treatments (Van den Bosch 1970, Kilgore and Douth 1967, and Pickett and MacPhee 1965). The conflicting results of these two sets of studies are partly explained by the nature of the pest insect-crop system and the frequency of insecticide applications. Such conflicts indicate, however, a role for computer simulations as an aid in forecasting the biological consequences of applying different levels of insecticide control on the pest populations and their parasites.

This paper demonstrates the applicability of computer simulation to research and management through the construction and use of system models in integrated forest pest management. A mathematical systems model can indicate what kind of information is required for understanding the biological structure of the system and prediction of system behavior with and without regulation. We examine the interactions among parasites and host (pest) densities and survival of host-parasite systems subjected to different levels of control by insecticides. We also examine cost-benefit functions associated with different levels of control.

Although the concepts used in these simulation studies are taken from field insecticide trials on western spruce budworm (*Choristoneura occidentalis* Freeman), and data from population research on the eastern spruce budworm (*Choristoneura fumiferana* Clem.) were used to describe the interaction; we do not suggest that the simulations mimic population dynamics of either budworm. Rather, we describe a very simple and general process that may pertain to other defoliators, with the aim of demonstrating the potential of simulation studies as aids in decisionmaking in forest insect pest management problems.

COMPONENTS OF THE PEST MANAGEMENT SYSTEM

Ideally a pest management system can be envisioned as a large model composed of different components or submodels. These components describe various biological and socio-economic processes and are linked in a manner to show the primary pathways of information flow that lead to decisionmaking. The nature of the linkages is important because inputs from one submodel can be the parameters for another.

The generalized forest pest management system model shown in *figure 1* has two structures—an inner research

and development core and an outer “management” structure. Our computer simulations focus on four components of the research and development core:

- Mathematical models of the population dynamics of the pest insect and its parasites.
- Mathematical functions for impact (usually damaging) of different population levels of the pest insect on generalized forest product yields or values.
- Estimates of the effectiveness of various control factors (parasites, insecticides) in suppressing and in preventing high populations of the pest insect.
- An economic framework for cost-benefit analyses of the various control options.

Our simulations do not include the forest stand dynamics component because it adds more complexity than we desire or need for our purpose. However, we will discuss this component below along with the others because it provides the linkage between the pest population dynamics and impact components. The impact and control components provide direct inputs into cost-benefit analyses required for decisionmaking on pest management activities within the forest resource management system. A more detailed description of these system components is given by Waters and Stark (1980).

Population Dynamics

Generally, models of population dynamics of pest insect species show how insect mortality is affected by population densities and forest conditions and identify key mortality agents. These models may indicate which mortality agents have the greatest potential for biological control. Generally these agents—parasites, predators, or disease-causing organisms—are density-dependent; that is, they respond to population changes of the pest insect species. Their potential can be enhanced occasionally by management actions, and although they may not adequately suppress epidemic pest populations, they may be effective in regulating low or endemic pest populations. Models of population dynamics may indicate how natural enemies of the pest may be made more effective. Perhaps some of the potentially more effective parasites are themselves regulated by alternate hosts or hyperparasites.

These models show whatever relationships may exist between insect survival and forest stand variables such as size and age of host trees, forest composition or habitat types, crown levels, stand densities and basal area, aspect, and topography. Consequently, the models serve to indicate the stand management or silvicultural treatments that may produce forest conditions less favorable to population increases of the pest insect. The models are also designed to mimic the effects of various kinds and dosages of chemicals. In particular, they describe the influence of these chemicals on the effectiveness of parasites, predators, and disease-causing organisms in controlling pest insect populations.

Forest Stand Dynamics

Models of stand dynamics and biomass production portray the ecological impact of pest population density levels, and of the duration of feeding injuries, on a variety of forest conditions or habitat types.

For example, defoliating insects consume the leaves of forest trees. If this activity is severe and sustained, it can lead to growth reduction, stem dieback, stunted and deformed trees, and eventually tree mortality over small or large areas. Defoliation can also reduce competition among surviving forest trees, however, and thus result in increased tree growth. The residual stand may actually be more productive than it would have been without the insect activity. Defoliation can increase the fall of nutrient-rich litter, stimulate the activity of decomposer organisms, and increase light penetration to the forest floor, thereby increasing the survival of seedlings, and the production of forage, or both. Defoliation can also increase water yield from the area.

Whether a particular level of insect activity is beneficial or injurious depends on the forest management objectives and plans of different ownership and user groups, the costs of effective control, the costs of alternative management plans if current plans are made unfeasible, and the vagaries of the market place. Economic impact models serve to determine values (losses and gains) affected by insect activities within the forest stand in relation to specific forest management plans.

Economic Impact

A model of economic impact describes both the values produced by forests under specific management plans and procedures and the influence of insect pest populations on this value production. Little or no economic damage may be caused by heavy defoliation over a short period of time, or severe damage may result from moderate defoliation over an extended period of time. The direct and indirect economic effects of defoliation by a forest insect pest species may be immediately obvious or may not be measurable until the end of the rotation period. Under certain conditions we may occasionally find that low to moderate pest population levels add value to forest stands by the end of the rotation period.

Economic impact models guide decisionmaking for control activities by establishing a means of benefit-cost analysis, leading to more efficient use of resources. The concept of "economic threshold" is a useful part of any benefit-cost analysis, and may be defined as the level at which the loss caused by the pest insect population just exceeds in value the cost of the control measures available (Geier and Clark 1961). Obviously, economic impact models must encompass the costs and effectiveness of various control strategies, including no control, and the short- and long-term value saved or lost by different con-

trol strategies initiated at different population densities and different times during the outbreak.

Control Systems

The effectiveness of the various materials, organisms, and techniques of vegetation management that either directly suppress insect pest populations or inhibit further population increase may be modeled as a control system. Materials applied include insecticides, microbials, and behavioral chemicals. Computer simulation of the control system can help in the evaluation of the effectiveness of various dosage levels of different materials on the pest insect and nontarget organisms.

Insecticides differ in their uses, properties, advantages, and restrictions. Predictions of the fate of each insecticide in various environments and effects on target and nontarget organisms can be made on the basis of the correlation of toxicological, chemical, and physical properties for each insecticide with the physical and biological environment and the representative phylum and order of organism treated. Computer simulation can aid the development of control systems that will allow the resource manager to use those insecticides that are currently available more intelligently and judiciously to avoid serious problems, and will help the researcher to develop more ecologically acceptable insecticides.

Direct control of insect pests by chemicals tends to be least expensive in the short run compared to other kinds of controls. If used repeatedly, however, chemical control decreases in effectiveness as pest populations become more resistant and economic and environmental costs increase. Direct control by certain biological organisms tends to be expensive in the short run, but if the organisms subsequently become established and effectively keep pest population levels below the economic threshold, then this control method becomes least expensive in the long run. Environmental costs associated with most forms of biological control are small.

If we include the environmental costs in with the economic costs of control, then some combination of biological and chemical control could be part of an optimal pest management program. To achieve this, information on the interaction of chemicals and various biological organisms such as parasites would be required. Modeling these interactions and the economic costs of control may allow us to devise optimum control strategies and policies for use of chemicals and other controls.

An optimal pest management program would distribute available controls (singularly or in combination) so that costs associated with forest product damage, controls, and environmental damage due to controls are minimized. An example of how the methods of optimal control theory can be applied to the problems of pest management and the results which may be expected has been described by Vincent (1975).

STRUCTURE OF THE MODEL

The basic structure of the model used for the present simulation is

$$N_{t+1} = N_t SC_t SG_t (1 - RP_t) F_t$$

in which

- N_{t+1} = number of pest insects at time $t + 1$
- SC_t = survival rate for the exposed population, N_t , from insecticidal applications during the interval from t to $t + 1$
- SC_t = survival rate for the exposed population, N_t , from other factors during the interval t to $t + 1$
- RP_t = mortality rate for N_t from parasitism during the time interval
- F_t = reproductive rate for N_t during the time interval.

The following general assumptions are made:

1. The pest host insect-parasite system is closed, with neither immigration nor emigration.

2. Generation survival (SG) is a constant.

These assumptions are unrealistic. Many unconsidered factors affect system dynamics. For example, death results from weather and from predation, disease, and accident. In real systems, many of these mortality agents are density dependent. Also, the intensity of many of them is determined by extrinsic or accidental events which affect population levels at various stages of an insect generation.

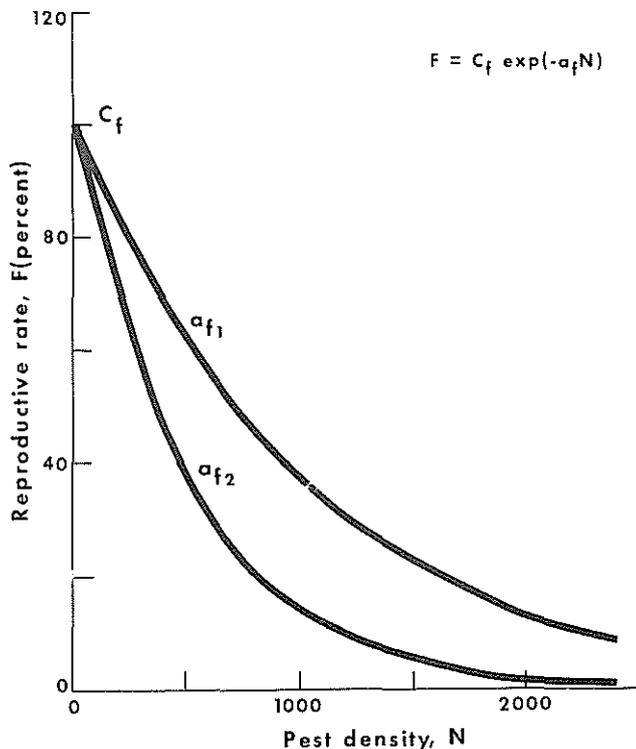


Figure 2—Fecundity function $F = C_f \exp(-a_f N)$; $C_f = 100$.

These two assumptions are necessary, however, because our intention here is to study certain simple effects. Our main rationale is that these merit attention before studies of compound effects.

3. SC—survival of pest insect under insecticidal control—is a constant in each simulation run, for a given case (set of system values), but varies from case to case.

4. F—reproductive rate—varies in response to density, N . It is assumed (*fig. 2*) that F has an upper limit (C_f) when density approaches zero, and that F diminishes exponentially at a rate a_f as N increases, such that

$$F = C_f \exp(-a_f N)$$

F is not permitted to decrease at very low population density as a result of mating failure or other phenomena affecting the reproductive process. The general form of this relation closely resembles natural events, however, and it is an acceptable approximation for our present purpose.

5. Parasite attack and adult parasite population dynamics are as defined by Watt (1959):

$$NA_t = P_t K [1 - \exp(-a_p N_t P_t^{1-b_p})]$$

in which

- NA_t = number of host insects attacked in generation t
- P_t = number of adult parasites present in generation t
- a_p and b_p = constants for parasite effectiveness
- K = maximum attacks per parasite

For a complete discussion of the derivation of this model, see Watt (1959); for examples of its application see Miller (1959) and *figure 3*. The constant a_p describes the parasite's searching ability in the absence of competition, and b_p describes competition among parasites for opportunities to attack hosts.

Briefly, the attack rate per parasite, NA/P , can attain a maximum, K , and diminishes as the ratio of hosts per parasite, N/P , diminishes.

We assume that parasite attack occurs early in the host's generation, that the survival of the parasite and that of the host are identically affected by the mortality factors, except for the insecticide applied, and that, after emergence, parasites are subject to an additional mortality factor (C_p , see assumption 7) before attacking the next generation of host insects.

6. Natural control of the pest host insect population results from reductions in reproductive rate (F) and from the effects of parasites, RP .

When some insecticides are applied against some forest pests, particularly immature stages of the spruce budworms containing developing parasites, differential mortality occurs among parasitized and nonparasitized insects (Eaton and others 1949; MacDonald 1959; Carolin and Coulter 1971; Williams and others 1969, 1979). The sur-

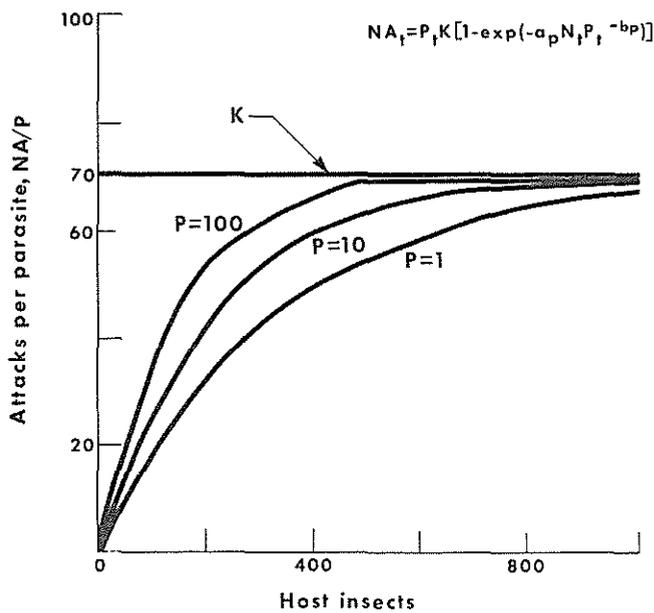


Figure 3—Number of attacks per parasite, NA/P as host-parasite ratio varies. $NA_t = P_t K [1 - \exp(-a_p N_t P_t^{-b_p})]$

vival rate of the relatively inactive, moribund parasitized larvae is higher because they are less exposed than the nonparasitized insects to other mortality factors, such as the insecticide spray droplets. This interpretation is particularly relevant for 5th and 6th instar western spruce budworm larvae parasitized by *Apanteles fumiferanae* Viereck and *Glypta fumiferanae* Viereck (Williams and others 1969, 1979). These parasites attack the 1st and 2d instars of the budworm, and except for some early emergence of *A. fumiferanae* from the 4th instar, their progeny emerge from 5th and 6th instars. A 5th- to 6th-instar budworm containing a fully developed parasite about to emerge is usually inactive and moribund. These host larvae are probably not as much exposed to insecticide droplets and residues as normal, highly mobile, actively feeding 5th to 6th instars.

We included this phenomenon in our model by making the insecticide more effective, by factor E , against nonparasitized than parasitized insects (fig. 4). The following relations then hold:

If

- PP = proportion of insects parasitized before spraying
- PN = proportion not parasitized before spraying
- RP = proportion parasitized after spraying
- SC = survival rate of total insect population from spraying
- LP = survival rate of parasitized insects from spraying
- LN = survival rate of nonparasitized insects from spraying
- E = ratio of LP to LN

then

$$LP - (E LN) = 0$$

$$(LP PP) + (LN PN) = SC$$

and

$$E(PP + PN) = \frac{SC}{LN}$$

$$RP = \frac{LP PP}{SC}$$

Solving for LP, LN, and RP yields

$$LN = \frac{SC}{1 + (E - 1)PP}$$

$$LP = E LN$$

$$RP = \frac{E PP}{1 + (E - 1)PP}$$

The relation between RP and PP for various values of E is shown in figure 4A. Analyses of data from Williams and others (1979) support our contention that E is dependent on SC. If this relation is valid, E is certainly dependent on the timing, method and quality of insecticide application, the type and physical properties of the insecticide, and the specific host-pest-parasite system under consideration.

We chose the relation $E = e^{a_e SC}$ (fig. 4B) because it is based on observed fact (Williams and others 1979) and logical reasoning. Experiments to test this hypothetical relation are particularly needed because the phenomenon has a profound effect on the results of simulation of insecticide applications in an integrated control program.

7. Our model component for changes in parasite populations subjected to insecticide treatments while in the host budworms reflects the differential survival of parasitized budworms over nonparasitized budworms, as well as other factors previously described.

$$\begin{aligned} P_{t+1} &= C_p N_t SC RP \\ &= C_p N_t SC \left(\frac{E PP}{1 + (E - 1)PP} \right) \end{aligned}$$

in which

C_p = parasite mortality in adult stage, and

$$PP = \frac{NA_t}{N_t}$$

8: An element in the system to be simulated is the degree of damage to the resource. We assume that each year the pest population produces some damage to the resource—damage that will occur either in the year of attack, or in some future year—for example, growth reduction in a perennial crop; or proportional mortality in an annual crop. Several cases are discussed below.

9. The following relations were used to derive the cost function: First, a relation usually exists between the dos-

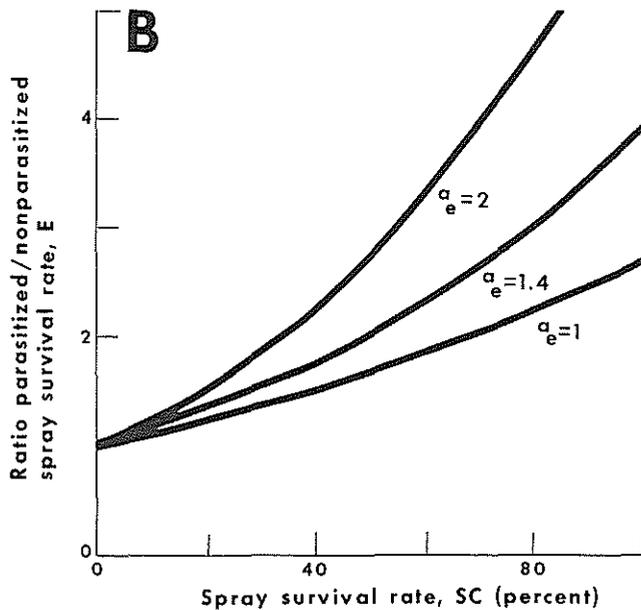
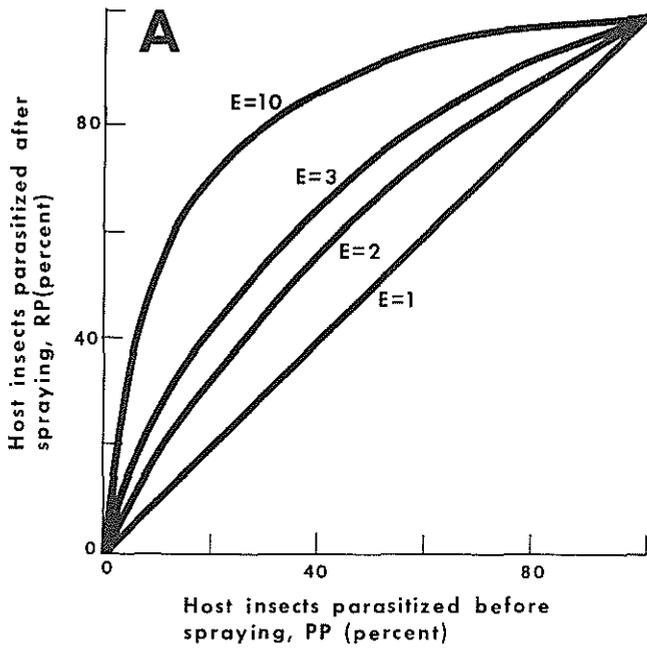


Figure 4—(A) Relationship between RP and PP as factor E varies. E is the ratio of the survival rate of the parasitized insects from spraying to that of the nonparasitized insects from spraying. (B) Relationship between E and SC for various values of a_e , a constant representing rates of increase ($E = e^{a_e SC}$).

age of any insecticide and the proportional mortality secured. Conventionally, a probit mortality, logarithmic dosage transformation produces an approximately linear relationship (Goldstein 1964, Finney 1971). We assumed a simpler relationship, that of an asymptotic exponential. The result assumes a greater effectiveness for insecticides at low dosages than is ordinarily obtained, and thus, a lower cost for any specified level of control below 50 per-

cent. For the purposes of this study we will exclude any environmental or social cost of using insecticides.

The function for cost was obtained as follows:

$$(1 - SC) = e^{-a_c INS}$$

in which

a_c = constant which establishes proportionality between units—that is, numbers or percent of insects killed and pounds of insecticide applied

INS = amount of insecticide.

Solving the above for INS, we obtain

$$INS = \frac{\ln SC}{-a_c}$$

or solving for mortality ($1 - SC$), we obtain

$$1 - SC = \frac{INS}{a_c}$$

For applying insecticide, as in aerial spraying, the costs incurred are fixed costs (FX) plus a variable amount proportional to the amount of insecticide applied (including application cost, cost of insecticide and so forth). Thus

$$COST_t = FX + C_c \left(\frac{\ln SC}{-a_c} \right)$$

in which C_c = variable cost per unit of insecticide.

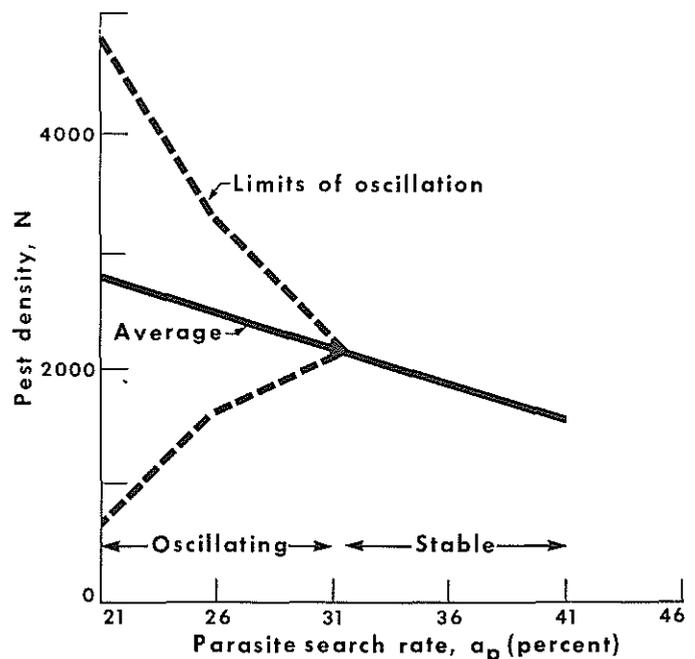


Figure 5—Result of varying parasite effectiveness constant a_p after 200 generations.

SIMULATIONS

To demonstrate the applicability of system simulation in integrated pest management in forestry, we conducted simulation runs using data drawn from the literature and analytic procedures developed from our study of the problem. The results of these simulations serve to illustrate certain basic points:

1. Intelligent multiple-use forest resource management (with respect to pest control) requires the development and early application of analytic methodology such as that represented by the simulations.

2. Forest insect population biologists must provide information in the form required by the analytic methodology referred to in 1, above.

3. The nature of the pest-forest interaction, and the estimated value of the damage caused to specific forest products by different population levels of the pest insect, must be known if the simulation is to be useful.

The values used in the experimental simulations were obtained from Miller (1959):

SG (generation survival from factors other than insecticides) = 0.4

C_r (upper limit of reproductive rate) = 0.100

a_f (rate that F diminishes exponentially) = 0.001

K (maximum attacks per parasite) = 0.70

b_p (constant for parasite effectiveness) = 1.8

C_p (added mortality factor for parasite after emergence) = 0.1

FX (fixed cost of insecticide) = 0.50

C_c (variable cost per unit of insecticide) = 0.50

a_c (constant for proportionality between units of insects killed and amounts of insecticide applied) = 0.001

Variation in Parasite Search Rate (a_p)

The model produces both stable and oscillating population densities after 200 generations, depending upon the value of a_p , the constant representing the parasite's searching efficiency. *Figure 5* depicts these results. In general, as a_p increases, the system becomes more stable, and the average or steady density decreases with increased parasite attack effectiveness. These results demonstrate that pest management can be obtained by improving parasite effectiveness, either by increasing the vulnerability of the host insect or the searching effectiveness of the parasite, or by finding new parasites with more effective searching abilities. Studies are needed, however, to test the feasibility of such efforts. The costs and benefits of the studies themselves must be investigated, with reference to their net effects on the host-parasite system. The accuracy of the model must also be tested, by examination of the effects of varying its parameters. Subsequently, additional

biological studies are needed to estimate the costs of modifying promising parameters.

Variation in Insecticide Survival Rate (SC)

The results of modifying both SC and a_p are shown in *figure 6A*. First, the intercept values on the y axis represent the values plotted in *figure 5*. Note that there is a separate curve for each value of a_p , relating pest density to SC. SC decreases from left to right—that is, mortality due to insecticide increases from left to right.

Two types of cases are possible. The first type includes those in which a_p has values which permit the system to oscillate. In these cases, a two-branched curve shows the limits of the oscillation. The second type includes those in which the values of a_p produce a stable system. In the oscillating system, as insecticide is applied at increasing levels, the amplitude of the oscillations changes. At the lower insecticide levels, amplitude increases; at higher levels, it decreases until a level is reached where the system becomes stable. The level at which the oscillation attains maximum amplitude increases with increasing parasite effectiveness. The level which produces a steady system decreases with increasing parasite effectiveness.

Similarly, in steady density systems, as insecticide levels increase, the steady density increases, then it decreases. The level which produces the maximum density increases as parasite effectiveness increases.

These results illustrate the need for a relevant framework for the development of methods for controlling insect population and minimizing forest pest impact. From the cases described by these simulations, it is evident that since damage is related to insect density, it may be more profitable to leave the system alone than to attempt control with low insecticide dosage rates.

A particularly important result is shown in *figure 6B*. The degree of steady density reduction obtained by increasing levels of control is plotted against the mortality rate. Clearly, the level of population suppression obtained is not proportional to the amount of control applied in the generation. Only when very high control rates or insecticide dosages are applied is much effect produced in the population. It appears that very high investments are worthwhile but moderate investments produce little effect.

A final important result from these simulations is the indication that parasites become extinct when sufficient insecticide is applied ($SC = 0.13$) to cause 87-percent mortality. At this point each host-parasite system behaves in the same way in response to the insecticide dosage, and all curves in *figure 6A* coalesce. In a real system, the presence of alternate hosts and invasion of parasites from surrounding untreated areas may maintain or reestablish the parasite population.

OPTIMIZING PEST MANAGEMENT

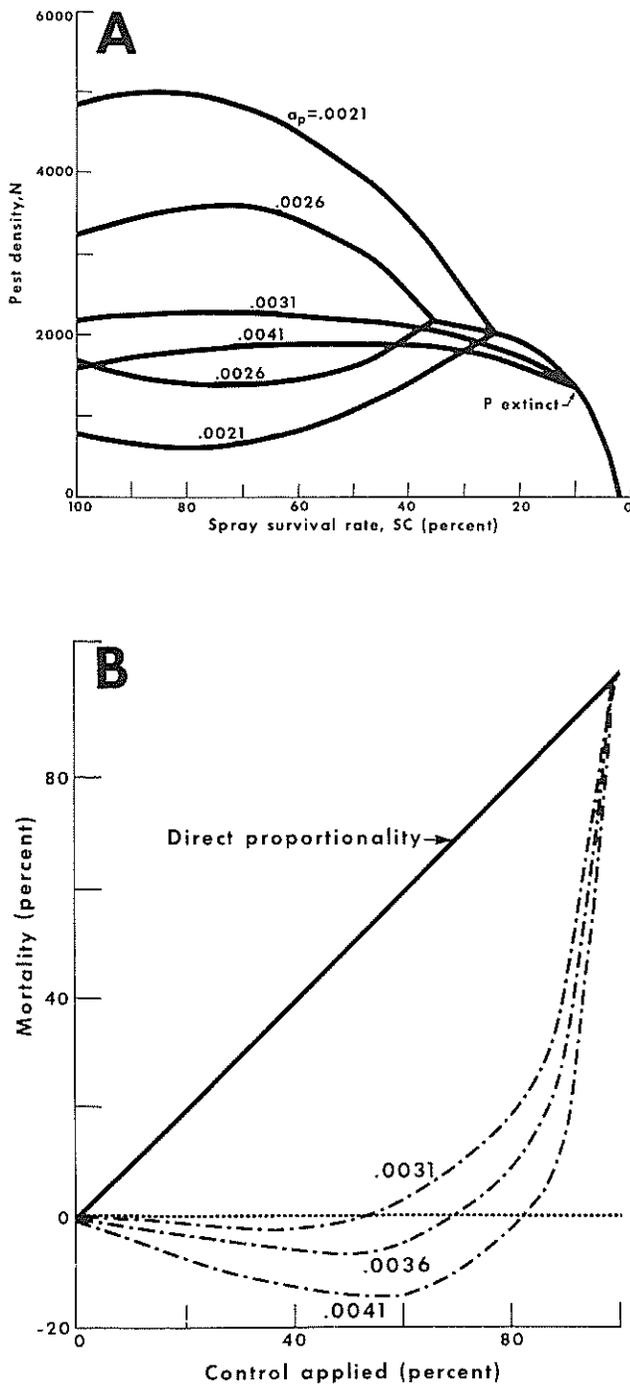


Figure 6—(A) Relationships between pest density and SC for various values of a_p . (B) Relationship between percent control applied with insecticides and actual reduction in population level for various values of a_p after 200 generations.

The preceding discussion suggests that the behavior of the pest-parasite population system under insecticidal control is complex; suppression of the pest is not proportional to insecticide dosage rate.

The most economical pest population level achievable through control can only be determined through cost-benefit analyses of the impact of pest insect populations on forest product values. First consider a simple example of the relation between damage value and pest density. We know that without insecticidal control our pest population has a density that depends on the parameters of the model, and that if $a_p = 0.0031$, the steady density is 2150. In figure 7A three similar cases are depicted in which there are simple linear relationships between the value of damage to different forest product values and pest density. Consider case A with pest density 2150 and value of damage about 350 units. If pest density is reduced to 0, all of this value will be gained. A linearly proportional gain occurs at intermediate pest densities. In case B, the maximum gain is greater—about 50 units, and in case C, a very high gain is possible.

In figure 7B these three gain curves are described as a function of pest density. The cost of obtaining this pest density, calculated as explained above, is also shown. Clearly, in case A, any insecticidal control operation will yield a net loss—the gain function is always less than the cost function. In case B, pest control does not become profitable until pest density is reduced to about 700; then there is a region of increasing net gain to a maximum, followed by a region of decreasing net gain to a point beyond which control rates that result in very low densities are again unprofitable.

In case C, in which there is a very rapid increase in gain as pest density declines, it will be maximally profitable to practice the highest possible rate of control because the point at which the gain function curve exceeds the cost function curve the most (point of maximum net gain) is in the vicinity of the intercept. Otherwise, some lower rate of population suppression is maximally profitable.

This simplified example demonstrates several fundamental points:

1. The cost and gain functions are necessary to determine optimal control rates.
2. The cost function cannot be derived without a thorough knowledge of the consequences of attempting population control. Results may not be those expected. In more realistic cases—where there are compound interactions among the mortality sources, or where integrated control through manipulation of several factors of mortalities or control methods is to be attempted—it will be necessary to observe and analyze system response in far greater detail than can be shown here.

3. The best control decision is based on the form of both the gain function and the cost function. The gain function depends on the relation between damage value and pest density in this case. This relationship, of course, is an important problem in insect impact studies. In this example we are concerned with the relation between insect densities and damage values. More generally, we must be concerned about relationships which depend on density, time of attack relative to the development of values in the tree species, physical location of attacks in timber, the interaction between pest control activities and the yield of other forest resource values, and so forth. Ultimately, we must be able to compute real cost and real gain in the system.

Consider an additional factor which complicates the simple linear density example. In *figure 8A* a threshold effect has been added to the previous linear case. Two different threshold densities, below which no damage occurs, are introduced. The consequences (*fig. 8B*) are that the point of maximum net gain is always less than complete control.

In additional simulation runs, we added more complexity to our examples by showing a curvilinear relationship between the amount or value of damage and pest density in

order to represent a situation where low insect populations or densities provide some benefit in forest value production. In *figure 8C*, the lower curve represents a situation in which there is actually some gross gain (a negative damage) from a low pest density. Clearly (*fig. 8D*), high control rates would not be selected. On the other hand, the upper curve in *figure 8C* would indicate a very high control rate.

In summary, we have clearly shown the kinds of data required for determining insect control strategies in timber management. The primary requirements are

- A thorough knowledge of the pest system, including effectiveness of natural control agents, and the consequences of introducing various degrees or rates of control into that system.
- The effectiveness and costs of alternative methods of control required to obtain various degrees of population reduction.
- An understanding of the relationship between pest population levels and units of damage.
- Knowledge of the value of the resource and units of damage.
- Ability to develop the cost and gain functions necessary to determine optimal control rates.

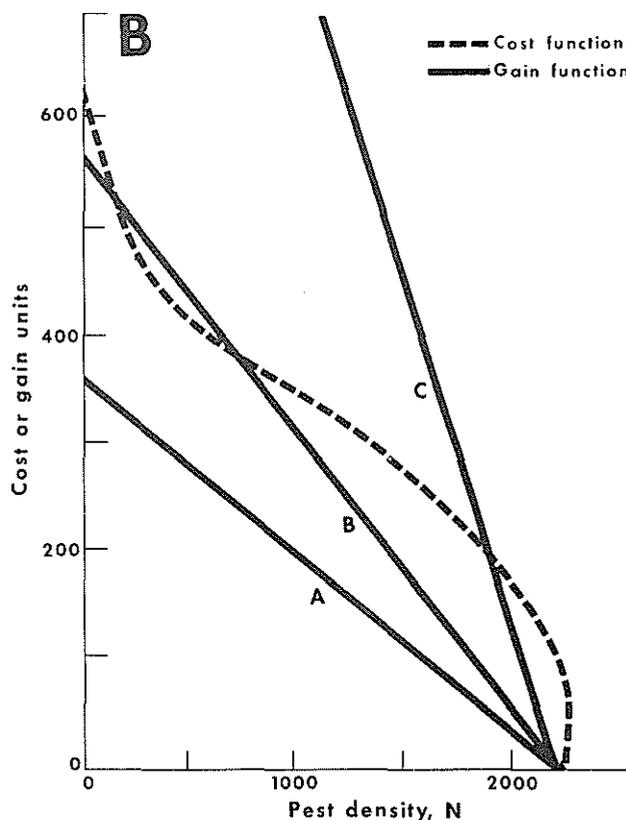
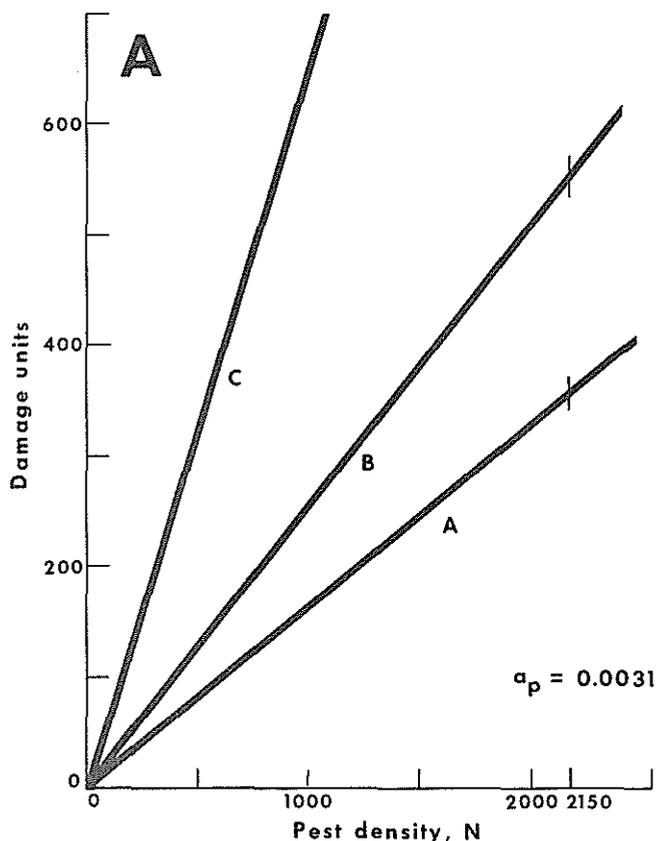


Figure 7—(A) Linear relation between the amount or value of damage and pest density for three cases of the parasite-host-pest system, with $a_p = 0.0031$. The steady density of the pest population is 2150. (B) Relationships between the gain curves of three cases or

situations and pest density for the parasite-pest system: $a_p = .0031$, and cost curve for the amount of control required to reduce the pest density from 2150 to 0.

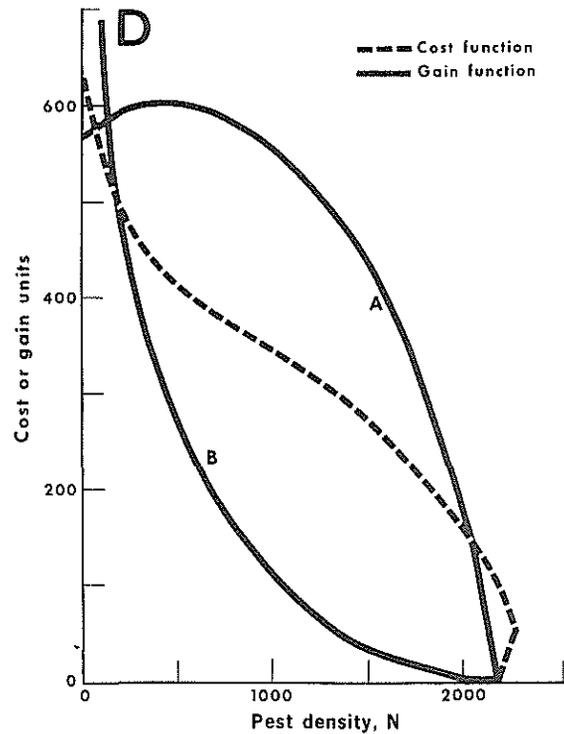
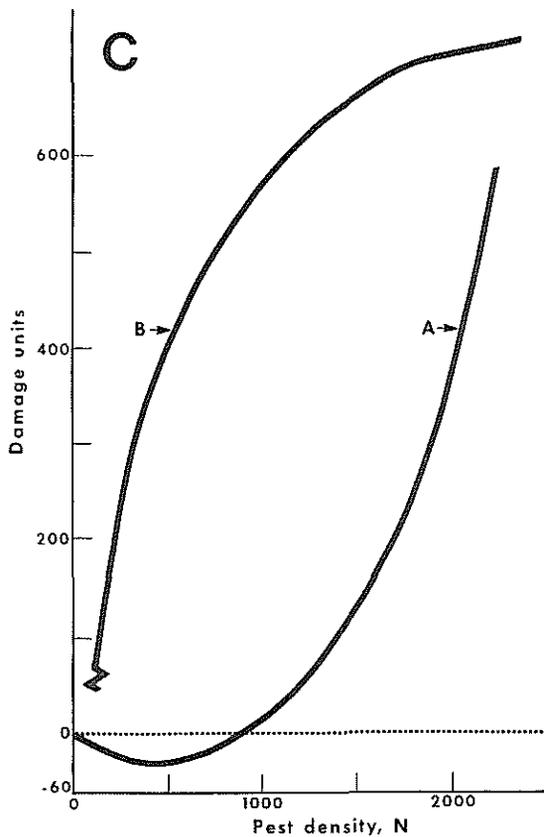
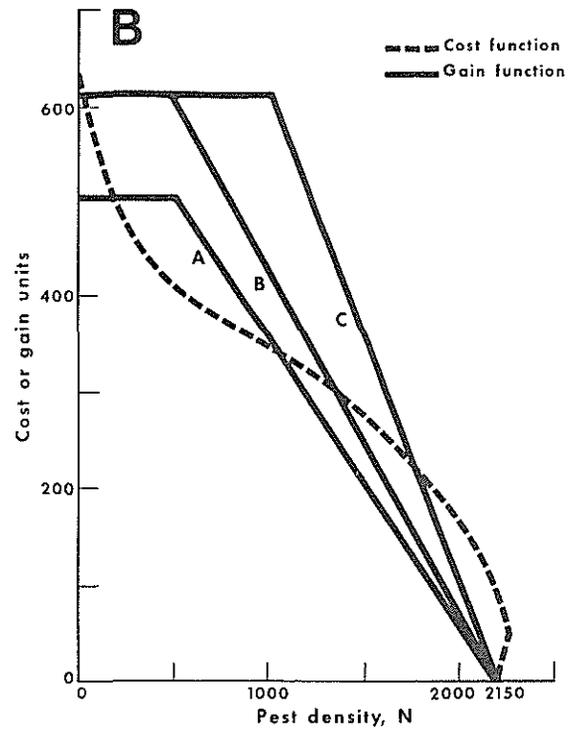
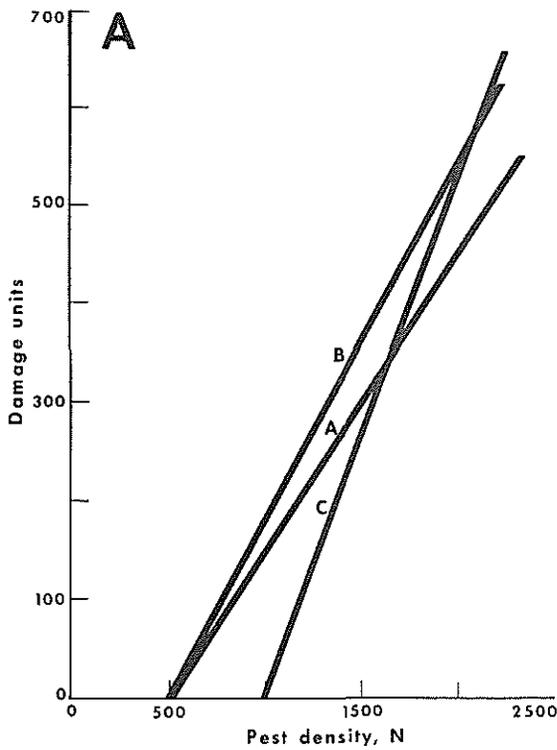


Figure 8—(A) Relationships between the amount or value of damage for the parasite-pest system ($a_p = .0031$) where no damage occurs until the pest population density reaches 500 (cases A and B) and 1000 (case C). The steady density for the pest population is 2150. (B) Relationship between the gain functions of cases A and B with a pest density threshold of 500 and case C with a pest density threshold of 1000, and cost curves for the amount of control required to reduce pest density of the parasite-pest system ($a_p =$

.0031) from 2150 to 0. (C) Curvilinear relationship between the amount or value of the damage and pest density for the parasite-pest system: $a_p = .0031$. The steady density of the pest population is 2150. Situation A represents small gains (negative damage) at pest densities from 0 to 800. (D) Relationship between the gain functions of cases A and B, pest density for the parasite-pest system: $a_p = .0031$, and cost curve for the amount of control required to reduce the pest density from 2150 to 0.

Perhaps the most important points that we have demonstrated are the analytical methodology necessary to determine the relationship between certain kinds of information required in decisionmaking for pest control, and the usefulness of computer simulation in experimenting with mathematical representatives of real world systems to predict the consequences of various management decisions.

REFERENCES

- Berryman, A. A.; Pienaar, L. V. **Simulation: a powerful method of investigating the dynamics and management of insect populations.** Environ. Entomol. 3(2):199-207; 1974 April.
- Campbell, Robert W. **Developing a pest population management system.** Proceedings of the Tall Timbers conference on ecological animal control by habitat management; 1971 February 25-27; Tallahassee, FL. Tallahassee, FL: Tall Timbers Res. Stn; 1972; 9-20.
- Campbell, Robert W. **The conceptual organization of research and development necessary for future pest management.** In: Stark, R. W.; Gittens, A. R., eds. Pest management for the 21st century. Nat. Res. Series 2. Moscow, ID: Idaho Res. Found., Inc.; 1973; 23-38.
- Carolin, V. M.; Coulter, W. K. **Trends of western budworm and associated insects in Pacific Northwest forests sprayed with DDT.** J. Econ. Entomol. 64(1):291-297; 1971 February.
- Eaton, C. B.; Beal, J. A.; Furniss, R. L.; Speers, C. F. **Airplane and helicopter spraying with DDT for spruce budworm control.** J. For. 47(10):823-827; 1949 October.
- Finney, D. J. **Probit analysis.** 3d ed. London: Cambridge University Press; 1971. 333 p.
- Geier, P. W.; Clark, L. R. **An ecological approach to pest control.** Proceedings of the 8th technical meeting of the International Union for Conservation of Nature and Natural Resources, 1961; Warsaw, Poland. 1961; 10-18.
- Goldstein, Avram. **Biostatistics. An introductory text.** New York: Macmillan Publishing Co., Inc.; 1964. 272 p.
- Holling, C. S. **An experimental component analysis of population processes.** Memoirs Entomol. Soc. Can. 32:22-32; 1963.
- Holling, C. S. **The analysis of complex population process.** Can. Entomol. 96(1-2):335-347; 1964 January-February.
- Holling, C. S. **The functional response of invertebrate predators to prey density.** Memoirs Entomol. Soc. Can. 48:3-86; 1966.
- Kilgore, W. V.; Douth, R. L. **Pest control, biological, physical and selected chemical methods.** New York: Academic Press; 1967. 447 p.
- MacDonald, D. R. **Biological assessment of aerial forest spraying against spruce budworm in New Brunswick III: Effects on two overwintering parasites.** Can. Entomol. 91(6):330-336; 1959 June.
- Miller, C. A. **The interaction of the spruce budworm, *Choristoneura fumiferana* (Clem.), and the parasite *Apanteles fumiferanae* Vier.** Can. Entomol. 91(8):457-477; 1959 August.
- Mott, D. Gordon. **Future pest management systems.** In: Stark, R. W.; Gittens, A. R., eds. Pest management for the 21st century. Nat. Res. Series 2. Moscow, ID: Idaho Res. Found., Inc., 1973; 73-92.
- Pickett, A. D.; MacPhee, A. W. **Twenty years experience with integrated control programs in Nova Scotia apple orchards.** Proceedings of the 12th International Congress on Entomology. London; 1971. 597 p.
- Van den Bosch, R. **Pesticides: prescribing for the ecosystem.** Environment 12(3):20-25; 1970 April.
- Vincent, Thomas L. **Pest management programs via optimal control theory.** Biometrics 31:(1)1-10; 1975 March.
- Waters, William E. **Evaluation of insect impacts on forest productivity and values.** Proceedings of the XVI IUFRO World Congress, Group 6; 1976 June 24; Oslo, Norway. Moscow, ID: University of Idaho; 1976; 15-18.
- Waters, William E.; Ewing, Bland. **Development and role of predictive modeling in pest management systems—insects.** Tummala, Ramamohan L.; Haynes, Dean L.; Croft, Brian A., eds. USA/USSR Symposium on long-term and short-term prediction models of insects, phytopathogens, and weed populations as they relate to crop loss; 1974 July 16-18. East Lansing, MI: Michigan State Univ.; 1976; 19-27.
- Waters, William E.; Stark, Ronald W. **Forest pest management: concept and reality.** Ann. Rev. Entomol. 25:479-509; 1980.
- Watt, K. E. F. **A mathematical model for the effect of densities of attacked and attacking species on the number attacked.** Can. Entomol. 91(3):129-144; 1959 March.
- Watt, K. E. F. **Mathematical models for use in insect pest control.** Can. Entomol. Suppl. 19; 1961. 62 p.
- Watt, Kenneth E. F. **Computers and the evaluations of resource management strategies.** Amer. Sci. 52(4):408-418; 1964 December.
- Watt, Kenneth E. F. **Ecology and resource management.** New York: McGraw Hill Book Co.; 1968. 450 p.
- Williams, Carroll B., Jr.; Walton, Gerald S.; Tiernan, Charles F. **Zec-tran and naled affect incidence of parasitism of the budworm *Choristoneura occidentalis* in Montana.** J. Econ. Entomol. 62(2):310-312; 1969 April.
- Williams, Carroll B., Jr.; Shea, Patrick J.; McGregor, Mark D. **Effects of aerially applied mexacarbate on western spruce budworm larvae and their parasites in Montana.** Res. Paper PSW-144. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 1979. 14 p.

Williams, Carroll B., Jr.; Shea, Patrick J. **Computer simulation for integrated pest management of spruce budworms.** Res. Paper PSW-159. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 1982. 11 p.

Some field studies of the effects of various insecticides on the spruce budworm (*Choristoneura* sp.) and their parasites have shown severe suppression of host (budworm) populations and increased parasitism after treatment. Computer simulation using hypothetical models of spruce budworm-parasite systems based on these field data revealed that (1) effective parasites produce greater stability in budworm populations than ineffective ones and are more resistant to changes induced by insecticides; and (2) the level of budworm population suppression in most budworm-parasite systems is not proportional to the amount of insecticide applied. Only high insecticide dosages produce any effect on the budworm population. Cost-benefit analyses showed that very high investments are worthwhile, but moderate investments produce little effect. The study demonstrated that the computer simulation process helps to define kinds of information needed for understanding the budworm-parasite system, and can predict system behavior under varying conditions.

Retrieval Terms: spruce budworms, insecticides, parasites, integrated pest management